



Introduced competitor reduces abundance of an imperiled cottontail

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Abstract Introduced species competing with native species can decrease the density and abundance of native species, causing concern for the persistence of native species populations. The presence of the introduced eastern cottontail (*Sylvilagus floridanus*—EC) in habitat patches with the imperiled New England cottontail (*Sylvilagus transitionalis*—NEC) can lead to interspecific competition. However, the degree to which this interspecific competition leads to changes in NEC relative abundance is unknown. We used open 2 species N-mixture models with directional interactions to determine how EC relative abundance at a site influences NEC relative abundance and how covariates affected both species' relative abundance. We found that EC relative abundance had a strong negative influence on NEC relative abundance, with an estimated effect of -0.163 , providing further evidence of interspecific competition between the 2 species. We found evidence of resource partitioning between the 2 species, where NEC relative abundance was positively influenced and EC relative abundance

was negatively influenced by vegetation heights of 0.5 to < 2.5 m. Overall, our results demonstrate the consequences of EC presence in native lagomorph ranges and the utility of N-mixture models for assessing the magnitude of interspecific competition between introduced and imperiled species.

Keywords Eastern cottontail · Interspecific competition · N-mixture models · New England cottontail

Introduction

Resource competition between introduced and native species has become increasingly common due to the prevalence of biological invasions globally (Wilcove et al. 1998; Galil 2007; Simberloff et al. 2013). Competition from introduced species can cause harm to native species populations, including reduction in fitness (Gurnell et al. 2004), introduction of novel pathogens (Vitule et al. 2009; Flory and Clay 2013; Tizzani et al. 2020), changes in morphology (Stuart et al. 2014) and decreases in abundance and density of native species (Duyck et al. 2004; Mazzamuto et al. 2017a). Examples of interspecific competition reducing native or rare species abundances and densities have been observed in fish (Robertson 1996), invertebrates (Duyck et al. 2004), and small mammals (Mazzamuto et al. 2017a). If native species are unable to shift their resource use to achieve coexistence,

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native species could experience population declines (Bøhn et al. 2008) or competitive exclusion could occur (MacArthur and Levins 1964). Understanding to what degree interspecific competition with introduced species affects native species abundance or density can be crucial for effectively managing native species populations.

The eastern cottontail (*Sylvilagus floridanus*; hereafter EC) is an example of an introduced species lowering the abundance of resident species populations. EC is the most widely distributed cottontail, commonly introduced for hunting purposes (Chapman and Litvaitis 2003; Bertolino et al. 2011; Hidalgo-Mihart et al. 2017; Delibes-Mateos et al. 2018). Anthropogenic influence, either through direct introductions or facilitating range expansion through habitat alteration, helps EC populations to expand easily into new areas (Chapman and Litvaitis 2003; Hidalgo-Mihart et al. 2017) and become overabundant (British Columbia Ministry of Forests 2022). Introductions of EC also influences native lagomorph populations around the world. For example, hunters introduced EC across Europe, but populations only became established and expanded in Italy (Silvano et al. 2000), where the native European hare (*Lepus europaeus*) resides. European hare and EC have differences in habitat preferences (Bertolino et al. 2013) and EC abundance does not directly affect European hare abundance (Cerri et al. 2017). However, the relationship between the European hare and its main predator, the red fox (*Vulpes vulpes*), became more negative where EC was more prevalent, reducing European hare abundance (Cerri et al. 2017).

EC has also been introduced into the northeastern United States for hunting purposes (Johnston 1972), where EC now co-occurs with the imperiled New England cottontail (*Sylvilagus transitionalis*; hereafter NEC). Stocking EC was common in New England in the early 1900s, where state agencies and private hunting clubs stocked EC from other parts of the United States until the 1950s (Johnston 1972). Prior to 1928, NEC was the only cottontail in New England (Johnston 1972). Today, EC is found throughout New England (Buffum et al. 2015). The reason EC has been successful at establishing outside of its native range is the ability to thrive in a wide variety of habitats, even highly urbanized, making it a habitat generalist (Chapman and Litvaitis 2003; Hunt et al. 2014). However, studies of EC habitat selection in

their introduced range and at different spatial scales have found evidence of habitat preference (Bond et al. 2002; Bertolino et al. 2011). In their native range, EC exhibited characteristics of a habitat generalist at the microhabitat scale but became more selective at larger spatial scales (Bond et al. 2002). In Italy, EC selected for habitat with less wetland surface area and patches with higher edge amounts (Bertolino et al. 2011). The ability of EC to occupy both urban areas and edge environments gives EC an advantage in the predominately exurban landscape of New England, where occupancy rates of the native NEC continue to decline (Rittenhouse and Kovach 2020).

Contributing factors to NEC population decline are habitat loss and the presence of an introduced competitor (Litvaitis et al. 2008; Kovach et al. 2022), but these threats are not mutually exclusive. NEC relies on early successional habitat with high stem density to survive because of the high amount of cover this habitat provides (Barbour and Litvaitis 1993; Litvaitis 1993, 2001; Cheeseman et al. 2018, 2019, 2021). Additionally, NEC requires large patches, close together to achieve gene flow and dispersal, and maximize survival (Barbour and Litvaitis 1993; Litvaitis and Villafuerte 1996; Fenderson 2010; Cheeseman 2017; Bischoff et al. 2023). However, early successional habitat is overall rare in the landscape (Litvaitis 1993; Rittenhouse et al. 2022) and remaining patches are typically small and fragmented (Bischoff et al. 2023) impeding the success of NEC habitat management efforts. Additionally, the presence of EC in the NEC range has complicated NEC management efforts (Cheeseman et al. 2021) and has led to interspecific competition (Probert and Litvaitis 1996; Cheeseman et al. 2018). Behavioral observations have found evidence of interference competition with no clear winner (Probert and Litvaitis 1996), and resource selection studies have found exploitative competition where EC displaces NEC into marginal or later successional shrublands when they co-occupy patches (Cheeseman et al. 2018). Despite evidence of interspecific competition occurring between the 2 species and the patch-level implications of this competition for habitat management, we still do not understand how this competition affects NEC populations and habitat management across large spatial scales.

Traditionally, interspecific competition between an introduced and native species is supported through observation studies (Probert and Litvaitis 1996),

radio-collaring individuals (Wauters et al. 2002; Mazzamuto et al. 2017b; Cheeseman et al. 2018), trap and removal (Mazzamuto et al. 2017a), or mark-recapture (Gurnell et al. 2004) in patches with and without the native species. However, observational, capture-recapture, and radio-tracking methods can be costly and constrain our inferences due to small sample sizes and limited spatial scales. With recent developments in N-mixture models, we can now use count data to create multi-species models with species interactions to assess the effect of ecological interactions, such as interspecific competition, across large spatial scales (Roth et al. 2016; Brodie et al. 2018; Kéry and Royle 2021).

Our goal is to determine whether and to what degree EC relative abundance influences the relative abundance of NEC. We used open N-mixture models with directional interactions (Kéry and Royle 2021) to test a negative association between the 2 species' relative abundances, where EC is the dominant species. We also identified habitat characteristics that uniquely influenced the relative abundance of each species at sites throughout Connecticut, United States. We predicted NEC relative abundance would be lower at sample areas with increased EC relative abundance. We hypothesized that the 2 species would diverge in their response to vegetation height, predicting that NEC would have higher relative abundance at sample areas with higher vegetation height and EC would have higher relative abundance at sample areas with lower vegetation height. Finally- because we observed that pellet detections were noticeably different in number between eastern and western Connecticut, we used derived parameters within the model to investigate differences in relative abundances between eastern and western Connecticut.

Methods

Study area

We focused the extent of the study area to Connecticut, United States, the portion of the NEC range with the highest number of occupied sites and most hectares of habitat compared to other states in the NEC range (Rittenhouse and Kovach 2020; Rittenhouse et al. 2022). Both cottontail species are found within Connecticut, but NEC is absent from the

central portion of the state (Fig. 1) where the Connecticut River and high development exist. Connecticut is a highly forested state, with roughly 60% of the land area covered by forests, and also highly developed, with roughly 19% of the land area covered by development (Arnold et al. 2020). Early successional habitats are rare within Connecticut, comprising approximately 3% of Connecticut's total land area (Rittenhouse et al. 2022). Precipitation in Connecticut occurs year-round, with an average annual precipitation totals of 1186.2 mm and the climate is temperate, with annual high monthly temperatures in the summer months (21.3–24.9 C; June–August) and annual low monthly temperatures in winter months (0.7–2.8 C; December–February; National Weather Service 2023).

Count and covariate data

We used data collected by the New England Cottontail Regional Monitoring Program from 2016–2021. The Regional Monitoring Program is a multi-state collaboration and range-wide survey where state biologists from Maine, Massachusetts, New Hampshire, Rhode Island, New York, and Connecticut collect cottontail fecal pellets at designated sites. The collective effort of the Regional Monitoring Program created an extensive multi-year dataset of pellet detection locations of both species. Observers visit sites each winter (from November to April) during conditions previously deemed favorable for pellet detection and quality: snow-covered ground, low temperatures, and 2–4 days after a snowfall or high wind event (Kovach et al. 2003; Brubaker et al. 2014; Whipps et al. 2020). Observers walked 5 to 6 parallel transects that were spaced more than 30 m apart within each site (Rittenhouse 2020, unpublished report). Observers chose the direction of the transects, so transect direction could differ between sites but was consistent within sites (Rittenhouse 2020, unpublished report). Observers searched up to 15 m on either side of the transect for a pile of cottontail pellets (Rittenhouse and Kovach 2020). Observers collected at least 1 pellet from the pile (hereafter referred to as sample) and placed the sample into a vial (Rittenhouse and Kovach 2020). Observers recorded GPS coordinates of the sample. Observers would only collect a sample if they had walked farther than 30 m since the previous sample was collected to ensure that samples were collected

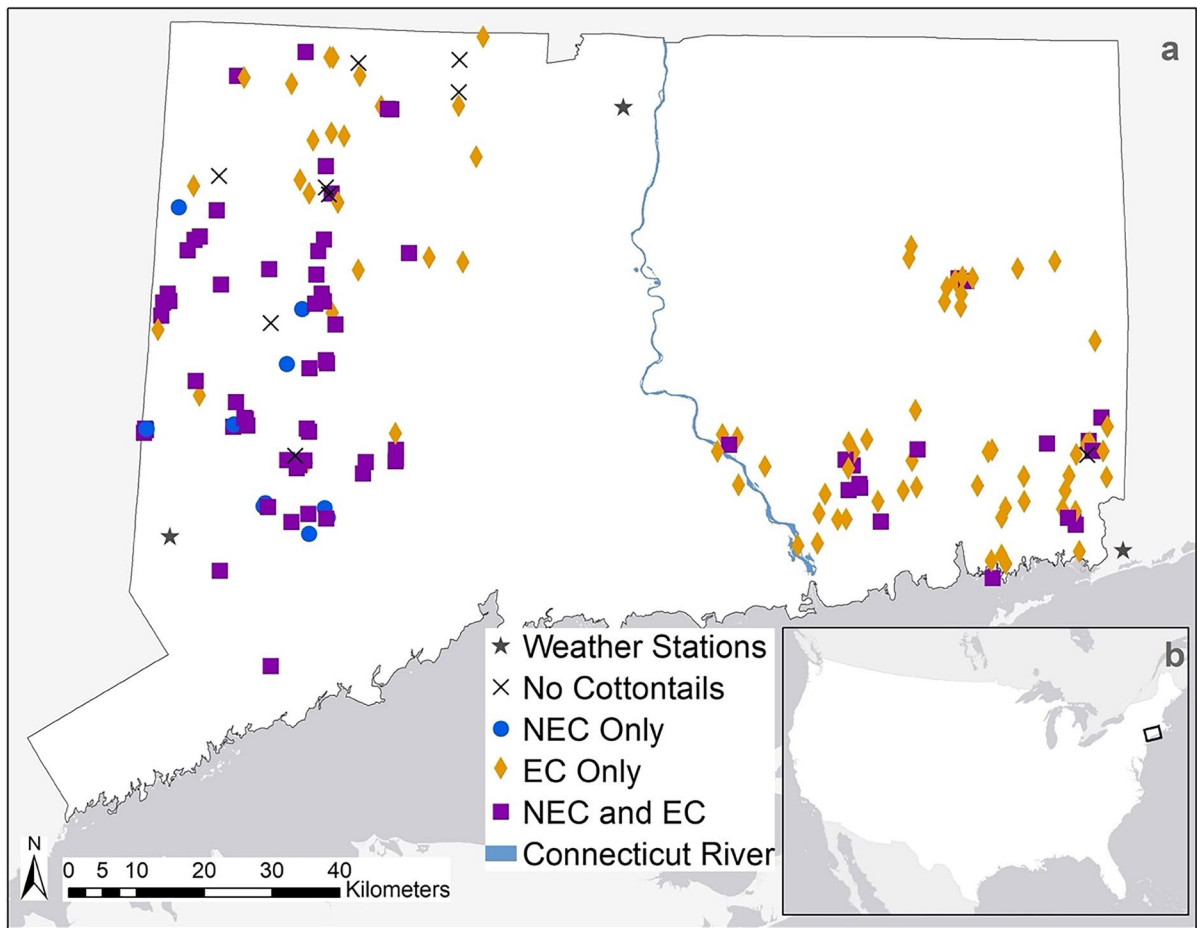


Fig. 1 Map of sites with no cottontails (black X's), only NEC (blue circles), only EC (orange diamonds), and both NEC and EC (purple boxes) locations over the 2016–2021 sample period in Connecticut, United States (Map a). Sites were selected for the New England Cottontail Regional Monitoring Program.

The Connecticut River (blue polygon) bisected western Connecticut and eastern Connecticut. The grey stars indicate the weather stations used to collect environmental data. Map b shows Connecticut (highlighted in the black box) in relation to the United States

from throughout the site (Rittenhouse 2020, unpublished report). Because the spatial distance between samples is larger than the average radius of a cottontail core area (Cheeseman 2017), we assumed that 1 sample represents 1 individual rabbit. This field protocol resulted in an average of 0–10 samples collected at each site for each visit.

Samples were processed at 2 laboratories (University of Rhode Island and University of New Hampshire) to identify the species of each sample. A fecal mitochondrial DNA analysis was used to extract high quality DNA and then a polymerase chain reaction was used to identify species (Litvaitis and Litvaitis 1996; Kovach et al. 2003; Whipps

et al. 2020). DNA was successfully extracted from over 99% of the samples, but when DNA was not extracted from the sample, we excluded the sample from the analysis. We cross referenced the species identification of each sample with the GPS location of the sample to create count data of the total number of pellets collected for each visit at each site for both species.

We defined the sample area by applying a minimum bounding polygon to all cottontail samples (i.e., both species and from all 5 winters) collected within a site. We identified 10 instances where the sample area could not be delineated using minimum bounding polygons due to observers collecting 2

or fewer samples at the site over the 5-year period. In these instances, we placed a 4.08 ha circle with a 114 m radius around the central coordinate of the site. The area of the circle was the maximum area searched during sampling (Rittenhouse 2020, unpublished report). Observers did not record the location of transects and thus we cannot define sample areas based on the extent of the area sampled. Over the 2016–2021 duration of this study, we defined 171 unique sample areas. Number of sample areas sampled in a given year and the number of visits to each sample area varied based on budget. There were 70 sample areas and 4 visits in 2016–2017, 106 sample areas and 4 visits in 2017–2018, 105 sample areas and 1 visit in 2018–2019, 75 sample areas and 2 visits in 2019–2020, and 53 sample areas and 2 visits in 2020–2021.

For each sample area, we calculated the area (ha), Euclidean distance to the nearest neighboring sample area (km), and Euclidean distance to the nearest forested-shrub wetland (km; Table 1). We retrieved the wetland information from the National Wetlands Inventory (NWI; US Fish and Wildlife Service 2020), and we selected a subset of wetland types of freshwater forested-shrub wetlands following the forested-shrub wetland list in Rittenhouse et al. (2022; Table S1 in Supplementary Information). Defining sample area based on location of cottontail samples means that the sample areas and subsequent covariate measurements were dependent upon where observers sampled and found samples within sites.

We used the Young Forest and Shrubland Vegetation Map to measure vegetation height proportions (Rittenhouse et al. 2022). The Young Forest and Shrubland Vegetation Map classified early successional vegetation type based on several factors, including ecological processes (succession,

disturbance and regeneration, and hydrology), vegetation height, percent vegetation cover by height category, previous land cover type, and time since disturbance (Rittenhouse et al. 2022). To measure vegetation height of sample areas, we used the canopy height model within the Young Forest and Shrubland Vegetation Map and the proportion of each vegetation segment within 5 vegetation height classes ranging from 0.0 m to above 10.0 m. We used the middle 3 height ranges, 0.5 to < 2.5 m ($\text{Height}_{0.5 \text{ to } < 2.5 \text{ m}}$), 2.5 to < 5.0 m ($\text{Height}_{2.5 \text{ to } < 5.0 \text{ m}}$), 5.0 to 10.0 m ($\text{Height}_{5.0 \text{ to } < 10.0 \text{ m}}$), to describe both typical shrub height as well as capture overstory trees (O'Connor 2015; Cheeseman et al. 2018). We measured the vegetation height proportion for each sample area by averaging vegetation height class proportions for all young forest and shrubland vegetation segments that fell within the boundaries of the sample area. Not all segments covered the entire sample area, so the average height proportion of the segments that did cover the sample area was the height proportion of the whole sample area. If sample areas did not contain any young forest and shrubland vegetation segments or if there was no vegetation of the specified height range within the sample area, those sample areas received a zero for that vegetation height class.

We used environmental covariates outlined in the Regional Monitoring Program Protocol (Rittenhouse 2020, unpublished report) and Brubaker et al. (2014) to estimate detection probability. Pellet detection is impacted by air temperature, snow depth, days since last snowfall and high wind events above 40 km/hr (Brubaker et al. 2014). Snow cover and low air temperatures are important for maintaining the quality of pellets and slowing degradation, ensuring biologists can extract DNA and identify species (Kovach et al. 2003; Whipps et al. 2020). We did not incorporate

Table 1 Sample area attributes used in the N-mixture model. Attributes were measured for all 171 sample areas within the study area, including sample areas with no cottontails, New England cottontail only, eastern cottontail only, and both cottontails

Variable	Definition	Mean	SD	Range
Area	Area of sample area (ha)	3.042	2.217	0.016–14.453
Distance	Euclidean distance to nearest sample area (km)	1.887	2.135	0.056–15.673
Wetland distance	Euclidean distance to nearest wetland (forested-shrub wetland) (km)	0.532	0.488	0.000–2.132
$\text{Height}_{0.5 \text{ to } < 2.5 \text{ m}}$	Proportion of sample area with 0.5 to < 2.5 m vegetation height	0.146	0.143	0.000–0.558
$\text{Height}_{2.5 \text{ to } < 5.0 \text{ m}}$	Proportion of sample area with 2.5 to < 5.0 m vegetation height	0.100	0.115	0.000–0.568
$\text{Height}_{5.0 \text{ to } < 10.0 \text{ m}}$	Proportion of sample area with 5.0 to < 10.0 m vegetation height	0.126	0.146	0.000–0.652

vegetation cover covariates into the detection process, because stem density does not influence cottontail pellet detection (Brubaker et al. 2014) and sampling occurs in winter, when leaves are not on vegetation and cottontail tracks are visible on the snow. We retrieved air temperature and snow depth measurements from data collected with the Regional Monitoring Program. Snow depth data was missing in 3% of visits. To ensure the model runs with missing covariate data, Kéry and Royle (2016) suggested replacing missing values with mean covariate values. We replaced missing covariate values with values from a probability distribution instead (normal distribution with the mean and standard deviation of the standardized values) to incorporate stochasticity. To address missing air temperature data and measure days since the last high wind event (days wind) and days since the last precipitation event (days snow), we retrieved data from the nearest weather station (Brubaker et al. 2014) using Weather Underground (Weather Underground 2023). We identified 3 major weather stations within the study area, Danbury Municipal Airport in Danbury, Connecticut, Bradley International Airport in Windsor Locks, Connecticut, and Westerly State Airport in Westerly, Rhode Island (Fig. 1). We chose to use days since the last high wind event of ≥ 32 km/hr rather than ≥ 40 km/hr because winds exceeding 40 km/hr were rare in Connecticut during our study period.

N-Mixture model

We used a Bayesian open 2 species N-mixture model with directional interactions (Kéry and Royle 2021) and sample area covariates to determine if EC relative abundance influences NEC relative abundance and to assess how covariates influence both species' relative abundance. Open models investigate both spatial and temporal changes in population sizes (Kéry and Royle 2021), thus we used count data of both species replicated at i sample areas ($i = 1, 2, \dots, 171$), j visits ($j = 1, 2, 3, 4$), and t winters ($t = 1, 2, 3, 4, 5$) in the model. We built the open multi-species N-mixture model following Kéry and Royle (2016, 2021). This model is a variant of other multi-species abundance and occupancy models (Waddle et al. 2010; Clare et al. 2016; Roth et al. 2016; Brodie et al. 2018). We also incorporated a zero-inflated variant to account for the high amount of zeros (roughly 50%

of observations) in our count data and random sample area ($\varepsilon_{i,t}$) and visit effects ($\varepsilon_{i,j,t}$) to capture unexplained variation in relative abundance and detection and reduce overdispersion (Joseph et al. 2009; Kéry and Royle 2016, 2021; Knape et al. 2018). We estimated realized relative abundance at each sample area, $N_{i,t}$, as a Poisson distribution of the expected relative abundance, $\lambda_{i,t}$, and the probability that a sample area is suitable for occupancy ($\Psi_{i,t}$), to account for zero-inflation. We also accounted for imperfect detection, where the count of individuals, ($C_{i,j,t}$) was modeled as a binomial distribution dependent upon $N_{i,t}$ and the probability of detecting individuals ($p_{i,j,t}$) (Royle 2004; Kéry and Royle 2021). We modeled relative abundance covariate effects as a log function and detection covariate effects as logit-link function (Kéry and Royle 2016, 2021). Since the interaction of interest here is directional (i.e., EC is dominant over NEC), there is an additional interaction effect in the NEC portion of the model, which determines if there is a directional interaction of a dominant species (EC) on the subordinate species (NEC; Waddle et al. 2010; Clare et al. 2016; Roth et al. 2016; Brodie et al. 2018). Where $\lambda_{i,t}^{NEC}$ is the expected relative abundance of NEC at winter t , γ is the effect of 1 EC at sample area i on the expected relative abundance of NEC at the sample area that same winter and $N_{i,t}^{EC}$ is the realized relative abundance of EC in the same winter. The interaction coefficient (γ) is measured for each sample area but is modeled across all sample areas within the study area.

$$\lambda_{i,t}^{NEC} = \log\left(\beta_0^{NEC} + \dots + \gamma * N_{i,t}^{EC}\right) \quad (1)$$

With N-mixture models, a dilemma where models either have good fit or reasonable estimates but not both frequently occurs, due to the strict assumptions of the model and high number of zeros often observed in count data (Joseph et al. 2009; Kéry and Royle 2016; Knape et al. 2018; Kéry 2018; Link et al. 2018; Duarte et al. 2018). When we ran Poisson N-mixture models with our data, posterior predictive checks indicated poor model fit (\hat{c} greater than 1.0). We conducted a model selection study, similar to Kéry and Royle (2016) and Knape et al. (2018), where we ran our count data with several N-mixture variants (zero-inflated Poisson [ZIP], negative binomial, ZIP with different combinations of random sample area and survey effects, and Poisson with random effects) and

posterior predictive checks to compare performance and determine a model with a low \hat{c} value and reasonable relative abundance estimates. The ZIP variant with random sample area and visit effects generated acceptable estimates, achieved ideal \hat{c} values (near 1.0), Bayesian p-values near 0.50, as well as \hat{R} values below the 1.10 threshold (Gelman and Rubin 1992; Kéry and Royle 2016), indicating this was an ideal model choice.

StateProcess :

$$z_{i,t} \sim \text{Bernoulli}(\psi_{i,t})$$

$$N_{i,t} \sim \text{Poisson}(\lambda_{i,t} * z_{i,t})$$

$$\log(\lambda_{i,t}) = \beta_0 + \beta_{\text{covariate}} * \text{covariate}_i + \varepsilon_{i,t}$$

$$\varepsilon_{i,t} \sim \text{norm}(0, \tau)$$

ObservationProcess :

$$C_{i,j,t} \sim \text{Binomial}(N_{i,t}, p_{i,j,t})$$

$$\text{logit}(p_{i,j,t}) = \alpha_0 + \alpha_{\text{covariate}} * \text{covariate}_{i,j,t} + \varepsilon_{i,j,t}$$

$$\varepsilon_{i,j,t} \sim \text{norm}(0, \tau_i)$$

A key component of the Bayesian framework is the prior distribution, so we used an informal sensitivity analysis to determine the most appropriate prior distributions for both model types following Northrup and Gerber (2018) and Kéry and Royle (2016). Few cases warrant informative priors, or priors based on tangible data/studies, so we followed recommendations for weakly informative priors (Kéry and Royle 2016; Northrup and Gerber 2018). We ran the sensitivity analysis starting with smaller precision values and then progressively used larger values to assess the effects of priors on model outputs (Northrup and Gerber 2018). Outputs were similar from the sensitivity analysis, thus we chose covariate priors with a normal distribution (mean of 0 and precision of 0.1) and a gamma distribution prior for the suitability parameter. The Bayesian framework of the model also allowed us flexibility in what parameters we measured. To calculate mean annual relative abundance in eastern and western Connecticut, we used derived parameters so sample sizes were not reduced. We coded all models in R 4.1.3 (R Core Team 2022) with the “jagsUI” package (Kellner and Meredith 2021).

Results

For the 2016–2021 sampling period, 9 sample areas had no cottontails, 10 sample areas had only NEC, 79 sample areas had only EC, and 73 sample areas had both NEC and EC (Fig. 1). Naïve average annual abundance for NEC ranged from 0.996 per sample area in 2016–2017 to 4.548 per sample area in 2020–2021 and naïve average annual abundance for EC ranged from 3.240 per sample area in 2016–2017 to 6.838 per sample area in 2018–2019 (Table 2). We found EC relative abundance was negatively associated with NEC relative abundance with an estimated interaction coefficient of -0.163 (95% CRI: $-0.213, -0.118$; Table 3, Fig. 2).

The relative abundance of both species responded similarly to spatial attributes of the sample area but differently to structural attributes of the sample area. Both species’ relative abundances positively responded to sample area with estimated effects of 0.289 (95% CRI: 0.117, 0.480) for NEC relative abundance and 0.175 (95% CRI: 0.093, 0.259) for EC relative abundance. However, vegetation height influenced the 2 species’ relative abundances differently. NEC relative abundance positively responded to $\text{Height}_{0.5 \text{ to } < 2.5 \text{ m}}$, with an estimated effect of 0.226 (95% CRI: 0.075, 0.391) while EC relative abundance negatively responded to $\text{Height}_{0.5 \text{ to } < 2.5 \text{ m}}$ with an estimated effect of -0.116 (95% CRI $-0.202, -0.030$). Distance to the nearest sample area, distance to the nearest forested-shrub wetland, $\text{Height}_{2.5 \text{ to } < 5.0 \text{ m}}$ and $\text{Height}_{5.0 \text{ to } < 10.0 \text{ m}}$ all had minimal influence on both species’ relative abundances (Table 3 and Fig. 3).

Snow depth and temperature were the 2 most influential covariates for detection. Detection probabilities of both species had negative associations

Table 2 Mean naïve relative annual abundance estimates for New England cottontail (NEC) and eastern cottontail (EC) in Connecticut from 2016–2021

Winter	NEC naïve abundance	EC naïve abundance
2016– 2017	0.996	3.240
2017–2018	1.038	4.455
2018–2019	3.895	6.838
2019–2020	2.415	5.859
2020–2021	4.548	3.913

Table 3 N-mixture model output for both New England cottontail (NEC) and eastern cottontail (EC)

Species	Parameter	Mean	SD	2.50%	97.50%	f	\hat{R}	
NEC	<i>Relative abundance</i>							
	Interaction effect	-0.163	0.024	-0.213	-0.118	1.000	1.000	
	Intercept	2.593	0.185	2.241	2.973	1.000	1.004	
	Area	0.289	0.092	0.117	0.480	1.000	1.000	
	Wetland distance	0.078	0.074	-0.062	0.228	0.858	1.000	
	Distance	-0.028	0.079	-0.185	0.127	0.638	1.000	
	Height _{0.5 to < 2.5 m}	0.226	0.080	0.075	0.391	0.998	1.000	
	Height _{2.5 to < 5.0 m}	0.006	0.104	-0.194	0.214	0.518	1.000	
	Height _{5.0 to < 10.0 m}	-0.131	0.105	-0.337	0.079	0.895	1.000	
	<i>Detection</i>							
	Winter 1 intercept	-0.659	0.526	-1.692	0.370	0.894	1.001	
	Winter 2 intercept	-1.304	0.349	-1.980	-0.607	1.000	1.002	
	Winter 3 intercept	0.840	1.061	-0.582	3.541	0.821	1.004	
	Winter 4 intercept	-0.040	0.470	-0.918	0.931	0.548	1.001	
	Winter 5 intercept	0.822	0.433	0.009	1.711	0.976	1.001	
	Snow	-0.305	0.110	-0.530	-0.095	0.998	1.000	
	Temperature	-0.175	0.144	-0.460	0.104	0.890	1.000	
	Days snow	0.013	0.105	-0.183	0.231	0.535	1.000	
	Days wind	0.108	0.109	-0.098	0.333	0.841	1.000	
	EC	<i>Relative abundance</i>						
		Intercept	2.049	0.071	1.917	2.195	1.000	1.003
Area		0.175	0.042	0.093	0.259	1.000	1.000	
Wetland distance		-0.035	0.041	-0.116	0.046	0.799	1.000	
Distance		-0.045	0.049	-0.143	0.052	0.821	1.000	
Height _{0.5 to < 2.5 m}		-0.116	0.044	-0.202	-0.030	0.996	1.000	
Height _{2.5 to < 5.0 m}		0.047	0.044	-0.039	0.134	0.856	1.000	
Height _{5.0 to < 10.0 m}		0.039	0.046	-0.052	0.129	0.807	1.000	
<i>Detection</i>								
Winter 1 intercept		-0.115	0.227	-0.554	0.335	0.696	1.001	
Winter 2 intercept		0.585	0.346	0.046	1.414	0.985	1.004	
Winter 3 intercept		2.995	1.445	1.100	6.604	1.000	1.002	
Winter 4 intercept		1.072	0.348	0.426	1.792	1.000	1.001	
Winter 5 intercept		-0.014	0.351	-0.638	0.740	0.542	1.001	
Snow		-0.207	0.084	-0.376	-0.046	0.994	1.000	
Temperature	0.249	0.086	0.080	0.421	0.998	1.000		
Days snow	0.092	0.090	-0.081	0.273	0.850	1.000		
Days wind	0.140	0.089	-0.034	0.317	0.942	1.000		
<i>Deviance</i>	2788.689	148.361	2492.956	3073.789	1.000	1.007		

Bolded values indicate where the 95% credible interval (2.50, 97.50%) for the parameter estimates did not overlap zero. F values are the proportion of the posterior distribution with the same sign as the mean parameter estimate. The \hat{R} values measure chain convergence, \hat{R} values below 1.1 indicate low Monte Carlo error for the parameter estimate

with snow depth, with estimates of -0.305 (95% CRI: -0.530, -0.095) for NEC and -0.207 (95% CRI: -0.376, -0.046) for EC (Table 3, Fig. 3). Temperature positively influenced EC detection with an estimated effect of 0.249 (95% CRI: 0.080, 0.421) and had no relationship for NEC detection

with credible intervals overlapping zero (95% CRI: -0.460, 0.104) (Table 3, Fig. 3).

The species composition of sample areas differed between eastern and western Connecticut. Most sample areas in eastern Connecticut had more EC than NEC and less frequently had sample areas with equal numbers of NEC and EC or sample areas with more

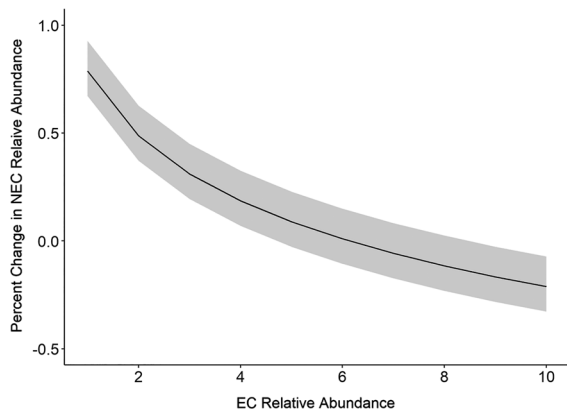


Fig. 2 Percent change in New England cottontail (NEC) relative abundance with the relative number of eastern cottontail (EC) at the same sample area within the same winter (black line). Grey polygon surrounding the estimate represents the 95% credible interval

NEC than EC. In contrast, western Connecticut had sample areas with mostly equal numbers (difference in relative abundance between the 2 species < 5) of both species or NEC relative abundance was higher than EC relative abundance (Table S2, Fig. 4).

Discussion

Our results provide a comprehensive measure demonstrating co-occupied sample areas have lower NEC relative abundance and provides further evidence that EC is a dominant competitor over NEC (Probert and Litvaitis 1996; Litvaitis et al. 2008). While we cannot confirm causation from these modeled results, interspecific competition between NEC and EC has been observed in both behavioral studies (Probert and Litvaitis 1996) and resource use studies (Cheeseman et al. 2018). Studies with other species have also found interspecific competition between introduced and native species lowered native species abundance and density (Duyck et al. 2004; Mazzamuto et al. 2017a). Additionally, the differences in responses of NEC and EC relative abundance patterns to vegetation height provides information for understanding how we can promote NEC populations in landscapes prevalent with EC. Overall, our results highlight the threat EC poses to native lagomorph populations.

Across the globe, native lagomorph species are declining (Schmidt et al. 2011; IUCN 2022) while

habitat generalist lagomorphs such as EC continue to expand (Chapman and Litvaitis 2003; Hidalgo-Mihart et al. 2017). This raises concern that the competition between native and introduced lagomorphs we observed in the northeastern United States could occur in other areas where native lagomorphs co-occur with EC. One possible explanation for why EC can outcompete native lagomorphs and live in such a wide variety of habitats is their large eye area and ability to detect predators at a larger distance compared to native lagomorphs (Smith and Litvaitis 1999). As urbanization is projected to increase (Jiang and O'Neill 2017), EC may be better suited for future landscape conditions than native lagomorphs that are restricted by habitat characteristics and sensitive to fragmentation.

Vegetation height may be one factor that can alleviate competitive interactions between NEC and EC. Our vegetation height results contribute to the body of evidence that resource partitioning occurs between both species (Buffum et al. 2015; O'Connor 2015; Cheeseman et al. 2018, 2021; Kilpatrick and Goodie 2020; Bischoff et al. 2023). Research focused on microhabitat, or the places cottontails sit within a patch, found that NEC sat at locations with vertical cover (i.e., vegetation height about 0.5 m) while EC sat at locations with more horizontal cover (i.e., vegetation below 0.5 m; O'Connor 2015). Cottontail resource selection studies at co-occupied patches found that NEC selected for areas with higher shrub height (> 0.5 m) to a stronger degree than EC selected for higher shrub height where EC was more prevalent (Cheeseman et al. 2018). In addition to differences in resource use, home range studies have found NEC and EC 95% and 50% home ranges overlap minimally, despite both species co-occupying sites (Kilpatrick and Goodie 2020). Resource or niche partitioning is a common response to new pressures from interspecific competition (MacArthur and Levins 1964; Wauters et al. 2002), thus NEC could be shifting resource use to reduce competitive pressures with EC. Our results and other studies demonstrating differences in resource use (O'Connor 2015; Cheeseman et al. 2018, 2021; Kilpatrick and Goodie 2020) further supports the relative abundance patterns we observed was due to interspecific competition.

The widespread introductions of EC through game clubs and state wildlife agencies across southern New England (Johnston 1972) is one explanation for the

Fig. 3 Plots of the effects of area and vegetation height 0.5 to < 2.5 m on New England cottontail (blue solid line) and eastern cottontail relative abundance (orange dashed line) and the effects of snow depth and temperature on New England cottontail (blue solid line) and eastern cottontail (orange dashed line) detection probability. The blue polygons indicate the variability surrounding New England cottontail estimates and the orange polygons indicate the variability surrounding eastern cottontail estimates

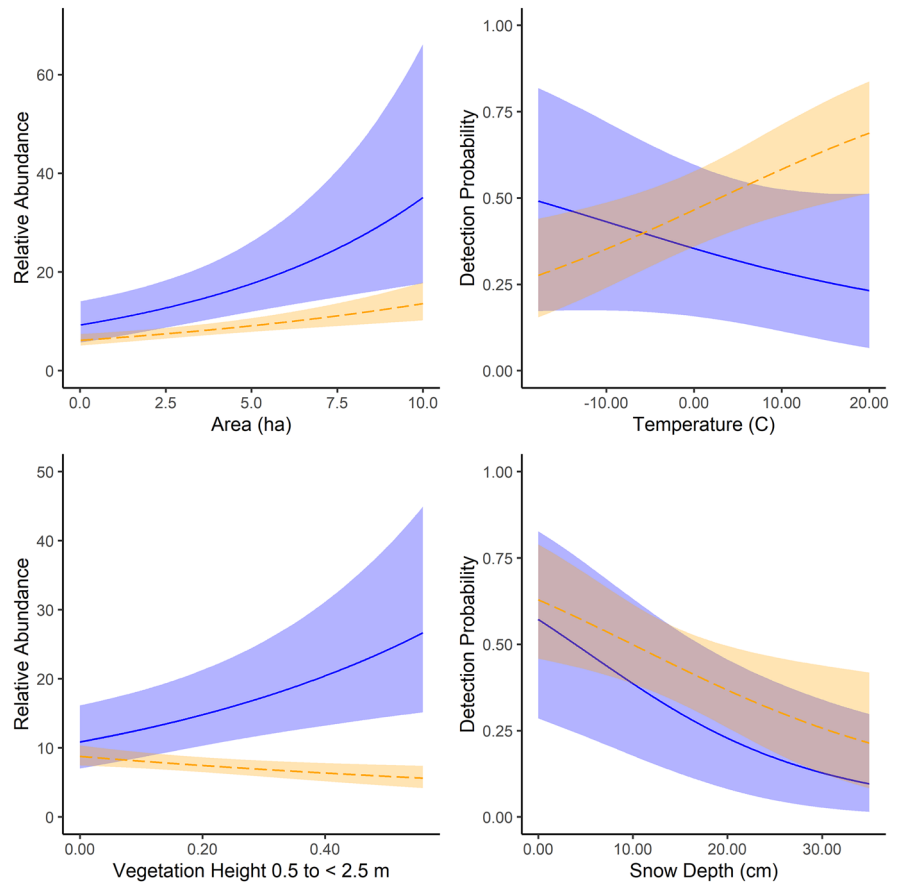
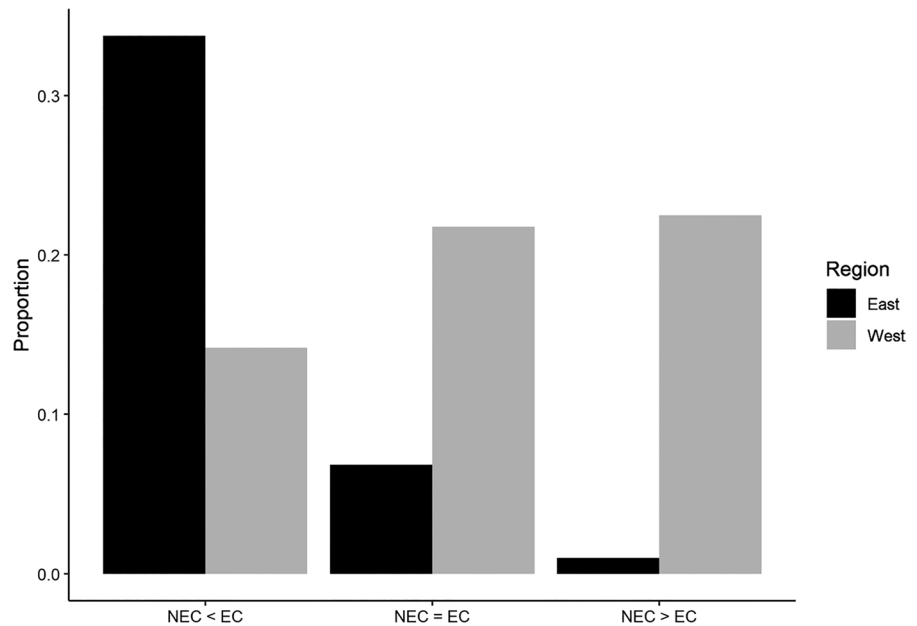


Fig. 4 Bar plot of the proportion of sample areas where New England cottontail (NEC) relative abundance was less than eastern cottontail (EC) relative abundance, NEC relative abundance and EC relative abundance were roughly equal (difference in relative abundance between the 2 species < 5), and NEC relative abundance was higher than EC relative abundance for all winters in the east and west regions of Connecticut



patterns of EC prevalence observed in Connecticut today, rather than natural range expansion of EC. We estimated that NEC annual relative abundance was higher in western Connecticut than eastern Connecticut. In comparison, we estimated that EC annual relative abundance was slightly higher in eastern Connecticut than western Connecticut, and thus this pattern does not align with the EC range expanding from New York eastward and northward into the NEC range. Historic records document that introductions were common and not spatially uniform across southern New England (Johnston 1972). In neighboring Rhode Island, EC were introduced at much higher numbers from the 1930 to 1950s while Connecticut allowed introduction of EC across the state until 1933 (Johnston 1972). Propagule pressure (i.e., number of introductions and/or the number of individuals introduced; Lockwood et al. 2005; Blackburn et al. 2011) could have caused EC populations in eastern Connecticut to be more successful compared to western Connecticut. Propagule pressure was also proposed as a reason why EC populations did not establish in Spain, since a survey of hunters revealed EC were introduced in only 6% of the localities (Delibes-Mateos et al. 2018). The higher EC propagule pressure in eastern Connecticut could also explain why our study and another density study found NEC densities are lower in eastern Connecticut patches compared to the patches sampled in other portions of the NEC range (Kristensen and Kovach 2018).

We demonstrate the utility of using N-mixture models for modelling ecological interactions between 2 species, specifically competition between a native and introduced species. Studies examining competition caused by introduced species present in a native species' range can have more intensive sampling techniques, such as removal experiments (Mazzamuto et al. 2017a) and mark-recapture (Gurnell et al. 2004). But these methods can be costly especially for rare species (Kilpatrick et al. 2013), are usually smaller sample sizes, and cannot always capture interactions between species. N-mixture models are a useful tool for modelling these ecological interactions when count data is the only data available. However, they must be used with care because they have notable limitations when model assumptions are violated (Kéry and Royle 2016; Knappe et al. 2018; Kéry 2018; Link et al. 2018;

Duarte et al. 2018). Specifically, N-mixture models are sensitive to overdispersion and zero-inflation (data with a high number of zeros), thus researchers must know how to identify and combat these sensitivities to achieve ideal model fit. Other drawbacks with using N-mixture models include the higher complexity of the modeling approach compared to other abundance estimation approaches and to collect extensive count data, several years of data collection and collaboration between multiple agencies is required. N-mixture models have allowed us to use preexisting datasets of counts and gain a more robust understanding of the relationship between the relative abundance of an introduced and native species within Connecticut. Thus, N-mixture models can be a practical tool for examining competition between an introduced and native species and making management decisions where introduced species are adversely influencing native species.

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Author Contributions All authors contributed to the design of the study. Model preparation and analysis was conducted by KEB. The first draft of the manuscript was written by KEB and all authors approve of the final manuscript.

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Data Availability The datasets analyzed during this study are available in the GitHub repository, https://github.com/kathryn-bischoff/NEC_EC_data_bio_inv_2023.git.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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