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FEATURED REVIEW

FLORISTIC CHANGE IN NEW ENGLAND AND NEW
YORK: REGIONAL PATTERNS OF PLANT SPECIES LOSS
AND DECLINE

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ABSTRACT. The wealth of historical botanical surveys in New England and New York allows ecologists to study changes in plant communities over time across well documented sites. Studies of floristic change in towns, counties, and preserves over the past 150 years reveal regional patterns of species loss and increasing proportions of nonnative species. These changes are often linked to land use change, deer herbivory, development pressures, and climate change. Here, we review patterns of change throughout the region and explore in-depth floristic change at a northern site: Mount Desert Island (MDI), Maine, which holds the largest section of Acadia National Park. We find floras across the region have lost, on average, one-quarter of their native species—ranging from a loss of 3.5% of species from the Finger Lakes Region in New York to a loss of 53.1% of species on Staten Island, New York. No variable that we examine (e.g., size of area, size of flora, conservation status, and data sources) explains differences in losses across all sites. Contemporary floras have higher percentages of nonnative species than historic floras: the percent of nonnatives in floras have increased by 1.5% to 19.7% across the region. We also explore a data set of 412 conspecifics found both on MDI and 324 km away in Concord, Massachusetts, and compare species-level changes in abundance over the past century to test whether changes in one location might be predictive of changes in the other. We find that at a community level, changes in abundance in Concord were predictive of changes on MDI—local floras throughout the region have lost roughly 25% of their original species over the last 50 to 150 years—but changes in abundance for particular species in

Concord were not predictive of how the same species changed in abundance on MDI. In New England, analyses of changes in nearby floras may help land managers and scientists understand community-level changes likely taking place, but we find that documenting and understanding changes in particular species requires targeted local study. Finally, we highlight the importance of context: understanding the survey effort, expertise, and goals of earlier botanists allows contemporary ecologists to make the most of the available historical ecological data.

Key Words: Acadia National Park, climate change, community ecology, Concord, Mount Desert Island, conservation, habitat loss, historical ecology, native species, nonnative species, plant biodiversity, species loss

The northeastern United States has an exceptionally rich history of botanical inventories pursued over the past two centuries by colonial surveyors (Cogbill et al. 2002), environmental writers (Miller-Rushing and Primack 2008), botanical collectors (Davis et al. 2015; Willis et al. 2017; Daru et al. 2017), professional and amateur scientists (Rand et al. 1894), and managers of conservation lands (Sorrie and Dunwiddie 1996). This inventory work has provided universities, libraries, archives, and herbaria with unique and valuable historical ecological records (Vellend et al. 2013a; McClenachan et al. 2015; Beller et al. 2017). Modern ecologists have returned to these records to understand historical conditions, landscape ecology and conservation (Foster and Motzkin 2003), changing community composition (Cogbill et al. 2002), species distributions (Bertin 2008), and phenology (Everill et al. 2014). Researchers have also used these historical records to evaluate the roles of European settlement (Thompson et al. 2013) and climate change (Parmesan and Yohe 2003; Primack and Miller-Rushing 2012) in driving ecological changes.

Over the past 40 years, a number of researchers have used the region's historical records to repeat past surveys of floras in New England and New York to understand how the flora and plant communities have changed over time (Table 1). Most studies covered roughly 50-100-year time periods between the late 19th or early 20th century to the late 20th or early 21st century. At the most basic level, these floristic change studies quantified changes in local species lists, and some included historic and contemporary information about the relative abundance of species and phenology. This research has relied on diverse sources of historical data—including species checklists, herbarium collections, and rigorous floral inventories—and covered different types of areas, including protected areas, towns, and entire counties.

In general, these resurveys have revealed trends of native species loss and increasing proportions of nonnative species during the 20th century. However, there has been no attempt to synthesize or compare the results of the many resurveys of floras in the northeastern United States. Such a review could yield insights into region-wide changes in plant communities and potential causal factors associated with different rates and types of change. It could also help ecologists identify vulnerable taxa, allow resource managers to compare the effectiveness of different conservation strategies, and test if changes in plant communities are specific to particular locations or whether floristic changes in one location might be used to estimate changes in another location.

The New England region is widely recognized as one of the most extensively collected, digitized, and digitally-accessible floras in the world; within this region Daru et al. (2017) found significant hotspots of herbarium sampling in Massachusetts and Connecticut. Our review of the geographic locations of floristic change studies parallels these herbarium results (Daru et al. 2017). We present thirteen floristic change studies: nine from Massachusetts, two from New York, one from New Hampshire, and one from Maine (Figure 1).

In Maine, Greene et al. (2005) conducted a floristic resurvey of Mount Desert Island (MDI), although discussions of floristic change since the early surveys of Rand and Redfield (1894) were limited. A more detailed assessment of botanical changes in Maine (or elsewhere in the north) could help ecologists understand changes in plant communities closer to the boreal-temperate forest boundary, a region that is likely to experience particularly dramatic climate-driven changes in the composition of dominant tree species (Fisichelli et al. 2013; Zolkos et al. 2014). In addition, MDI, Maine is the only northeastern floristic change site within a national park; this conservation history and the remote location of the site provides an example of floristic change under reduced development pressure. In contrast, Middlesex Fells Reservation near Boston has been protected since 1894, but the Boston suburbs sprawled around—and through, via an eight lane highway—the area, severely fragmenting it and cutting it off from surrounding forests (Drayton and Primack 1996; Hamlin et al. 2012). In rural western Massachusetts, Skinner and Mount Holyoke Range State Parks have escaped these recent development pressures, but logging, grazing, and agriculture were active through the first half of the 20th century (Searcy 2012). Many protected areas in northern New England—e.g., Baxter State Park, the White and Green Mountain National Forests, Acadia National Park—are larger and have had less

Table 1. Floristic change surveys from the Northeastern United States.

Location	Historical flora	Present flora	Size of study area (ha)	Historical Species	Species Extant	Species Extirpated (%)	Historical natives (%)	Present natives (%)	Conservation Status (yes/no)	Citation
Maine										
MDI	1880-1894	1985-2010	28000	730	829	106 (15.8%)	82.2	75.4	yes	McDonough MacKenzie et al. 2018
Massachusetts										
Broadmoor Brook	1969-1980	2008-2009	246	562	499	177 (31.49%)	73.49	71.94	yes	Standley, L.A., 2015
Concord	1888-1902	2003-2007	6700	479	589	115 (24.01%)	75	61	yes	Willis et al. 2008; Primack, R., Miller- Rushing, A., Dharaeeswaran, K., 2009
Harvard Forest	1908-1911, 1933-1934, 1947	2004-2005	6700	637	729	79 (12.40%)	85.87	78.05	yes	Jenkins, J., G. Motzkin, and K. Ward, 2008
Middlesex Fells	1894-1896	2003-2011	1400	680	851	187 (27.50%)	83.83	64.86	yes	Hamlin, Bryan T., et al. 2012
Mt Holyoke Range	1860-1952	1999-2007	unclear	370	834	39 (10.54%)	97.84	82.01	n/a	Searcy, K.B., 2012
Nantucket	1899-1919	1980-1996	14000	1136	1265	326 (28.70%)	69	61	yes	Sorrie, Bruce A., and Peter Dunwiddie. 1996
Needham	1880-1885	2000-2002	3250	691	628	287 (41.53%)	81.48	67.99	no	Standley, Lisa A. 2003
Worcester City	1879-1955	1994-2001	9740	733	650	147 (20.05%)	n/a	n/a	no	Bertin, R.I., 2002
Worcester County	1899-1950s	1985-2012	391900	1040	1024	91 (8.75%)	n/a	n/a	n/a	Bertin, R.I., 2013

Table 1. Continued.

Location	Historical flora	Present flora	Size of study area (ha)	Historical Species	Species Extant	Species Extirpated (%)	Historical natives (%)	Present natives (%)	Conservation Status (yes/no)	Citation
New Hampshire	1903-1911	1978-1985	17.4	265	243	108 (40.75%)	n/a	95.88	yes	Holland, M.M., Sorrie, B.A., 1989
Three Mile Island										
New York	1879*	1977-1981	15760	1133	961	602 (53.13%)	80.8	66.49	no	Robinson, G.R., Yurina, M.E., Handel, S.N., 1994
Staten Island										
Finger Lakes	1886	2005	970000	1545	1976	54 (3.50%)	81.55	61.84	no	Marks, P.L., Wesley, F.R., Gardescu, S., 2008

*focus on 1879 here

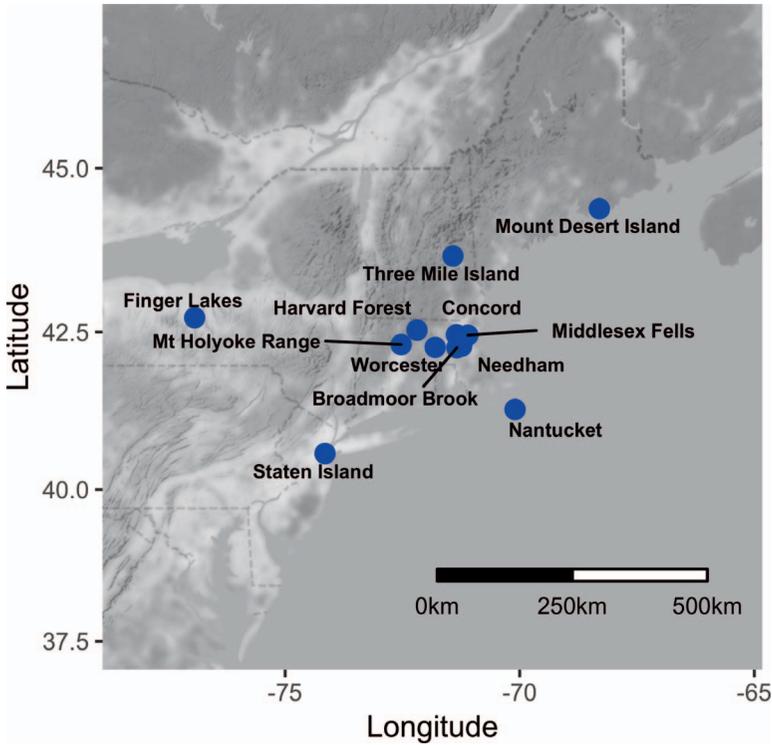


Figure 1. Map of thirteen floristic change studies from New England and New York included in this review. Here, the label ‘Worcester’ indicates the floristic change studies for both the city of Worcester and Worcester county. More information on the original papers documenting floristic change at each location can be found in Table 1. Created with ggmap (Kahle and Wickham 2013), map tiles by Stamen Design, under CC BY 3.0, data © OpenStreetMap contributors.

intensive, contemporary development in and around them, but this type of landscape is underrepresented in the region’s floristic change literature.

Here, we review the existing resurveys of New England and New York floras and make a detailed examination of the resurvey of MDI, Maine. We look critically at the varied historical records underpinning floristic change studies, present a framework for evaluating the historical ecological data in floristic change studies, and examine the biases in these resources. We also assess regional patterns and compare in detail species-level changes in abundance at two sites

Table 2. Framework for comparing floristic change across diverse resurvey studies. Here, we compare the quality of historical floristic data sources across thirteen floristic change studies in New England and New York. The presence of each component is derived from the methods of each resurvey study.

Location	Intention to document an entire flora	Voucher specimens from fieldwork	Field notes from fieldwork	Published flora (* = unpublished)	Contemporary feedback (correspondence, additions to the flora)
Maine					
MDI	X	X	X	X	X
Massachusetts					
Broadmoor Brook	X		X		
Concord			X		
Harvard Forest	X	X		X*	
Middlesex Fells	X	X	X	X	X
Mt Holyoke Range		X			
Nantucket	X			X	
Needham	X	X		*	
Worcester County	X	X			
Worcester City		X		X	
New Hampshire					
Three Mile Island	X	X	X		
New York					
Staten Island	X			X	
Finger Lakes	X			X	

(MDI, Maine, and Concord, Massachusetts) to test the degree to which floristic change at one location can be used to inform understanding of change at another location in the region. This work highlights the potential and assesses the limits of historical ecological resources in documenting floristic change and supporting conservation management decisions.

MATERIALS AND METHODS

A framework for comparing floristic change across diverse resurveys. Assessments of floristic change are limited by the historical data that are available. Frequently these data—herbarium specimens, unpublished manuscripts, or historic inventories—are incomplete or biased in some way (Table 2). As a result, defining a framework for comparing these historical surveys is an important part of our methods for this research.

Individual botanists collecting plant specimens or observations often have different goals and tendencies (e.g., intensive collecting of rare species, focusing on invasive species, collecting data during particular seasons), and may not share a common goal of surveying the complete flora of a region (Searcy 2012; Vellend et al. 2013a; Bertin 2013; Daru et al. 2017; Guerin et al. 2018). Historical floras that are based solely on herbarium specimens are subject to spatial, temporal, trait, phylogenetic, and collector biases (Wehi et al. 2012; Willis et al. 2017; Guerin et al. 2018). In a review of over 600,000 digitized herbarium specimens, Daru et al. (2017) confirm that New England's herbarium specimens disproportionately represent herbs and trees over other growth forms; they tend to have been collected from locations near roads, and during spring and summer (see also Guerin et al. 2018). Herbaria specimens accompanied by field notes and floras provide valuable context for collections. Unpublished manuscripts and inventories may be incomplete or of unknown quality (Angelo 2014b; Standley 2015). Both published and unpublished floras may contain errors of identification or omissions due to species being overlooked or ignored, though these may be alleviated to some extent by voucher specimens collected by the authors or their contemporaries (Greene et al. 2005; Hamlin et al. 2012).

The ideal historical floristic data source for resurveying and assessing plant-community changes would include these components: one or more expert botanists intending to document an entire flora; extensive fieldwork documented in both field notes (which often capture goals and effort and can reveal biases) and herbarium specimens; time spent in herbaria to reexamine and verify identification of existing collections; and a published flora with contemporary feedback, including correspondence with other scientists and additions to the flora published in subsequent years (Table 2). Data sets meeting these criteria are rare but do exist. For example, Rand et al. (1894) set out to document the entire flora of MDI, left abundant field notes and herbarium specimens, and made addendums as further exploration yielded new information (Rand et al. 1894; Rand 1908; Stebbins 1929).

By way of comparison, the 1895 flora of Middlesex Fells was recorded on index cards and likely undercounted certain species; for example, aquatic and wetland plants and grasses appear to have been underreported in the historical flora (Hamlin et al. 2012). Further, the elderly botanist responsible for surveying trees for the historical flora likely had limited access to the interior of the park. Thus the resurvey of the flora of the Middlesex Fells found that the Fells lost 125 native

species (21.9% of the historic native flora), which was offset by the “appearance” of many new native species, some of which were probably present but overlooked during the 1895 surveys (Hamlin et al. 2012; Primack and Miller-Rushing 2014a).

Because of these common undercounts and biases, “net loss of native species”—a metric commonly used in studies of change in species richness—is problematic for comparisons across floristic change studies. The “net loss of native species” in a particular location is influenced by the intensity of both the original survey and the resurvey. Native species that were present but overlooked in earlier floras, especially floras with patchy survey effort, can “appear” in contemporary floras, artificially reducing the net loss of native species. Thus, in our comparison of changes in floras across the region, we describe loss of species without accounting for the addition of new species—that is, we report the number of species included in the historical flora and the proportion of those species that are no longer documented in the current flora (Table 1). This method is still susceptible to recent resurveys of floras that may have overlooked species that were actually present, exaggerating the extent of species loss (Angelo 2014a, 2014b). We tried to guard against this by including resurveys that were intentional and thorough (Table 1).

Changes in the flora of Mount Desert Island, Maine. MDI, Maine is located ~445 km northeast of Boston, Massachusetts. Approximately 44% of the 280-km² island comprises the MDI unit of Acadia National Park (Greene et al. 2005). Acadia National Park was first established as Sieur de Monts National Monument in 1916. The area of the park has expanded over time through purchases and donations of private land, creating a variety of irregular-shaped park units surrounded by villages and fragmented by park roads, carriage roads, and hiking trails.

MDI is located in the northeastern mixed forest ecoregion province of New England (Harris et al. 2012). The Atlantic Ocean moderates MDI’s maritime climate with cool summers and mild winters. Mean July high temperatures are 25°C, mean minimum January temperatures are -10°C, and annual average precipitation is 123 cm (Greene et al. 2005). The coarse-grained granite bedrock geology of the island is visible on the open summits and ridges of low dome-shaped mountains that rise over 300 m in elevation. Glaciers carved variations in slope and topography, creating a mosaic of conditions from exposed headlands to sheltered salt marshes: the lowlands are generally poorly drained, and soils are generally acidic. The biophysical diversity of the island supports heterogeneous and varied

habitats (Greene et al. 2005). The island comprises less than 1% of Maine's land area, but includes over half of the state's plant species (Greene et al. 2005).

HISTORICAL DATA. Edward Rand et al. (1894) documented the flora, including the relative abundance for each species, of MDI in the late 19th century. This published flora represented the culmination of fieldwork that began in 1880 and continued through 1894. Rand began his fieldwork as a Harvard undergraduate when he joined the Champlain Society, a student group dedicated to studying the natural history of MDI on summer field trips (Schmidt 2014). In collaboration with local botanists, Rand spent these summer trips compiling species lists of the vascular plants of the island and continued his botanical work for fourteen years. The 1894 *Flora of Mount Desert Island, Maine* includes narrative abundance descriptions for every species Rand and his colleagues recorded on the island. Only two other studies in our review, Concord, Massachusetts and Staten Island, New York, include abundance descriptions noted by historical botanists and used in the contemporary assessment of floristic change (Robinson et al. 1994; Willis et al. 2008). Though Rand was an amateur botanist, he was a founding member of the New England Botanical Club and his flora was thorough and well received by the scientific community (Robinson 1925). We qualitatively assessed Rand's survey effort and goals through the detailed log books in which the Champlain Society recorded their daily activities. These are held in the Mount Desert Island Historical Society archives and are available online (Mount Desert Historical Society 2018).

CONTEMPORARY DATA. The late botanist Craig Green and colleagues documented the contemporary flora of MDI and other sections of Acadia National Park through surveys between 1980 and 2005 (Greene et al. 2005). The data set underpinning this flora was then published as *The Plants of Acadia National Park* with notations of species abundance (Mittelhauser et al. 2010). We restricted our analyses to their observations on MDI, equivalent to the area covered by Rand et al. (1894). Mittelhauser et al. (2010) also compiled a list of locally extirpated species (i.e., species not documented in the region since 1980) based on historical accounts of the flora in the literature, including Rand et al. (1894), and

specimens in the region's herbaria. In our study, we build on both Greene et al. (2005) and Mittelhauser et al. (2010) by providing a more detailed analysis of changes in species abundance on MDI.

ANALYSIS OF FLORISTIC CHANGE. We created a database for each species listed in the 1894 and the 2005 floras (Rand et al. 1894; Greene et al. 2005). We noted species that were absent from the 1894 flora but appeared in *Rhodora* as early 20th century addendums to the flora of MDI (Rand 1908; Stebbins 1929); however, no historical abundance data were available for these species. We cross-referenced historical names and matched them to present-day nomenclature (Haines 2011). We excluded subspecies and varieties from our dataset and focused on assessing changes in abundance at the species level, consistent with the floristic change studies from the region in the literature. We also removed cultivated species and records we could confirm were false identifications through annotated voucher specimens.

To calculate changes in abundance, we used the categories provided by Mittelhauser et al. (2010): common, occasional, uncommon, rare, and extirpated. Rand's narrative notes on abundance were not so easily delineated, so we created a logic tree to aggregate the 1894 abundance descriptions for each species into one of these categories (excluding "extirpated"). We considered species not documented in 1894 or later addendums to be new arrivals to the flora; we considered species not documented in 2005 to be locally extirpated. We calculated change in abundance as the difference between a species' relative abundance in 1894 and 2010, both in terms of direction (increase, no change, or decline) and magnitude; declining three categories (e.g., from common to rare) constituted a larger decline than declining one category (e.g., from uncommon to rare). We also placed each species in one of six broad habitat categories (freshwater aquatic and wetlands, coastal, grasslands and fields, mountains, roadsides and disturbed, and woods) based on descriptions in Rand et al. (1894) and Mittelhauser et al. (2010) and following methods in Primack et al. (2009) and Standley (2003). We recorded 'habit' (i.e. tree, shrub, annual herb, perennial herb) for each species based on the USDA Plants database (USDA, NRCS, 2018). We categorized perennial graminoid species as 'graminoid' and categorized annual graminoids as annual herbs. We used chi-squared analysis (X^2) to compare changes in relative abundance across habitat types.

Changes in local floras across New England and New York. We compiled data on floristic change from 13 sites across central and southern New England and New York (Tables 1, 2). We began this review using Bertin's (2013) study, which compared native species loss in Worcester County, Massachusetts with eight other locations. To this list we added Three Mile Island, New Hampshire (Holland and Sorrie 1989), Concord, Massachusetts (Willis et al. 2008; Primack et al. 2009), Broadmoor Brook, Massachusetts (Standley 2015), and MDI, Maine (Greene et al. 2005). We did not consider the flora of Springfield, Massachusetts because the *Vascular Flora of Springfield* was not readily available online or in print.

Among these 13 studies, 10 drew on historical datasets that began in the 19th century (MDI, Concord, Holyoke Range, Needham, Middlesex Fells, Nantucket, Staten Island, the Finger Lakes, Worcester, and Worcester County). Only Broadmoor Brook relied on historical data collected after 1955. The size of the study areas ranged from 17.4 ha (Three Mile Island) to 970,000 ha (Finger Lakes), with a mean area of 128,569 ha and a median area of 6,700 ha. For the Mount Holyoke Range study, there is no clearly defined study area, and the most recent floral survey likely exceeds the area covered by historic data (Searcy 2012). We included both Worcester County, Massachusetts (Bertin 2013) and two locations in the county: the city of Worcester (Bertin 2002) and Harvard Forest (Jenkins et al. 2008). Many sites comprise or contain conservation lands: Broadmoor Brook is a Mass Audubon sanctuary; Middlesex Fells has been a state reservation since 1894; roughly 60% of all-natural areas in Concord are undeveloped or conserved; and about 44% of MDI is protected as a part of Acadia National Park (Table 1). The northernmost sites were MDI (44.3° N latitude), Three Mile Island (43.7° N), and Finger Lakes (42.7° N). The northernmost point in New England is at roughly 47.3° N latitude, so much of New England's northern flora still lacks an assessment of floristic change (Figure 1).

Across these studies, we compared the loss of native species and identified taxonomic groups and habitat types that lost disproportionate numbers of species. We used linear models to test the relationship between the size (area and number of species) of studies and the rate of species loss, and a Welch two-sample t-test to test the relationship between the conservation status and the rate of species loss. We used a simple yes/no metric of "conservation status": sites that were described as defined by or containing significant conservation land in the original floristic change paper (MDI, Concord, Broadmoor Brook, Middlesex Fells, Harvard Forest, and Three Mile

Island) were assigned positive “conservation status”, all other sites were not. We excluded two sites from these analyses: Mt Holyoke, which lacks an estimate of site size, and Worcester County, which contains Harvard Forest and the city of Worcester, and which also focused exclusively on native species.

Comparing species-level changes in relative abundance in Concord and Mount Desert Island. The floras of Concord and MDI (~324 km apart) are linked by shared species and similar histories of high-quality, detailed botanical research (Primack and Miller-Rushing 2012). Concord and MDI also share the rare feature that they include data describing the relative abundance of taxa in the late 19th century and today. Staten Island, New York is the only other floristic change study in our review with abundance descriptions consistently noted by historical botanists (Robinson et al. 1994). The unpublished historical notes of Hosmer (1888-1902) (Primack and Miller-Rushing 2012) and the published flora of Rand et al. (1894) captured the presence and abundance of plant species at the end of the 19th century. In both cases, an expert botanist made dedicated efforts to capture data across a single location over many years, resulting in detailed and high-quality records.

It is important to recognize that Concord and MDI differ in key characteristics that could cause divergent patterns in floristic change over the past century. For example, (1) MDI has a relatively maritime climate compared to Concord’s more continental climate (Greene et al. 2005; Primack et al. 2009); (2) temperatures have warmed more than twice as much in Concord due to the urban heat island effect (Primack and Miller-Rushing 2012); (3) Concord has experienced more development than MDI, though a majority of the land area at both sites remained protected or undeveloped (Primack et al. 2009; Harris et al. 2012).

Intriguingly, Concord and MDI also share a connection to Henry David Thoreau. Alfred Hosmer, the shopkeeper who recorded the historical flora of Concord used in this analysis may have been inspired to compile data by his admiration for Thoreau’s natural history writing (Primack et al. 2009). On MDI, Edward Rand found a mentor and collaborator in summer resident Annie Sawyer Downs, who contributed to Rand’s botanical surveys (Rand et al. 1894). Downs had grown up in Concord, and as a child she learned botany from Thoreau (Harding 1992).

In Concord, Primack and Miller-Rushing (2012) began recording flowering phenology in Concord in 2003 in an effort to repeat observations of flowering times noted by Thoreau and Hosmer (Miller-

Rushing and Primack 2008; Primack and Miller-Rushing 2012). When species that Hosmer recorded as common in Concord proved difficult to find, they broadened their study beyond phenology to document the contemporary abundance and assess changes in the relative abundance of species between the late 19th and the early 21st centuries (Primack et al. 2009). The resulting data were documented in two main publications (Willis et al. 2008; Primack et al. 2009), and were subject to later scrutiny (McDonald et al. 2009; Willis et al. 2009; Angelo 2014a; Primack and Miller-Rushing 2014a; Willis and Davis 2014; Angelo 2014b; Primack and Miller-Rushing 2014b), which ultimately did not change the conclusions of their work.

The Concord floristic change dataset did not include the complete flora—it omitted graminoids, spore-bearing vascular plants, and nonvascular plants—and the fieldwork was not intended to document every vascular plant in the town of Concord (Angelo 2014b; Primack and Miller-Rushing 2014b). However, Primack et al. (2009) did estimate current abundance (or local loss) of each of the 479 species that Hosmer documented in the late 1800s. For a thorough record of the vascular flora of Concord, consult Angelo (2018). Primack et al. (2009) categorized species abundance as common (three or more populations in Concord) or uncommon. They further divided the uncommon species (one or two populations) into rare (populations only found in one location) or infrequent (populations found in two locations). They also aggregated Hosmer's descriptions of relative abundance into these categories to facilitate analyses of abundance changes over time (Primack et al. 2009). Mittelhauser et al. (2010) used similar categories of relative abundance of plants on MDI: common, occasional, uncommon, rare, and extirpated. We did not attempt to make absolute comparisons between the categories of relative abundance used on MDI (Mittelhauser et al. 2010) and Concord (Primack et al. 2009), instead we focused on analyzing the *relative* changes (increase, no change, decline, new arrivals, and local extirpations) at these locations.

We used data from the flora of Concord (occurrence, relative abundance, and trait data) as presented in Willis et al. (2008), and the flora of MDI based on Mittelhauser et al. (2010) for our comparison of species-level changes in relative abundance. To determine if changes in abundance in Concord correlated with changes in abundance for the same species on MDI, we used chi-squared analyses (X^2) and odds ratios. To test whether species distribution (i.e., more northern or southern distributions) was related to changes in abundance in both locations, we used the mean latitude metric developed by Willis et al.

Table 3. Changes in abundance of taxa recorded by Rand in 1894 through 2010. Nine species were recorded in 1894 without an abundance description and are omitted from this table.

Abundance Shift 1894-2005	Percent of Rand's Flora	n
Locally extirpated	15.8	106
Decline	34.4	231
No Change	30.4	204
Increase	19.4	671

(2008). We used linear models with change in abundance in a location (Concord or MDI) as the response variable, and mean latitude as an explanatory factor. We could not use a simpler county-based method of analysis adopted by Bertin (2013) and Searcy (2012) because MDI occurs too near the northern edge of New England. All analyses were performed in R version 3.3.3 (R Core Team 2017).

RESULTS

Changes in the flora of Mount Desert Island, Maine. The historical flora of MDI comprised 730 species: 680 in Rand et al. (1894), and another 50 additions published as addendums (Rand 1908; Stebbins 1929). The flora of MDI included 829 vascular plant species in 2005; of these, 205 species were new arrivals since Rand et al. (1894) and addendums (Rand 1908; Stebbins 1929) (Table 3). Of the 680 species recorded by Rand et al. (1894), 15.8% are no longer found on MDI, 34.4% declined in abundance, 30.4% experienced no apparent change in abundance, and 19.4% increased in abundance [9 species from Rand et al. (1894) did not have an abundance description]. The proportion of native species on the island dropped from 82.2% in 1894 to 75.4% in 2010.

When we considered the magnitude of change, most of the species in the 1894 flora experienced no change (33.0%) or declined by one abundance category (32.5%)—e.g., dropped from occasional to uncommon [as in the case of *Lactuca canadensis* L. (wild lettuce) and *Trillium undulatum* Willd. (painted trillium)] or rare to extirpated [as in the case of *Lilium canadense* L. (Canada lily) and *Eleocharis parvula* Roem. & Schult. (low spike-rush)]. Few species increased from rare to common (4 species, 0.6%), a shift of three categories, or dropped from common to extirpated (8 species, 1.2%), a shift of four categories. The four species that did increase from rare to common included one native, *Ambrosia artemisiifolia* L. (common ragweed), and three nonnatives, *Veronica officinalis* L. (common speedwell), *Galium mollugo* L. (wild

madder), and *Barbarea vulgaris* W. T. Aiton (winter cress). Eight species (1.2%) that were common in 1894 are now extirpated, including three graminoid angiosperms (*Panicum dichotomum* L., *Muhlenbergia schreberi* J. F. Gmel., *Carex tribuloides* Wahlenb.), three perennial herbs (*Antennaria plantaginifolia* L., *Sisyrinchium angustifolium*, Mill., and *Galium triflorum* Michx.), an annual herb (*Hedeoma pulegioides* L.), and a club moss (*Huperzia lucidula* Michx.). Twenty-five species declined by three categories (common to rare, or occasional to extirpated). Among native species, 16.6% increased in abundance, while 48.8% declined in abundance or were extirpated. In contrast, 32.2% of nonnative species increased in abundance, while 39.8% declined in abundance or were extirpated.

Several families experienced particularly high rates of species loss. Among families with seven or more species represented in the historical flora (Rand et al. 1894; Rand 1908; Stebbins 1929) the mean rate of species loss was 14.7% and the mean rate of species decline was 34.6%. Six families lost at least a third of their species: Liliaceae (42.9%), Lamiaceae (42.9%), Orchidaceae (42.9%), Amaranthaceae (37.5%), Caryophyllaceae (36.4%), and Apiaceae (33.33%). In addition, 68.8% of Juncaceae species, 57% of Lycopodiaceae species, and 71.4% of Violaceae species declined in abundance between the 19th and 21st centuries (Table 4).

Woody species comprise 17.4% of the historical flora (127 species) and had low rates of local extirpation. No tree species and only a single vine species, *Clematis virginiana* L. (virgin's bower) disappeared from MDI. Six shrub species, including *Clethra alnifolia* L. (coastal sweetpepperbush), *Crataegus chrysocarpa* Ashe (goldenberry hawthorn), *Ribes americanum* Mill (American black currant), *Salix lucida* Muhl (shining willow), *Rubus setosus* Bigelow (setose blackberry), and *Rubus frondosus* Bigelow (Yankee blackberry) were extirpated. While 61.5% of the historical flora was herbaceous, 93.3% of all locally extirpated species were herbs (99 species); of these 25 were annuals (21.7% of the historic annuals), 71 were perennials (15.1% of the historic perennials), and 3 are listed as displaying both annual and perennial duration (20% of the historic herbaceous species listed as both) (USDA, NRCS 2018).

Herbs represent 74.1% of the new species on MDI; another 19.0% of new arrivals are shrubs and 4.9% are trees. New herbs include (but are not limited to) native *Euphrasia randii* Robins. (Rand's eyebright), *Trillium cernuum* L. (nodding trillium), and *Caltha palustris* L. (marsh marigold), and nonnatives *Suaeda maritima* L. (low sea blite), *Lythrum salicaria* L. (purple loosestrife), and *Fallopia japonica* Houtt. (Japanese

Table 4. Summary of species loss and decline 1894-2005 across families with at least seven species on Mount Desert Island.

Family	Lost (%)	Decline (%)	Species Count
Adoxaceae	0.0	16.7	7
Amaranthaceae	37.5	25.0	16
Apiaceae	33.3	33.3	17
Asteraceae	17.1	30.0	93
Betulaceae	0.0	0.0	9
Brassicaceae	16.7	8.3	23
Campanulaceae	28.6	42.9	8
Caprifoliaceae	0.0	50.0	9
Caryophyllaceae	36.4	13.6	26
Cyperaceae	9.2	50.0	105
Dryopteridaceae	0.0	40.0	7
Ericaceae	0.0	35.7	30
Fabaceae	6.3	50.0	26
Hypericaceae	14.3	14.3	11
Juncaceae	12.5	68.8	18
Lamiaceae	42.9	21.4	16
Lentibulariaceae	12.5	37.5	9
Liliaceae	42.9	0.0	7
Lycopodiaceae	14.3	57.1	9
Myrsinaceae	0.0	60.0	8
Onagraceae	11.1	66.7	12
Orchidaceae	42.9	38.1	23
Orobanchaceae	16.7	33.3	7
Pinaceae	0.0	57.1	10
Plantaginaceae	20.0	26.7	23
Poaceae	9.6	36.5	72
Polygonaceae	7.1	28.6	20
Potamogetonaceae	0.0	16.7	11
Ranunculaceae	15.4	23.1	15
Rosaceae	15.8	42.1	64
Rubiaceae	12.5	12.5	10
Salicaceae	10.0	30.0	12
Typhaceae	0.0	40.0	7
Violaceae	14.3	71.4	9

knotweed). The new trees include natives *Picea rubens* Sarg (red spruce), *Pinus banksiana* Lamb. (Jack pine), *Acer saccharum* Chapm. (sugar maple), *Betula cordifolia* Regel (heart-leaved paper birch), and *Fraxinus pennsylvanica* Marshall (green ash); nonnatives *Pinus sylvestris* L. (Scots pine), *Sorbus aucuparia*, L. (European mountain ash), *Tilia platyphyllos* Scop. (largeleaf linden), and *Tilia cordata* Mill. (littleleaf linden); and the nonnative invasive *Acer platanoides* L. (Norway maple). Four new vines appeared: *Adlumia fungosa* Aiton

Table 5. Species loss and proportion of native taxa by habitat categories on Mount Desert Island.

Habitat	Proportion of Flora	Species Loss (%)	1894 Native (%)	2010 Native (%)
Aquatic and Wetlands	35.6	8.1	95.2	93.2
Coastal	8.1	13.2	86.7	87.9
Grasslands and Fields	13.9	13.8	67	56.3
Mountains	3.0	10.7	95.5	96
Roads and Disturbed Areas	16.4	12.4	26.4	24.6
Woods	4.1	8.5	97.1	90.7

(Allegheny vine), the nonnative *Vicia tetrasperma* L. (lentil vetch), and nonnative invasives *Celastrus orbiculata* Thunb. (Oriental bittersweet) and *Lonicera japonica* Thunb. (Japanese honeysuckle).

For the 243 species listed as common in the historical flora, 84.4% are now ranked as common (93) or occasional (112), though 3.3% (8) have become locally extirpated. For the species listed as rare in the historical flora, 35.7% are now locally extirpated. Today, 106 species from the 1894 flora appear to have been extirpated; of these locally extirpated species, 48.1% were rare in 1894, 23.6% were uncommon, 20.8% were occasional, and 7.5% were common.

Every habitat on MDI lost species between 1894 and 2005 (Table 5). All habitat categories lost statistically indistinguishable proportions of their species, between 8.1 and 13.8% ($X^2 = 4.65$, $df = 6$, $p = 0.59$) (Table 5). Thirty-eight species were not assigned a habitat category due to missing historic or USDA habitat information or historic information that was very broad (“various habitats”, “dry and damp ground”) or edaphic-related (“dry soil”, “wet ground”). Sixteen (42.1%) of these uncategorized species were locally extirpated; while this percentage is high, it is based on a relatively small sample size.

We also considered changes in the proportion of species in each habitat that were native to the area (Table 5). All habitat categories except two (mountain and coastal) currently have lower proportions of native species than they did in 1894. The roadside habitat — which supported a much lower proportion of native species than all other habitats in both time periods — shifted by less than two percent, from 26.4% native taxa to 24.6%. No other habitat in either time period contained fewer than 56% native species (or more than 44% nonnative species). The mountain habitat, which supported the fewest taxa in both time periods, supported a single nonnative species in 1894 (*Sagina nodosa* subsp. *nodosa* L. knotted pearlwort) and gained six additional native species by 2010. These “new” mountain species included

Vaccinium boreale I. V. Hall & Aalders (northern blueberry), which was very likely present in 1894 but not recognized by botanists as an individual species until the 1970s (Kloet 1977). In contrast, the proportion of natives in aquatic and wetland categories decreased by 2.6% (from 95.2% native to 93.2%), grasslands and fields by 10.7% (from 67.0% to 56.3%), and woods by 6.4% (from 97.1% to 90.7%).

The loss of historically occurring native species was offset by the arrival of new species, mostly nonnative species — MDI has lost 85 historically occurring native species and 21 historically occurring nonnative species but has added 38 new native species and 61 nonnative species (Table 6). The addition of new species occurred across all habitat types. The grasslands and fields habitat, and roadsides and disturbed habitat, experienced many new additions relative to the total number of species in those habitat types, and new species were mostly nonnative. Aquatic and wetlands were unusual in that they added more native species (28) and nonnative (8) after accounting for the loss of historically occurring species and new arrivals. Coastal and mountain habitat types added the fewest new species, including no net change in nonnative species (Table 6).

Some past studies of floristic change (e.g., Primack et al. 2009) excluded graminoids, ferns and allies, and conifers, essentially limiting their studies to other flowering plants, here referred to as “wildflowers”. On MDI, excluding these categories would leave 682 species. The historical wildflower flora comprised 534 species: 496 in the 1894 flora (Rand et al. 1894), and another 38 additions published in the addendums, but without abundance data (Rand 1908; Stebbins 1929). Of the 496 wildflowers recorded in 1894 with abundance data, 17.8% are no longer found on MDI, 30.6% declined in abundance, 32.9% experienced no apparent change in abundance, and 19.4% increased in abundance. The proportion of native wildflower species on the island dropped from 76.6% in 1894 to 70.4% in 2005.

Changes in local floras across New England and New York. Historical floras comprised between 265 species (Three Mile Island) and 1,545 species (Finger Lakes), with a mean of 772 species (Table 1). Across these floristic change studies in New England and New York, species loss ranged from a low of 3.5% in the Finger Lakes Region to a high of 53.1% on Staten Island (Robinson et al. 1994; Marks et al. 2008; Marks and Canham 2015). The mean species loss across all locations was 25.2%.

We expected that large study sites and sites with conservation lands would experience lower rates of species loss. However, there was no relationship between site size and species loss (linear regression, $F_{1,9} =$

Table 6. Changes in the native and nonnative flora of Mount Desert Island (MDI) by habitat category and across the entire flora (bottom row). The increased species richness in MDI's current flora is a result of lost native species and the arrival of new, mostly nonnative species since 1894.

Habitat Category		Native	Nonnative
Coastal	Historic Count	52	8
	Current count of historically occurring species	45	5
	Net change in historically occurring species	-7	-3
	Total Current Count	58	8
	Net Change in Total Species	+6	0
Grasslands and Fields	Historic Count	67	33
	Current count of historically occurring species	52	49
	Net change in historically occurring species	-15	-3
	Current Count	63	49
	Net Change	-4	+16
Mountains	Historic Count	21	1
	Current count of historically occurring species	18	1
	Net change in historically occurring species	-3	0
	Current Count	24	1
	Net Change	+3	0
Roadsides and Disturbed	Historic Count	29	81
	Current count of historically occurring species	22	69
	Net change in historically occurring species	-7	-12
	Current Count	33	101
	Net Change	+4	+20
Aquatic and Wetlands	Historic Count	259	13
	Current count of historically occurring species	235	12
	Net change in historically occurring species	-24	-1
	Current Count	287	21
	Net Change	+28	+8
Woods	Historic Count	136	4
	Current count of historically occurring species	121	4
	Net change in historically occurring species	-15	0
	Current Count	147	15
	Net Change	+11	+11
Uncategorized	Historic Count	23	3
	Current count of historically occurring species	9	1
	Net change in historically occurring species	-14	-2
	Current Count	13	9
	Net Change	-10	+6

Table 6. Continued.

Habitat Category		Native	Nonnative
All Habitats	Historic Count	587	143
	Current count of historically occurring species	502	122
	Net change in historically occurring species	-85	-21
	Current Count	625	204
	Net Change	+38	+61

3.93, $p = 0.079$), or between presence of conservation land and species loss (t test, $t = 0.42$, $df = 5.9$, $p = 0.69$). While the smallest site (Three Mile Island) experienced the greatest percent species loss and the largest site (Finger Lakes) experienced the smallest percent species loss, among the sites between 246 and 28,000 ha there is no pattern in percent species loss scaling with size. Sites with reported conservation land lost between 12.4% (Harvard Forest) and 40.8% (Three Mile Island) of their historical floras (Table 1). In comparison, the sites without reported conservation land lost between 3.5% (Finger Lakes) and 53.1% (Staten Island) of their historical floras. A model including site size, conservation status, and the interaction of size and conservation was not significant (linear regression, $F_{3,7} = 2.30$, $p = 0.165$). The size of the historical flora was also not significantly correlated with percent species loss (linear regression, $F_{1,9} = 0.69$, $p = 0.427$). In locations where the floras were resurveyed multiple times (Concord and Staten Island) species loss was concentrated in the most recent time period (Robinson et al. 1994; Primack et al. 2009).

DIFFERENCES AMONG HABITATS. Species losses at MDI, Staten Island, Concord, and the Finger Lakes Region were not associated with a particular habitat—that is, no habitat lost a notably higher or lower proportion of its species than other habitats (Robinson et al. 1994; Marks et al. 2008; Primack et al. 2009). These results contrast with changes in Worcester County where large declines in field species matched large declines in the extent of field habitats (Bertin 2013). The Mount Holyoke Range study did not specifically test for differences in species loss across habitats, but did note that reductions in logging and grazing activity, and subsequent forest growth in previously open habitats, may have contributed to losses of shade-intolerant species (Searcy 2012). Standley (2003) reported that in Needham, Massachusetts, cultural grassland/wet meadow habitats lost the greatest proportion of species, but the study did

not test for a significant relationship between habitat and species loss.

DIFFERENCES ACROSS TAXONOMIC GROUPS. Particular families lost disproportionate numbers of species across New England and New York. Losses and declines in Orchidaceae were particularly severe and widespread (Standley 2003; Primack et al. 2009; Bertin 2013). On MDI, 80% of orchids declined in abundance or were locally extirpated. In Massachusetts, Middlesex Fells lost 44% of its orchids; 56% of the remaining orchid species declined in abundance between the late 1800s and now (Hamlin et al. 2012). In Concord 62% of orchids were lost from a flora of 21 species reported in the 1970s. Six of the eight orchids that remain in Concord are now rare (Primack et al. 2009). In addition to the Orchidaceae, Liliaceae and Violaceae have also lost exceptionally large proportions of their species across New England and New York (Holland and Sorrie 1989; Robinson et al. 1994; Standley 2003; Primack et al. 2009; Searcy 2012; Bertin 2013).

Comparing species-level changes in relative abundance in Concord and Mount Desert Island. There are 412 plant species that were recorded in both Concord and MDI—58.4% of the total Concord flora and 43.7% of the total MDI flora. Historical relative abundance was documented in both locations for 254 of those species; the remaining 158 species were new to one or both locations in the most recent floral resurveys. We analyzed the whole conspecific dataset (412 species), as well as the subset of species with historical abundances in both locations (254 species). We found that changes in the relative abundance of the same species in the two locations were unrelated. With three categories of possible change (increase, decrease, or no change), we expect 33.3% of species will shift in the same direction simply by chance even if abundance changes in the two locations are random and unconnected. Of 412 species that occurred both in Concord and on MDI, less than one third (129 species) experienced the same type of change in both locations. Fifty species declined in abundance and 21 were extirpated from both Concord and MDI. However, 98 species declined in abundance in Concord but maintained or increased in abundance on MDI; 77 species declined in abundance on MDI but maintained or increased in abundance in Concord. An odds ratio test confirmed that declines and losses in Concord were not statistically associated with declines and losses on MDI (odds ratio = 0.72); a second odds ratio test of just species lost found the same result

(odds ratio = 0.52). An odds ratio of 1.0 would indicate that change in abundance in one location is not associated with change in abundance in the other. As these odds ratios are less than one, a species' decline or loss in Concord is actually correlated with lower odds of that species experiencing the same change in abundance on MDI.

We found no statistically significant relationship between mean latitude and local change in abundance for the species that occurred in both Concord and MDI (linear regression, $F_{1,210} = 1.38$, $p = 0.24$ for MDI abundance change; linear regression $F_{1,210} = 3.41$, $p = 0.06$ for Concord abundance change). For this subset of the flora in both locations, species with northern distributions were no more likely to decline in abundance than were species with southern distributions. A linear regression for the whole Concord flora confirmed the original finding of Willis et al. (2008) that mean latitude is correlated with change in abundance for the species that occur there ($F_{1,421} = 3.88$, $p = 0.049$, $R^2 = 0.01$). However, the subset of Concord-only species in our conspecific dataset (perhaps representative of more southern elements) is not driving this trend ($F_{1,163} = 2.06$, $p = 0.15$).

DISCUSSION

Changes in the flora of Mount Desert Island, Maine. The flora of MDI is one of the best-documented floras in the northeastern United States. Both the historical flora (Rand et al. 1894) and recent resurvey (Greene et al. 2005) were undertaken by expert botanists, committed with the intent of documenting the complete flora, and were complimented by extensive notes and the collection of voucher specimens. Given the quality of the record, we can be particularly confident in the documented changes in the flora.

The trends in floristic change on MDI generally matched those of other locations in the region—i.e., substantial losses and declines in the abundance of native species, with especially high losses of certain taxa (mainly herbs), such as species in the Orchidaceae (orchids), Liliaceae (lilies), and Lamiaceae (mints), across most floras in the region. Likewise, we detected similar rates of loss across habitat types and overall gains in the proportion of the flora that is nonnative. These losses and declines of native species occurred despite MDI's northern, rural location and the protection of much of MDI as a national park since 1916.

Potential causes of these floristic changes on MDI include development pressure, such as road and housing construction, high visitation rates (~2.5 million visits per year for much of the 20th

century), human-caused fire (6,596 ha of the 28,000 ha island burned in 1947), deer browse, and other local disturbances. However, the similarity in losses across habitats (e.g., wetlands, coastal areas, grasslands and fields, wooded areas), suggests that more uniform large-scale factors—such as climate change, acid rain, and nitrogen deposition—likely played important roles, as they appear to have in other floras in the region (Willis et al. 2008; Bertin 2013).

Herbs were disproportionately represented among the species lost (93.3% of locally extirpated species were herbs) and gained (74.1% of new additions were herbs) on MDI since 1894, even though these species represented just 61.5% of the historical flora. It is not clear why herbs are more prone to shifts than woody species, although it is possible that their relatively short life spans make their populations more dynamic and responsive to environmental change than woody species.

The losses of historically occurring native species were offset by additions of new species, mostly nonnative species (Table 6). Thus, the total species richness of the MDI flora has increased since 1894 from 730 to 829. “New” additions to a flora may reflect species that were present but undetected in earlier surveys and counts of new species can be difficult to interpret in studies where herbarium specimens alone comprise the historic flora. Here, evidence of thorough and sustained historic survey effort on MDI is documented in field notes and addendums, bolstering confidence in the count of new additions (Table 2). Much of the gains occurred through the additions of new, nonnative species in grasslands and fields, and roads and disturbed habitats. A surprising number of new native species arrived in MDI’s aquatic and wetland habitat types as well, perhaps aided by increased opportunities for long-distance dispersal by humans on boats. In total, the change in species richness on MDI—losses in historically occurring native species replaced largely by additions of new nonnative species—follows broader patterns of change observed in other ecosystems across the world (Vellend et al. 2017b; Primack et al. 2018; Cardinale et al. 2018).

Changes in local floras across New England and New York. Although the general patterns of changes in local floras in the region were consistent (as described in the previous paragraph), the degree of loss of native species varied substantially—some locations lost only a small percent of species (e.g., the Finger Lakes Region, MDI, and the city of Worcester), while others lost more than 40% of their native plant species (e.g., Three Mile Island, Needham and Staten Island) during the 20th century. There were no obvious patterns distinguishing locations that experienced particularly high or low

losses. Site size, the size of the historical flora, and the presence of protected areas were not related to variation in the loss of species in our models.

Some of the variation in species loss was likely related to local variation in the many drivers of species loss and decline, including: stochastic extinctions, development pressures, climate change, and ecological succession (Willis et al. 2008; Primack et al. 2009; Searcy 2012; Hamlin et al. 2012; Bertin 2013). Our framework for comparing floristic change across diverse resurvey studies highlights the variation in sampling intensity in different surveys (Table 2); with this in mind, we explore some local variation in drivers of species loss and decline. On MDI and in Concord, we found that rare species with small populations were more likely to become extirpated than common species, something that has been noted at other sites as well (Farnsworth and Ogurcak 2006; Gerke et al. 2014). For example, on MDI nearly half (46.4%) of the species that were lost were classified as rare in 1894. Although Acadia National Park has existed for over a century (established in 1916), substantial areas of MDI have still been developed over that time, both inside of the park (e.g., parking lots, motor roads, trails, carriage roads, and campgrounds) and outside its boundaries (e.g., roads, villages, summer homes, and campgrounds) (Vaux et al. 2008). In addition, the protected landscape on MDI has experienced successional changes as young forests have matured after a period of logging and farming during the 1800s, and additional disturbances (hurricanes, nor'easters, a major human-caused fire in 1947) occurred during the following century (Harris et al. 2012; Miller-Rushing et al. 2016). Nitrogen deposition, mercury deposition, tropospheric ozone, and other pollutants have also increased since the 1894 flora was completed (Greene et al. 2005; Harris et al. 2012). Most notably, the climate has changed substantially—e.g., warmer temperatures, more precipitation, and longer growing seasons (Monahan and Fisichelli 2014; Monahan et al. 2016). Tracing the specific causes of the decline or loss of any single species is beyond the scope of these floristic change studies—there are many candidate causes and interactions among them. However, the cumulative effects of these changes alter the environmental conditions and rare and endangered species are likely the most vulnerable to extirpation due to their low number of initial populations and, often, the small size of these populations.

ROLE OF PROTECTED AREAS. The role of development pressures and conservation practices in floristic change is challenging to

assess from the diverse studies and study locations. MDI and Middlesex Fells, a protected area about 9 km northwest of Boston, share similar conservation histories, and the sizes of their historic and extant floras are comparable, and yet the Middlesex Fells lost 28% of its original flora while MDI lost only 16% of its flora (Hamlin et al. 2012). Both landscapes have been protected for over 100 years—Middlesex Fells was protected as a reservation in 1894—but while MDI has remained an isolated and largely rural outpost, the city and suburbs of Boston sprawled around Middlesex Fells (Hamlin et al. 2012). Perhaps this divergent land-use history around the two parks provides some explanation as to why the Middlesex Fells lost more of its species than did MDI.

The state parks of the Mount Holyoke Range in western Massachusetts provide another example of long-term floristic change in a protected landscape. In these state parks, Searcy (2012) reported some of the lowest rates of species loss and among the highest proportion of native taxa in a contemporary flora in New England. In terms of losses of native species and gains in nonnative species, MDI (which contains a rural national park) fell between Middlesex Fells (a reserve embedded in a thoroughly urban landscape) and the Mount Holyoke Range (a patchwork of state parks in rural Massachusetts). This result is a bit surprising given that MDI represents a larger study area, a century of federal protection, a rural location, and a more detailed, consistently recorded historical flora (Tables 1, 2). However, the lower rate species loss in the Mount Holyoke Range may be an artifact of a contemporary resurvey which likely involved a greater survey effort and a larger survey area than the historical flora (Searcy 2012).

Ultimately, our analysis of the role of conservation land in floristic change was limited by the available data from the original floristic change studies. We employed a simple binary metric (“conservation lands present”) that encompassed a range of protected statuses — including a Mass Audubon sanctuary, a state park, a research forest, and a national park — of varying ages. Of course, several of the main threats to native plant species, including climate change, pollution, and exotic species, do not respect park boundaries and are likely to act across the whole landscape regardless of the conservation status of a particular parcel. Future studies of regional patterns in floristic change might consider more nuanced and/or quantitative metrics such as percent conserved land or percent undeveloped land as measured in aerial photographs and GIS layers. However, without assessing differences in the underlying historical flora data (Table 2), it will be challenging to accurately compare rates of species loss across any site-level traits.

DIFFERENCES AMONG HABITATS. Our comparisons of species loss across different habitats in contrasting study locations were limited by the use of different habitat categories in each study. The habitats were not standardized in number or detail, and although many studies included a generalized ‘woods’ or ‘forest’ habitat, some, like the Needham study (Standley 2003) considered ‘white pine/oak woods’ separately from ‘rich woods.’ Methods for assigning categories ranged from author’s personal experiences in the field site to consulting published plant atlases (Robinson et al. 1994; Primack et al. 2009; Bertin 2013). In the wild, many species grow across gradients of habitats or in a variety of habitats, and these situations were treated differently in different studies. In addition, habitat analysis can be biased in historical data; for example, open fields and grasslands have declined dramatically in abundance across New England since the 19th century due to agricultural abandonment, but many historical floras under sampled or excluded graminoids which are common in these habitats (Primack et al. 2009; Hamlin et al. 2012). In Concord, where graminoids were excluded, the lack of a relationship between species loss and habitat category may be an artifact of excluding graminoids in analyses of changes in grassland habitats. However, on MDI, the historical and contemporary floras included graminoids and still found no relationship between species loss and habitat, despite substantial loss of open habitats and gains in closed-canopy forests between the historic and contemporary floral surveys. This suggests that the lack of a relationship between species loss and habitat types is a real pattern. In fact, in the grassland and field habitat on MDI 12.2% of species were lost over this time period, but the coastal habitat, which did not change or expand in any substantial way, experienced a higher proportion (15.8%) of species loss.

DIFFERENCES ACROSS TAXONOMIC GROUPS. The Orchidaceae (orchids), Liliaceae (lilies), and Violaceae (violets) lost disproportionate numbers of species across the region in many of these studies. Because plants collectors and botanists are often especially eager to collect these plants due to their attractive flowers, it is likely that these families were historically well-documented in voucher specimens and the losses and declines in these families reflect true changes in abundance (Daru et al. 2017).

The cause of these losses is likely due to the combined effects of deer herbivory, habitat loss, acid rain, nonnative earthworms, and nitrogen deposition (Craven et al. 2016; Fisichelli and Miller 2018). The thorough historical flora on MDI also allowed us to identify high rates of species decline in families that may have been less well-documented in other locations, such as Juncaceae (rushes) and Lycopodiaceae (clubmosses) (Table 4).

Comparing species-level changes in relative abundance in Concord and Mount Desert Island. Even though similar proportions of species were lost from Concord and MDI, there was no significant correlation between how particular species changed at the two sites; that is, whether a species increased, decreased or remained the same at one site had no relationship to what the species did at the other site. The relative abundance of less than one-third of species shifted in the same direction (increase, decrease, or no change) at both locations. This lack of correlation suggests that data from well-studied floras outside of a particular location may not be helpful for anticipating changes in the local abundance of particular species—at least not when the locations are this far apart (~324 km) and different in setting (e.g., coastal vs inland, and rural vs suburban). Even though there are many ecological similarities between Concord and MDI, as reflected by largely overlapping floras, the individual species are responding differently at the two sites. This finding underscores the importance of using local data to inform local decision-making. Native plant species are declining region-wide, but species with vulnerable populations in southern New England are not necessarily declining in abundance in northern New England, and a plant species may be declining in abundance on MDI while a conspecific population may be stable or increasing in abundance in Concord.

What is driving these different trends in abundance change in conspecifics in Concord and MDI? The differences in climate (e.g., coastal MDI versus inland Concord)—soils, disturbances (e.g., development, pollution, storms), and other local conditions may affect species differently across these two locations (Greene et al. 2005; Primack et al. 2009). In addition, the location of each site with respect to species' ranges may be important. Populations at the trailing edge, core, and leading edge of a range often display different trait plasticity and genotype diversity and may be limited by different forces (for example abiotic vs biotic forces at northern vs southern edges) (Willis et al. 2008; Woolbright et al. 2014; Sheth and Angert 2016; Morellato et al. 2016). Studies in New England have found that northern taxa were more likely to decline in abundance or disappear from localities than

more southern taxa (Willis et al. 2008; Searcy 2012; Bertin 2013); however, this relationship was not significant for the set of conspecifics that occurred both in Concord and on MDI. The link between mean latitude and change in relative abundance may be relatively weak compared to other factors—e.g., species traits like phenology or sensitivity to pollution, and local differences in species interactions—making this effect difficult to detect.

How do changes in local floras in New England and New York compare to change elsewhere? Changes in New England and New York generally fit patterns reported globally in plant species diversity trends, particularly in terms of declines in the abundance of native species and the replacement of many of the lost species with nonnative species. Globally, the loss of local species and arrival of nonnative species at a site is often balanced such that, on average, changes in local plant species richness show no general trend towards declining or increasing local-scale species richness (Vellend et al. 2013a, 2017a). We found that species richness increased since 1894 on MDI due to the addition of new nonnative species (Table 6). However, as we recognize in evaluating other data sets from New England and New York, historical data used in both local and global analyses may be missing certain types of species because of the goals, collection strategies, and other hidden circumstances of past botanical work. In one common situation, species identified as “newly arrived” in modern floras may have occurred in a flora in the past, but may not have been documented if the species was rare or botanical collectors were biased against certain taxa, collection locations, or seasons of collecting (Daru et al. 2017). Underreporting of historical occurrences can lead to false conclusions of changes in species richness that could influence trends calculated from many local data sets (Gonzalez et al. 2016; Cardinale et al. 2018).

The length and quality of records and the resulting analyses of changes in local floras in New England and New York are exceptional. Meta-analyses of changes in species richness, local extinctions, abundance of native species, or other characteristics of local plant diversity rarely include resurveys that cover 75 years or more (Vellend et al. 2013b; Murphy and Romanuk 2013; Wiens 2016). In Europe, many long-term historical data sets describing plant diversity exist, but few entire (or nearly entire) floras have been resurveyed and analyzed like those included in this study (Gregor et al. 2012; Grass et al. 2014; Worz and Thiv 2015). We know of no other region outside of Europe with data sets describing changes in plant occurrences and abundance as numerous as those found in New England and New York.

Conclusions and recommendations. Detailed historical records like those summarized in these floristic change studies provide valuable opportunities for understanding trends in local plant biodiversity and for informing the management of rare species. Floristic change studies may also provide insight into ecological stressors and threats, whether those threats are local, like development pressure, regional, like air pollution, or global, like climate change (Greene et al. 2005; Bertin 2008; Harris et al. 2012). Although native species were lost throughout the region, there were surprisingly large amounts of variation in the degree and nature of changes in plant communities. The wide range of rates of species loss, and the lack of correlation between loss and the size of study areas or conservation status, indicates that individual stressors like development are probably not driving differences in floristic change across the region—rather the variation among sites likely reflects a complexity of factors driving species loss and changes in abundance.

In conclusion, our review of floristic change across New England and New York yields the following suggestions for assessing the regional vulnerability of plants:

1. Analyses of changes in nearby floras may help land managers and scientists understand broad, community-level changes in species richness and relative abundance, but local study is likely required to understand local changes in the abundance of particular species.
2. Rare species are more likely to disappear from localities than species ranked as common, occasional, or uncommon. This reinforces our understanding that rare species are particularly vulnerable and efforts to identify, protect, and monitor local populations of rare species should be continued.
3. Species within particular taxonomic groups (e.g., Orchidaceae, Liliaceae, Violaceae) have declined in abundance disproportionately to other groups throughout New England and New York. Other taxa have declined in particular locations (e.g., Juncaceae and Lycopodiaceae on MDI), and local data is needed to identify these site-specific declines. Like rare species, species in these groups appear vulnerable and deserve special consideration for monitoring and management.
4. No single habitat type appears to be more (or less) vulnerable to species loss and decline than any other. This finding suggests that the large-scale drivers of species loss are common across all habitat types (e.g., climate change, air pollution or deposition).
5. Nonnative species are becoming more common in floras throughout the region as native species decline in abundance.

Our recommendation here is not new, but we recommend that managers monitor and manage (to the extent practical) nonnative species that are likely to become invasive and harm native species and ecosystem processes. Targeting particularly invasive species will be important for maintaining the ecological integrity of protected areas as ecological communities continue to change.

6. Resurveys of historical floras are among the best available methods for assessing changes in the abundance of plant species over time; however, the method is susceptible to biases resulting from the methods or motives of particular researchers (past or present). Researchers and managers should use these resources when possible but should also be aware of their limitations.
7. Present-day botanists should renew efforts to document current floras in well-targeted areas to provide detailed baseline data for future scientists. Based on our review of historical studies, we suggest that published floras, voucher specimens, and detailed field notes are most important to creating useful records for botanists working to understand floristic change in the decades to come. As the availability and quality of detailed floras increases, the work of future botanists interested in comparative longitudinal studies will become easier and broader conclusions can be drawn.

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