

## Articles

# High Similarity in Winter Diet between Imperiled New England Cottontail and Invasive Eastern Cottontail

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## Abstract

Ongoing declines in the imperiled New England cottontail *Sylvilagus transitionalis* have coincided with the introduction and expansion of the closely related eastern cottontail *Sylvilagus floridanus*. These paired population trends have led to the inference of competition between the two species. Competition between native and introduced species has often involved overlapping use of food resources, but limited effort has been spent to analyze the diets of New England cottontail and eastern cottontail and to evaluate the potential for resource competition. We used microhistologic analysis of fecal pellets to assess the winter diets of both species and we compared diet composition with available plant communities to evaluate their preferences for dietary items across southern New England and southeastern New York. We found no differences in diets between New England cottontail and eastern cottontail, although diets did differ between regions within the study area. Diet preferences also were consistent between the species and largely excluded nonnative plant genera. Our results demonstrate that these species are generalist herbivores and that there is high potential for competition for food resources in the winter between them, although the present lack of diet partitioning may indicate the presence of other factors limiting competition. This study highlights the need for careful evaluation of interactions between native and nonnative species, a prerequisite for developing conservation plans that appropriately account for interspecific competition.

Keywords: early successional forest; herbivore; invasive species; microhistologic; resource competition; *Sylvilagus floridanus*; *Sylvilagus transitionalis*

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## Introduction

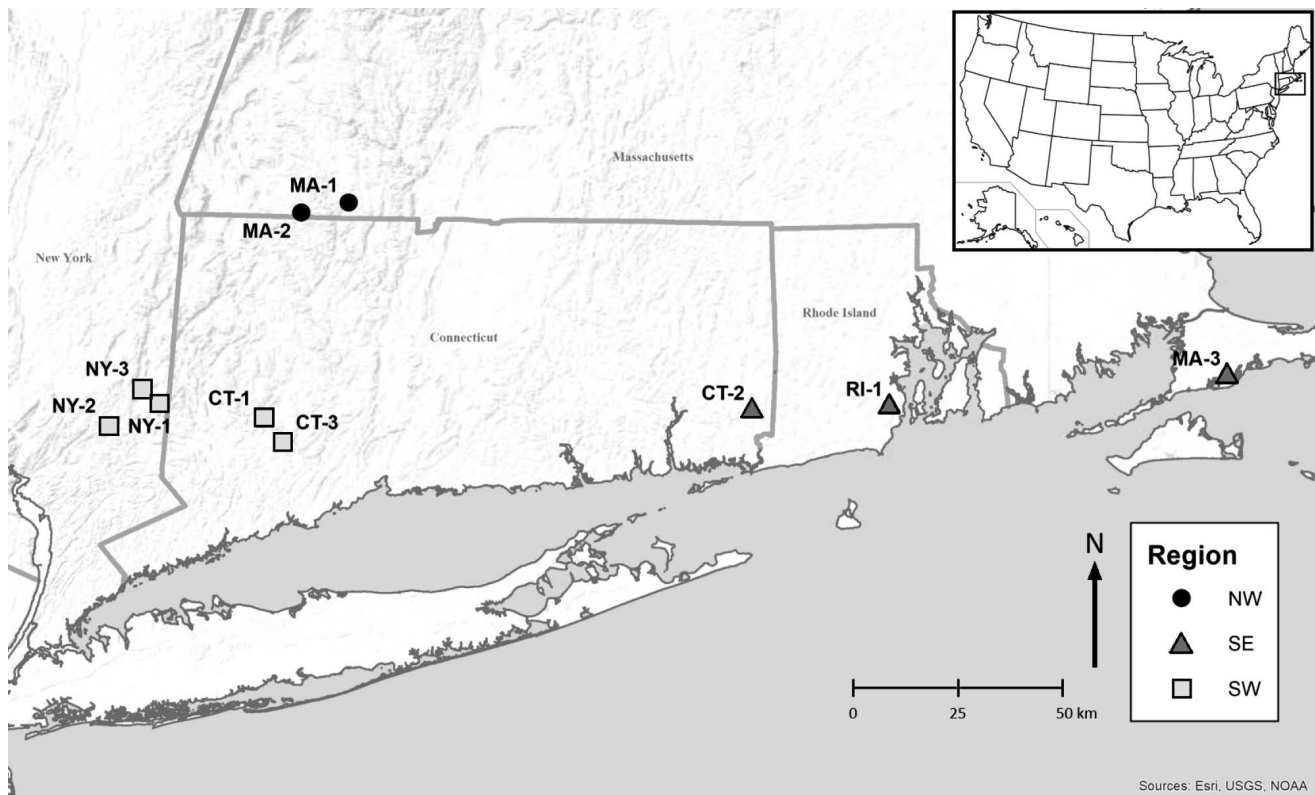
Invasive species have been implicated in the decline of a wide range of species of conservation concern, including plants, insects, and vertebrates (Clavero and García-Berthou 2005; Dueñas et al. 2018). Negative correlations between the arrival of invasive species and native species populations are likely related to the novel interspecific interactions that arise when species are introduced to new areas (Pearse and Altermatt 2013; Grether et al. 2017), and particularly competition between species of similar trophic position (Callaway and Ridenour 2004; Gurnell et al. 2004; Kirchbaum et al. 2010). Competition may involve indirect interactions mediated by predators or parasites (Noonburg and Byers 2005; DeCesare et al. 2010), but also can involve direct competition for limited resources (Stockley and Bro-Jørgensen 2011; Grether et al. 2017). Limiting resources include habitat features such as shelter or nest sites (Newton 1994), but have most often been associated with food resources (Belovsky 1986; Arsenault and Owen-Smith 2002). Accordingly, the diets of invasive species regularly overlap with those of native species, including cases with declines in the native species (Baldi et al. 2004; Miranda et al. 2012; Ustups et al. 2016). These findings have led to a growing recognition of the need to consider species interactions, and particularly competition, when designing and evaluating conservation strategies (Sinclair and Byrom 2006; Wittmer et al. 2013). Consideration of competition between invasive and native species is particularly important in the context of broader conservation concerns, such as habitat loss, where competition may exacerbate ongoing declines (Wiens et al. 2014). Moreover, even if competitive interactions do not actively accelerate the loss of imperiled species, they may still inhibit the population growth and recovery of those species (Hamel et al. 2013; Chen et al. 2020). Thus, evaluating the potential for competition between native and invasive species for food resources is an important part of developing conservation strategies.

The New England cottontail (NEC) *Sylvilagus transitionalis* is a native species to the northeastern United States that has experienced a drastic decline in its distribution over the last century (Litvaitis et al. 2004; Rittenhouse and Kovach 2020), coincidental with the spread of a nonnative competitor, the eastern cottontail (EC) *Sylvilagus floridanus*. The distribution of NEC is restricted to four isolated populations across the states of Maine, New Hampshire, Massachusetts, Rhode Island, Connecticut, and New York east of the Hudson River (Fenderson et al. 2011; Sullivan et al. 2019). This decline has been most closely associated with the loss of early successional habitat because NEC is an obligate early successional specialist (Litvaitis and Villafuerte 1996; Litvaitis et al. 2008) and has led to region-wide conservation efforts (Fuller and Tur 2012). Primary conservation actions have included the restoration of approximately 35,000 acres of early successional forest and a program for captive breeding and translocation. During this same period, the closely related and ecologically similar EC has expanded

throughout the historical range of NEC. The EC is a habitat generalist (Chapman et al. 1980) and an invasive species east of the Hudson River. First recorded in the area in the 1930s (Dalke and Sime 1938), EC are now more common than NEC throughout much of New England (Probert and Litvaitis 1996; Sullivan et al. 2019). This overlap in range, combined with the trophic similarities between the two species, creates great potential for competition between NEC and EC (hereafter collectively referred to as “both cottontail species” or “cottontails”), which could undermine NEC conservation efforts. To date, though, there has been limited research aimed at understanding potential competition between both cottontail species, with most studies focused on interference competition mediated through dominance relationships (Probert and Litvaitis 1996) and range shifts (Cheeseman et al. 2018). Importantly, the potential for exploitation competition between both cottontail species over food resources remains untested, although early evidence suggests that the winter diet of both species is dominated by stems from woody plant species, with more grasses and forbs consumed in the summer (Chapman 1975; Chapman et al. 1980).

The purpose of this study was to assess competition for food resources between NEC and EC in southern New England and New York by evaluating the similarities and overlap in winter diet composition and preferences. Given the close phylogenetic relationship between both species (Silva et al. 2019), a baseline expectation would be high overlap between their diets. Accordingly, the two species were not distinguished from one another in an early study on cottontail diets in Connecticut (Dalke and Sime 1941). A diet selection study of both cottontail species, caught from the wild in Massachusetts and held in captivity, found a similar diet preference between the species in the summer, but a difference in their preference diet in the winter (Pringle 1960). High dietary overlap also has been observed in other cases involving the introduction of congeneric lagomorph species (Reid 2011). On the other hand, there is evidence for diet partitioning between other sympatric lagomorphs that has alleviated exploitation competition (Chapuis 1990; Katona et al. 2004), and both species have likely co-occurred in the northeastern United States for at least several decades, providing time for diet partitioning to develop. Similarly, a previous study of cottontail habitat use in southeastern New York found evidence for resource partitioning on the basis of patch successional stage (Cheeseman et al. 2018), which might translate to differences in diet if there is high turnover in plant assemblages among stages. When EC are in low abundance, NEC occupy areas with a wider range of canopy closure values. However, when EC are in high abundance, NEC are found in areas with higher canopy closure values (Cheeseman et al. 2018). Consequently, we expected to find differences in the winter diet between both species, with NEC consuming more shrubs and fewer grasses than EC because of their preference for patches with dense understorey (Litvaitis et al. 2003; Mayer et al. 2018). We also expected that, if there is winter diet partitioning between both cottontail species,





**Figure 1.** Sites in southern New England and southeastern New York where we collected pellets between November and March of 2011 to 2013 for analysis of New England cottontail *Sylvilagus transitionalis* and eastern cottontail *Sylvilagus floridanus* diets. We divided sites into three regions with varying plant communities: a coastal, lowland region (southeast [SE]); an inland, higher-elevation region (northwest [NW]); and a region with intermediate elevation and distance to the ocean (southwest [SW]). We found and collected only New England cottontail pellets from sites CT-2 and CT-3.

there also could be differences between the species in diet usage. This study is an important step toward understanding the competitive interactions between both cottontail species and informing conservation plans for an imperiled species in the context of a relatively recent invasion.

### Study Site

We conducted this study in collaboration with state and federal biologists throughout southern New England and southeastern New York as part of a broader effort to assess the geographic ranges and habitat use of both cottontail species with winter pellet surveys (sensu Buffum et al. 2015). The process of selecting survey sites varied depending on the needs of individual states, but generally the state and federal biologists focused efforts on areas where at least one of the following was true: 1) NEC was known to occur, 2) vegetation was suitable for NEC, or 3) wildlife management was a high priority. Ultimately, 10 sites produced large-enough pellet samples for diet analysis (Figure 1). Sites were roughly spread across three regions: a northwest region (NW) with two sites in western Massachusetts; a southwest region (SW) with three sites in southeastern New York and two sites in western Connecticut; and a southeast region (SE) with one site each in eastern Connecticut,

Rhode Island, and eastern Massachusetts (Figure 1). Although all sites were characterized by a mixture of shrubland, grassland, and mature forest, these regions occurred along a continuum of elevation and proximity to the ocean, potentially producing differences in their plant communities. Specifically, the NW region was the farthest inland and characterized by the highest elevations, whereas the SE region was the most coastal with the lowest elevations. Although we detected both cottontail species at the majority of these sites, the surveys used for this study were not exhaustive enough to provide reliable estimates of the relative density of each species.

### Methods

#### Fecal pellet collection

We collected cottontail fecal pellets between February 2011 and March 2013 during the winter (November to March) when snow cover made cottontail pellets readily visible (Brubaker et al. 2014). We conducted pellet surveys at least 48 h after a snow event, with a minimum wait of 72 h if the snowfall was greater than 30 cm. Each survey covered a square plot between 1 and 4 ha in size and consisted of perpendicular transects over that area spaced by approximately 30 m. In sites with enough

habitat, multiple adjacent plots were surveyed. Cottontail pellets were typically clustered within survey sites, and at four sites (NY-1, NY-2, and NY-3, and CT-2) we found multiple clusters separated by more than 220 m. A comparison of this distance with cottontail home ranges (Cheeseman et al. 2019) strongly suggests that pellets in different clusters were produced by different individuals, and so we considered these clusters to be separate samples. State and federal biologists collected pellets grouped in a single pile (within approximately 20 cm of one another) into sterile 15-mL tubes and sent them to the University of Rhode Island Wildlife Genetics and Ecology Laboratory, Kingston, Rhode Island for species identification.

We extracted deoxyribonucleic acid (DNA) from fecal pellets in each tube and used mitochondrial DNA sequencing to identify the species of origin of fecal pellets using the protocol described by Sullivan et al. (2019). Briefly, we extracted genomic DNA from each fecal pellet using the Qiagen QIAamp DNA stool mini kit (Qiagen Sciences, Maryland) according to manufacturer's instructions. We amplified an approximately 480-base-pair portion of the mitochondrial DNA control region using forward primer L15934 (Litvaitis et al. 1997) and reverse primer H16442 (Sullivan et al. 2019). We determined the species of origin of the amplified DNA by comparing the unknown sequence with reference sequences that included all known haplotypes from NEC, EC, and snowshoe hare (*Lepus americanus*; Sullivan et al. 2019).

After species identification, we assigned the pellets in each tube to a cluster on the basis of its location and we combined tubes from each species and cluster into 22 single-species composite samples (NEC,  $N = 13$ ; EC,  $N = 9$ ) to have enough fecal material for microhistologic analyses. We found both cottontail species at every survey site except CT-2 and CT-3, where we detected only NEC. Composite samples included pellets from 1 to 12 tubes, totaling at least 2, but up to 24, pellets. We assumed pellets from the same tube to be from the same individual, whereas pellets from different tubes may have been from different individuals. We carried out this work under the approval of the University of Rhode Island Institutional Animal Care and Use Committee (AN11-012-11).

### Microhistologic analyses

Analysis of fecal samples is a common and reliable method for noninvasively characterizing animal diets (Holechek et al. 1982; Mayes and Dove 2000). Therefore, we submitted composite samples for each cottontail species to the Washington State University Wildlife Habitat and Nutrition Laboratory, Pullman, for microhistologic analysis of diet composition, a widely used method for assessing herbivore diets (Mayes and Dove 2000; Baldi et al. 2004; Sangiuliano et al. 2016; Kalb et al. 2018). Briefly, the process involved preparation of samples by grinding, washing, and filtering samples,

with subsequent steps to extract, bleach, and stain plant fragments (Davitt and Nelson 1980). We prepared extracted plant tissues from each sample on microscope slides and then identified them to genus or nearest structural grouping by observing diagnostic microhistologic features of cellular structure (Holechek et al. 1982). The amount of plant tissue available for analysis depended on the number of fecal pellets collected, resulting in two to eight slides being prepared for each composite sample. We examined each slide with 25 randomly placed microscope views, resulting in 50 to 200 views for each diet sample (50:  $N = 3$ ; 100:  $N = 6$ ; 200:  $N = 13$ ). We reported results as percent diet composition calculated as the area covered by each plant category within random microscope views, divided by the total area of microscope views for that composite sample (Sparks and Malechek 1968; Davitt and Nelson 1980).

### Plant availability

Diet items may be consumed because they are actively selected over other options or because no other options are present. Therefore, evaluating animals' preferences for diet items requires a comparison of the items consumed with the availability of those diet items (Alldredge and Ratti 1986; Thomas and Taylor 2006). Accordingly, after pellet surveys, we selected a random pellet location for each pellet cluster as the center point for a  $50 \times 50$  m vegetation survey site to establish the availability of dietary plants. Within each vegetation survey site, we placed six  $1\text{-m}^2$  quadrats at predetermined random locations on either side of transects running N-S and E-W through the center point, for a total of 12 quadrats. We then counted the number of available stems ( $<5$  mm in diameter, 0–0.5 m above ground) of each woody shrub species within each quadrat to estimate vegetation density. We counted clusters of forbs and grasses as single stems and we visually identified the species of vegetation. We recorded availability within each vegetation survey site as the percent stem composition, calculated as the number of stems for a given plant genus in all quadrats divided by the total number of stems counted in all quadrats for that site.

### Data analysis

Before analysis of both cottontail species' diet composition and preference, we identified trace components as diet items that averaged less than 1% of diets and never exceeded 5% of the diet in any given composite sample, which we then aggregated into a single variable. We characterized the diets of each cottontail species by calculating several metrics of diet diversity, including richness, evenness, the Shannon index, and the Simpson index (Hill 1973). Traditional statistical analyses designed for normally distributed data are inappropriate for raw compositional data because of its scale invariance and subcompositional coherence (Aitchison and Egozcue 2005). Therefore, we used





recommended adjustments for our compositional data: putatively left-censored (i.e., zero) diet proportions in our data set were replaced via multiplicative log-normal imputation (Martín-Fernández et al. 2012; Palarea-Albaladejo and Martín-Fernández 2015) and we transformed diet proportion data using a centered log-ratio transformation (van den Boogaart and Tolosana-Delgado 2008). The centered log-ratio transformation is appropriate for data like ours, which is characterized by relative distance and nonmeaningful total amounts and has been used previously to analyze mammalian diet composition (e.g., Soininen et al. 2013).

To investigate the factors influencing diet composition, we first characterized broad associations among transformed diet proportions by reappportioning variance in the data set among new, orthogonal dimensions with a principal components (PCs) analysis (Haerdle and Simar 2015). We retained all components that accounted for a greater proportion of cumulative variance than expected given an even distribution and we used a broken-stick model to evaluate the loadings of diet items on extracted PCs (Peres-Neto et al. 2003). We then used linear models to test the influence of cottontail species and region on PCs and metrics of diet diversity while controlling for the influence of effort in the micro-histologic analyses as represented by number of views. In cases where we found evidence for strong effects of region ( $\alpha = 0.05$ ), we compared regional means with Tukey honestly significant difference post hoc tests (Hothorn et al. 2008). We also directly investigated the similarity between both cottontail species' diets by calculating four indices of diet overlap used in related studies: Renkonen's similarity index, Horn's index of similarity, the simplified Morisita index, and Shoener's index of overlap (Katona et al. 2004; Kalb et al. 2018). For all of these indices, 0 indicates no overlap in diet and 1 indicates complete overlap in diet. The data set of diet proportions used for comparisons between both cottontail species is available (Table S1, *Supplemental Material*).

To assess both cottontail species' preferences for dietary items, we calculated the Johnson's rank preference index for each diet item (Lechowicz 1982; Alldredge and Ratti 1986). To do so, we ranked plant genera (including aggregated trace genera) in ascending order from most to least common in composite samples and availability plots. We gave genera that did not occur in a given sample or availability plot the highest numeric rank possible (18) and then calculated the preference index for genus at each site by subtracting diet sample ranks from availability ranks. We evaluated overall preference by calculating the mean difference for each plant genus and considered a genus preferred if the mean was positive and the 95% confidence interval did not overlap zero. We then used a linear model to test the influence of cottontail species and region on preference indices for each plant genus. The data set of diet ranks used for assessment of both cottontail species' prefer-

ences is available (Table S2, *Supplemental Material*). We used  $\alpha = 0.05$  as a benchmark of effect strength for linear models and conducted them in R version 3.6.2 (R Core Team 2019).

## Results

The fecal samples included 10 NEC and 9 EC mitochondrial DNA haplotypes (Table S3, *Supplemental Material*). Most of the haplotypes were previously identified by Sullivan et al. (2019), but we identified two NEC and one EC new haplotype (GenBank accession numbers OP679797, OP679798, and OP679799, respectively) that differed from previously accessioned haplotypes by one or two nucleotides. Most composite diet samples included only one haplotype, but two NEC and one EC composite sample each included three haplotypes.

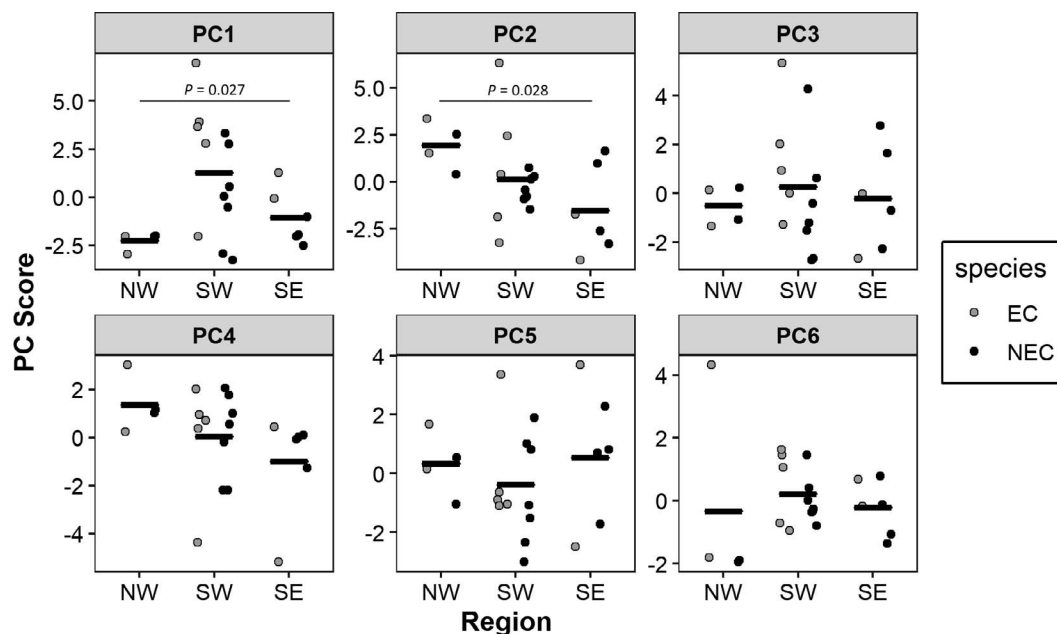
We detected 50 different genera of plants in the cottontail pellets collected, of which only 17 constituted more than 1% of the average diet or more than 5% of any single sample. The remaining trace genera included *Agrostis*, *Ailanthus*, *Alnus*, *Amelanchier*, *Aronia*, *Berberis*, *Brassica*, *Carex*, *Celastrus*, *Clethra*, *Fagus*, *Gaylussacia*, *Hamamelis*, *Ilex*, *Kalmia*, *Ligustrum*, *Lindera*, *Lonicera*, *Morella*, *Ostrya*, *Panicum*, *Populus*, *Potentilla*, *Prunus*, *Rhamnus*, *Rhus*, *Ribes*, *Sassafras*, *Smilax*, *Toxicodendron*, *Tsuga*, *Ulmus*, and *Vitis*. We reduced the dimensions of the 17 most common genera, aggregated trace genera, and two additional categories of dietary plant material (unknown shrubs and unknown conifers) with a principal components (PCs) analysis and retained six components representing 80.8% of the cumulative variance (Table 1). Retained components represented various combinations of diet items, with substantial loadings from two to six plant genera. There was strong evidence that scores for both PC1 ( $F_{2,17} = 4.50$ ,  $P = 0.027$ ) and PC2 ( $F_{2,17} = 4.42$ ,  $P = 0.028$ ) were related to region (Figure 2), with post hoc tests indicating that these effects were primarily driven by a contrast between the NW and SW regions for PC1 ( $P = 0.034$ ) and a contrast between the NW and SE regions for PC2 ( $P = 0.066$ ). There was little evidence to suggest that diet composition, as indicated by components, was related to rabbit species (Figure 2; Table S4, *Supplemental Material*) and correspondingly, all indices of overlap between both cottontail species' diets had values over 0.8 (Table 2). Diet richness ( $17.3 \pm 1.0$ , mean  $\pm$  SE), evenness ( $0.71 \pm 0.08$ ), and both indices of diet diversity (Shannon index:  $2.01 \pm 0.13$ ; Simpson index:  $0.75 \pm 0.04$ ) were unrelated to rabbit species or region (Table S4, *Supplemental Material*).

Both cottontail species exhibited varying preferences for diet items (Table 3). Preferred plant genera included *Quercus*, *Corylus*, *Betula*, *Sorbus*, *Salix*, *Vaccinium*, and *Spiraea*, whereas both cottontail species selected trace plant genera, in aggregate, less often than they were available and EC avoided the genus *Rosa*. However, there was weak evidence that Johnson's rank preference indices were related to either region or rabbit species (Table S5, *Supplemental Material*), with the exception of



**Table 1.** Loadings and cumulative variances of components extracted from a principal components (PCs) analysis of diet items consumed in varying proportions by New England cottontail *Sylvilagus transitionalis* and eastern cottontail *Sylvilagus floridanus* in southern New England and southeastern New York. We estimated diet proportions of different plant taxa via microhistologic analysis of cottontail fecal pellets collected from 14 sites across southern New England and southeastern New York between November and March of 2011 to 2013. Asterisks denote loadings considered to be important for given components.

	PC1	PC2	PC3	PC4	PC5	PC6
Cumulative variance	0.227	0.400	0.535	0.649	0.748	0.808
Plant taxa						
<i>Abies</i>	0.286*	0.218*	-0.021	-0.158*	-0.029	0.158*
<i>Acer</i>	-0.219	0.148	0.029	0.048	-0.085	-0.044
<i>Betula</i>	-0.317*	0.098	-0.003	0.281*	-0.258*	0.065
<i>Carya</i>	-0.075	0.038	0.178	-0.062	0.152	-0.568*
<i>Cornus</i>	-0.078	-0.303*	0.152	-0.035	-0.200	0.015
<i>Corylus</i>	-0.028	-0.162	-0.220	0.210	-0.505*	-0.030
<i>Elaeagnus</i>	0.436*	-0.270	0.547*	0.262	-0.207	0.111
<i>Lyonia</i>	0.241*	0.135	-0.091	-0.100	-0.031	0.064
<i>Poa</i>	0.154	-0.178	-0.085	-0.239	0.390*	0.001
<i>Quercus</i>	-0.132	-0.175	-0.189	-0.166	0.032	0.171
<i>Rosa</i>	-0.300*	0.114	-0.025	0.200	-0.033	0.116
<i>Rubus</i>	0.458*	0.097	-0.566*	0.394*	0.111	-0.208
<i>Salix</i>	-0.140	0.210	0.273	0.505*	0.526*	0.102
<i>Sorbus</i>	-0.270	-0.191	-0.129	-0.097	0.198	0.064
<i>Spiraea</i>	-0.065	-0.015	0.026	-0.164	0.155	0.389*
<i>Vaccinium</i>	0.028	-0.388*	0.151	-0.111	0.095	-0.421*
<i>Viburnum</i>	-0.030	0.580*	0.154	-0.279*	-0.200	-0.317*
Unknown conifer	0.221	0.210*	0.159	-0.246	-0.048	0.310*
Unknown shrub	-0.027	-0.083	-0.209	-0.040	0.013	0.055
Trace genera	-0.141	-0.082	-0.133	-0.206	-0.075	-0.032



**Figure 2.** Relationships between diet composition, region, and species for New England cottontail *Sylvilagus transitionalis* and eastern cottontail *Sylvilagus floridanus*. We estimated diet composition via microhistologic analysis of cottontail fecal pellets collected from 14 sites across southern New England and southeastern New York between November and March of 2011 to 2013. Panels separate the top components extracted from a principal components analysis of diet items used to reduce the dimensions of diet composition and points (gray = eastern cottontail, EC; black = New England cottontail, NEC) depict the component scores for individual sites. Horizontal bars indicate mean scores for different regions in which we collected samples.

**Table 2.** Indices of overlap between New England cottontail *Sylvilagus transitionalis* and eastern cottontail *Sylvilagus floridanus* diets at 14 sites in southern New England and southeastern New York between November and March of 2011 to 2013. We calculated overlap indices from the relative proportions of individual diet components estimated via microhistologic analysis of fecal pellets. For each index, 0 indicates no overlap and 1 indicates complete overlap.

Index	Value
Renkonen	0.801
Horn	0.936
Morisita	0.949
Schoener	0.804

*Corylus*, which was more strongly favored by NEC than by EC ( $F_{1,12} = 10.630$ ,  $P = 0.007$ ).

## Discussion

We found that cottontails in southern New England and southeastern New York had relatively broad diets, with the individual or individuals at each cluster consuming an average of 17 different plant genera ranging from conifers to grasses. Similarly, the diversity of cottontail diets as indicated by the Simpson index was reasonably close to the maximum value of 1, and diversity as indicated by the Shannon index was comparable with or greater than that estimated for other lagomorphs, where values generally ranged between 1 and 2 (Chapuis 1990; Bonino and Borrelli 2006). These findings confirm that both cottontail species in this area are largely dietary generalists in the winter and therefore capable of using areas with a wide range of plant communities. Nevertheless, a subset of plant genera constituted the bulk of cottontail diets and all but 1 of the 17 most prominent plant genera were composed of trees or shrubs (the exception being *Poa*, a genus of grasses). This result is consistent with findings about the importance of woody shrub density in determining cottontail occupancy (Litvaitis et al. 2003; Cheeseman et al. 2018; Mayer et al. 2018). Cottontail diets in southern New England have been relatively consistent in composition and diversity over time, with a study in Connecticut during the 1930s recording observations of rabbits consuming 14 of the 17 most prominent plant genera in our samples and a total of 55 different plant genera (Dalke and Sime 1941).

Although our sample size was apparently sufficient to capture the breadth of cottontail diets, a result potentially supported by the combining of pellets from multiple individuals into composite samples, it was ultimately limited. Such small sample sizes inevitably reduced our power to statistically resolve subtle differences between species and regions, meaning that our findings of no differences between species in diet composition and no differences between species or regions in diet diversity must be interpreted with caution. Nevertheless, the fact that our analyses produced a mix of strong and weak evidence suggests that some effects were large enough in magnitude to be

**Table 3.** Johnson's rank preference index for plant genera consumed by New England cottontail *Sylvilagus transitionalis* and eastern cottontail *Sylvilagus floridanus* at 14 sites in southern New England and southeastern New York between November and March of 2011 to 2013. We estimated plant consumption by cottontails via microhistologic analysis of fecal pellets and compared them with measurements of the composition of available vegetation. Values represent mean differences between used and available ranks of plant genera composing more than 1% of the average cottontail diet, with 95% confidence intervals (CIs) in parentheses. Plant genera are ordered from most to least preferred by New England cottontail. Asterisks indicate CIs that do not overlap 0 for at least one of the two cottontail species; dash indicates no data.

Plant taxa	New England cottontail, mean (95% CI)	Eastern cottontail, mean (95% CI)
<i>Quercus</i> *	12.0 (7.7, 16.3)	9.1 (3.7, 14.6)
<i>Corylus</i> *	11.1 (4.9, 17.3)	8.1 (3.2, 13.1)
<i>Betula</i> *	10.7 (5.8, 15.7)	9.1 (2.0, 16.3)
<i>Sorbus</i> *	10.5 (7.4, 13.6)	5.6 (0.4, 10.8)
<i>Salix</i> *	10.2 (6.1, 14.2)	7.3 (2.2, 12.4)
<i>Vaccinium</i> *	9.1 (4.1, 14.1)	9.9 (3.9, 15.8)
<i>Spiraea</i> *	6.2 (3.5, 8.9)	7.9 (3.3, 12.5)
<i>Carya</i>	4.2 (−2.4, 10.8)	6.1 (−2.4, 14.7)
<i>Acer</i>	3.2 (−2.1, 8.5)	−1 (−9.1, 7.1)
<i>Elaeagnus</i>	2.4 (−1.3, 6.0)	5 (−0.5, 10.5)
<i>Rubus</i>	1.8 (−3.4, 7.1)	0.1 (−7.7, 7.9)
<i>Viburnum</i>	1.6 (−3.9, 7.2)	−1.1 (−11.1, 8.9)
<i>Cornus</i>	1.5 (−4.5, 7.4)	−2.7 (−12.9, 7.5)
<i>Poa</i>	1.2 (−0.5, 2.9)	2.3 (−2.6, 7.1)
<i>Abies</i>	—	4.7 (−1.7, 11.2)
<i>Lyonia</i>	−0.9 (−4.5, 2.7)	4.1 (−1.6, 9.9)
<i>Rosa</i> *	−1.6 (−9.7, 6.4)	−10.6 (−16.1, −5.0)
Trace genera*	−3.2 (−4.8, −1.6)	−8.1 (−14.1, −2.2)

detectable despite the limitations of sample size, and any effects missed due to low power are correspondingly smaller in magnitude.

Contrary to our expectations, we failed to find strong evidence for differences between the winter diet composition of both cottontail species and a correspondingly high overlap between the overall diet of the two species. In particular, our results contrast those of Pringle (1960), who found a difference in the vegetation preference of both cottontail species during the winter. However, the Pringle (1960) study analyzed the selection of wild-caught cottontails in captivity, whereas we studied cottontail diet in the wild, which could explain the difference between our results. In addition, our microhistologic results in wild individuals are consistent with the direct observations of Dalke and Sime (1941), who found consistent diets among all cottontails throughout their study area in Connecticut. Corresponding to the high overlap in both species' diets, we did not find the expected difference in grass consumption between species. Instead, both species primarily consumed grasses in only trace amounts, meaning that any differences between the species in habitat use did not translate into differences in winter diet. However, cottontail grass consumption may increase and diverge between species in other seasons when grasses are more



active and have higher nutritional content (McDonald et al. 2011).

The overlap in diet between both cottontail species has several implications for the potential resource competition between the two species. First, competition can influence the success of imperiled species by synergistically interacting with other drivers of population dynamics (Hamel et al. 2013; Wiens et al. 2014; Chen et al. 2020). Thus, the high degree of overlap suggests that competition for food resources is likely to occur when the two species co-occur at high densities and may be a contributing factor in the ongoing decline or slow recovery of NEC. Nevertheless, decades of co-occurrence of both species produced no discernible partitioning in cottontail diets, which suggests that competition between these species has, in effect, not been strong enough to prompt any long-term dietary adaptation. Our analysis of diets focused exclusively on winter months, and so partitioning may occur during other seasons. However, winter also is the season with the fewest high-quality food resources available for herbivores and therefore the period in which we would expect to see the strongest competition that could lead to resource partitioning. For diet generalist species such as these cottontail species, a lack of resource partitioning may indicate that competition is limited by the top-down effects of keystone predation (Paine 1969; Amarasekare 2008; McPeck 2014) or may indicate the presence of spatial or temporal partitioning of resource use (Orlando and Hall 2015; Soto and Palomares 2015). It also is possible, although unlikely, that they did not come into contact at our study sites until relatively recently. In either case, diet partitioning may still be an available mechanism to relieve future resource competition between the two species.

Competition can be particularly strong among generalist species like cottontails (Belovsky 1986; Stephens et al. 2019), and so there may be a notable risk of NEC being outcompeted by EC in the absence of future partitioning. Combined with recent evidence of other negative impacts of EC on NEC persistence, including prompted shifts in habitat selection (Cheeseman et al. 2018), apparent range exclusion (Cheeseman et al. 2020), and higher tick loads on NEC compared with EC (Mello 2018), this result suggests the need for a more comprehensive and coherent approach to the management of the NEC–EC relationship. Moving forward, it will be important for NEC conservation planners to evaluate the degree of resource competition between both cottontail species, and in future cases where there are high cottontail densities and strong competition is confirmed, it may be necessary to implement more active measures to reduce competition. Additionally, although overall densities may drive competition at a given site, it also is possible that the relative densities of the two species help shape the outcomes of competitive interactions. Evaluating the relationship between relative densities and diet was beyond the scope of this study and may be an important line of future research.

Despite the similarity between both species' diets, cottontails did not consume consistent diets throughout

our study area as represented by PC1 and PC2 varying across regions. In both cases, the strongest contrasts between regions involved the NW region, suggesting that climatic differences over our study area, resulting from changes in elevation and proximity to the ocean, produce enough variation in plant communities to noticeably alter both cottontail species' diets. For example, PC1 was positively related to the more southerly genus *Lyonia* (maleberry) and negatively related to the more cold-hardy *Betula* (birches), and correspondingly we observed higher values in the SW region and lower values in the NW region. Similarly, PC2 was positively related to *Abies* (firs), other conifers, and viburnum and we observed higher values in the NW region. Regions also likely differed in the degree of human influence on their plant communities, which led, for example, to a positive relationship between PC1 and the nonnative genus *Elaeagnus*. These factors provide plausible general explanations for much of the observed variation in both cottontail species' diets, but it is important to note that each occurs along a gradient that is only loosely captured here because of our small sample size. In certain cases, local variation in these and other factors (e.g., soil type; Latham 2003; Lawes et al. 2013) may be more important than regional trends. Nevertheless, these results do demonstrate that both cottontail species are capable of using a wide range of plants in different areas.

Differences in plant usage across regions may result from varying diet preference and not just differences in plant availability (Manly et al. 2002; Thomas and Taylor 2006). However, we found no influence of region on diet preferences of both cottontail species, suggesting that their diets were more strongly influenced by the availability of different plants in those regions. Overall, both cottontail species did display preferences for many plant genera, including *Quercus*, *Corylus*, *Betula*, *Sorbus*, *Salix*, *Vaccinium*, and *Spiraea*. This result strongly contrasts with the results of a recent study on NEC diet preferences on Cape Cod (Etkind 2020), with *Betula* being the only plant genus found to be preferred in both studies. Meanwhile, *Quercus* and *Vaccinium*, two of the genera found to be preferred in our study, were avoided in Etkind's study. At present, it is unclear what factors may have contributed to these differences, but one possibility is that the spatial arrangement or richness of diet items differed between study areas, leading to changes in cottontail foraging behavior (Bergman et al. 2005; Milligan and Koricheva 2013). Alternatively, the nutritional value of plants, and particularly nitrogen, may have varied across study areas or periods (Duquesnay et al. 2000; Kontsiotis et al. 2015). Of interest, cottontails only consumed trace amounts of many of the plant genera containing widespread nonnative species, including *Ailanthus*, *Berberis*, *Brassica*, *Celastrus*, *Ligustrum*, *Lonicera*, and *Rhamnus* (Bates et al. 1976), and trace genera in aggregate were avoided by both cottontail species. Similarly, neither of the likely nonnative plant genera consumed in nontrace quantities (*Elaeagnus* and *Rosa*) was preferred and *Rosa* was actively avoided by EC. Thus, it does not appear that areas containing high





proportions of introduced vegetation are likely to provide high-quality forage for either cottontail species. This result is consistent with the findings of Cheeseman et al. (2020) but would be further reinforced with a direct analysis of the nutritional content of known diet items. If this finding is confirmed, the support of native shrubland communities rich in regenerating oak *Quercus* and hazelnut *Corylus* could be a useful management step toward assisting the recovery of NEC.

## Supplemental Material

Please note: The *Journal of Fish and Wildlife Management* is not responsible for the content or functionality of any supplemental material. Queries should be directed to the corresponding author for the article.

**Table S1.** Proportions of plant taxa found in the fecal pellets of New England cottontail *Sylvilagus transitionalis* and eastern cottontail *Sylvilagus floridanus* through microhistological analysis. We collected pellets between February 2011 and March 2013 during the winter (November to March) at 14 sites across southern New England and southeastern New York. These pellets represent the winter diet of these species.

Available: <https://doi.org/10.3996/JFWM-22-015.S1> (3 KB TXT)

**Table S2.** Used and available rankings of plant taxa in areas occupied by New England cottontail *Sylvilagus transitionalis* and eastern cottontail *Sylvilagus floridanus* in southern New England and southeastern New York. We derived data on used ranks from proportions found in fecal pellets collected between February 2011 and March 2013 during the winter (November to March) at 14 sites across the study area and analyzed by microhistology. We collected data on available ranks during subsequent vegetation sampling.

Available: <https://doi.org/10.3996/JFWM-22-015.S2> (2 KB TXT)

**Table S3.** Summary of New England cottontail *Sylvilagus transitionalis* and eastern cottontail *Sylvilagus floridanus* fecal pellets and corresponding mitochondrial DNA haplotypes used for species identification for composite diet samples. We collected pellets between February 2011 and March 2013 during the winter (November to March) at 14 sites across southern New England and southeastern New York. We compared unknown mitochondrial DNA sequences with reference sequences of known haplotypes.

Available: <https://doi.org/10.3996/JFWM-22-015.S3> (23 KB XLSX)

**Table S4.** Type III ANOVA results for models explaining the composition and diversity of New England cottontail *Sylvilagus transitionalis* and eastern cottontail *Sylvilagus floridanus* winter diets, as quantified by microhistologic analysis of fecal pellets. We collected pellets between February 2011 and March 2013 during the winter

(November to March) at 14 sites across southern New England and southeastern New York. PC1, PC2, etc., refer to models in which the response variable was a principal component characterizing broad patterns of diet composition (see Table 1). Predictor variables included in each model were species (New England or eastern cottontail), region (NW, SW, and SE; see Figure 1), and scans, the number of microscope views with which each sample was examined.

Available: <https://doi.org/10.3996/JFWM-22-015.S4> (19 KB DOCX)

**Table S5.** Type III ANOVA results for models explaining the preferences of New England cottontail *Sylvilagus transitionalis* and eastern cottontail *Sylvilagus floridanus* for dietary plants, as quantified by a Johnson rank index comparing the ranked availability of plant genera with the ranked proportions of those genera in fecal pellets. We collected pellets between February 2011 and March 2013 during the winter (November to March) at 14 sites across southern New England and southeastern New York. PC1, PC2, etc. refer to models in which the response variable was a principal component characterizing broad patterns of diet composition (see Table 1). Predictor variables included in each model were species (New England or eastern cottontail), region (NW, SW, and SE; see Figure 1), scans (the number of microscope views with which each sample was examined), and the availability rank of the relevant plant genus. There was no variation in availability across samples for *Salix*, *Sorbus*, *Spiraea*, or unknown shrubs (\*), and so we did not include availability as a predictor variable in those models.

Available: <https://doi.org/10.3996/JFWM-22-015.S3> (26 KB DOCX)

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