



RESEARCH ARTICLE

Exotic- and native-dominated shrubland habitat use by fall migrating Swainson's Thrushes and Gray Catbirds in Michigan, USA

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Submitted February 10, 2017; Accepted September 28, 2017; Published December 13, 2017

ABSTRACT

The ability to locate high-quality stopover habitat has fitness implications for migrating landbirds, and alteration of stopover habitats due to human land-use change, including the introduction of nonnative plants, has been identified as a conservation concern. We tested whether the use and selection of shrublands dominated by exotic plants differed from that of native-dominated shrublands. Specifically, we compared capture rates, transfer rates between habitats, within-foraging-range habitat selection, and food items of Swainson's Thrushes (*Catharus ustulatus*) and Gray Catbirds (*Dumetella carolinensis*) between exotic- and native-dominated shrublands in Michigan, USA, during fall migration of 2012 and 2013. Capture rates were >20% higher for thrushes and >250% higher for catbirds in native shrubland. Capture–recapture data showed that birds moved from exotic to native shrubland at higher rates than vice versa. For radio-tagged thrushes and catbirds, native shrubland was ~30% more likely to be used than expected by land cover at the within-foraging-range scale. Thrushes, but not catbirds, avoided exotic shrubs within their foraging ranges. Native *Lindera benzoin* fruit was >50% more likely to be found in fecal samples from both bird species in native-dominated shrubland than in exotic-dominated shrubland, and was the predominant food item in the former habitat type. Collectively, our results suggest that fall migrating Swainson's Thrushes and Gray Catbirds select, and hence occur at higher densities in, predominantly native shrublands rather than exotic-dominated shrublands. One mechanism for this pattern may be their preference for certain native fruits, such as *L. benzoin*. Our results suggest that native shrubland may be an especially important stopover habitat for frugivorous birds during fall migration.

Keywords: bird migration, stopover, habitat selection, habitat quality, invasive shrub, resource use, fruit, radio-telemetry

Uso de hábitat de matorral dominado por exóticas y nativas por migrantes de otoño de *Catharus ustulatus* y *Dumetella carolinensis* en Michigan, EEUU

RESUMEN

La habilidad de localizar hábitat de parada de alta calidad tiene implicancias para la adecuación biológica de las aves terrestres migratorias, y la alteración de los hábitats de parada debido al cambio antrópico de uso del suelo, incluyendo la introducción de plantas no nativas, ha sido identificada como una preocupación de conservación. Evaluamos si el uso y la selección de matorrales dominados por plantas exóticas y por plantas nativas difirieron entre sí. Específicamente, comparamos tasa de captura, tasa de transferencia entre hábitats, selección de hábitat dentro del rango de forrajeo e ítems de forrajeo de *Catharus ustulatus* y *Dumetella carolinensis* entre matorrales dominados por exóticas y nativas en Michigan, EEUU, durante la migración de otoño de 2012 y 2013. Las tasas de captura fueron >20% más altas para *C. ustulatus* y >250% más altas para *D. carolinensis* en el matorral nativo. Los datos de captura–recaptura mostraron que las aves se movieron desde el matorral exótico al nativo a tasas más altas que a la inversa. Para los individuos de *C. ustulatus* y *D. carolinensis* marcados con radios, el matorral nativo tuvo ~30% más probabilidad de ser usado que lo esperado en base a la cobertura del suelo a la escala dentro del rango de forrajeo. *C. ustulatus*, pero no *D. carolinensis*, evitó los arbustos exóticos adentro de su rango de forrajeo. El fruto nativo de *Lindera benzoin* presentó >50% más probabilidad de ser hallado en muestras de ambas especies de aves en el matorral dominado por nativas y fue el ítem alimenticio predominante en este tipo de hábitat. En conjunto, nuestros resultados sugieren que los migrantes de otoño de *C. ustulatus* y *D. carolinensis* seleccionan y por ende aparecen a mayores densidades en los matorrales predominantemente nativos que en los matorrales dominados por exóticas. Un mecanismo para explicar este patrón pueden ser sus preferencias por ciertos frutos nativos, como los de *L. benzoin*. Nuestros resultados sugieren que el matorral nativo puede ser un hábitat de parada especialmente importante para las aves frugívoras durante la migración de otoño.

Palabras clave: arbusto invasivo, calidad de hábitat, fruto, migración de aves, parada, radio telemetría, selección de hábitat, uso de recursos

INTRODUCTION

Conservation of migratory landbirds requires habitat management throughout the entire annual cycle (Moore et al. 2005), and high mortality has been reported during the migratory phase (Silllett and Holmes 2002). Because migration is physiologically demanding and landbirds generally carry insufficient fat stores to complete migration in a single flight bout, they must stop en route to rest and refuel (Moore et al. 2005, Klaassen et al. 2012). Hence, their ability to locate high-quality stopover sites undoubtedly has fitness consequences (Dierschke 2003, Smith and Moore 2003, Newton 2006). During fall migration, fruit is a major food resource for many landbird species (Parrish 1997, Smith et al. 2007, 2013), and its quality and quantity are likely key factors determining stopover habitat quality. Unfortunately, stopover habitat is being altered by human land-use changes (Wilcove and Wikelski 2008), including the introduction of exotic shrub species (Suthers et al. 2000, Catling 2005, Smith et al. 2013). In the Midwestern United States, exotics such as autumn olive (*Elaeagnus umbellata*), honeysuckles (*Lonicera* spp.), multiflora rose (*Rosa multiflora*), and common buckthorn (*Rhamnus cathartica*) have become common and widespread and are considered ecologically invasive (Borland et al. 2009, USDA NRCS 2015). It is known that landbird migrants consume the fruits of these and other exotic shrubs in fall (White and Stiles 1992, Suthers et al. 2000), but more research is needed on the value of exotic shrubs relative to their native counterparts during migration (Smith et al. 2013, Ewert et al. 2015).

Studies on exotic and native fruits have indicated that native fruits tend to have greater fat and energy density, whereas exotic fruits tend to contain more sugar and water (Smith et al. 2007, 2013). For example, it has been estimated that birds need to consume up to three times the wet mass of exotic *E. umbellata* fruits compared with those of the native common winterberry (*Ilex verticillata*) to obtain the same amount of energy (Smith et al. 2007). While energy content alone may not dictate a bird's fruit preferences (see experimental results in Drummond 2005), in general, energetically rich native fruits appear to be consumed first by migrants (White and Stiles 1992, Stiles 1993, Smith et al. 2013).

However, the use and selection of exotic-dominated shrublands by fall migrating landbirds are less clear and likely depend on landscape context. For example, in a mosaic of forest, urban, and agricultural land in Pennsylvania, USA, the abundance of birds was positively correlated with the abundance of exotic *Lonicera* fruits

(Gleditsch and Carlo 2011). At a Michigan, USA, stopover site, long-term capture–recapture data revealed that frugivorous migrants that arrived late in fall were still able to gain fat and mass after most native fruits were depleted (Craves 2009). These studies evaluated the use of exotic shrubs and fruits across a landscape in which native counterparts were rare (Gleditsch and Carlo 2011) or within shrublands composed of both exotic and native shrubs (Craves 2009). Few studies have compared migrant use between shrubland habitats that are predominantly exotic or predominantly native (Ewert et al. 2015).

We aimed to determine whether habitat use and selection by 2 migrating landbird species, Swainson's Thrushes (*Catharus ustulatus*) and Gray Catbirds (*Dumetella carolinensis*), differed between shrubland dominated by exotic plants (hereafter, exotic shrubland) and shrubland dominated by native plants (hereafter, native shrubland). We compared capture rates, transfer rates between habitat types, and within-foraging-range habitat selection ratios of thrushes and catbirds. We also compared food items of birds between these habitat types to investigate the relationship between diet and habitat use.

METHODS

Study Site and Species

We conducted our fieldwork in a state-managed wildlife area near East Lansing, Michigan, USA (Rose Lake Wildlife Research Area, 42.811972°N, 84.384917°W). The study site (370 ha) existed within an agricultural and suburban landscape, and exotic and native shrublands occurred at similar latitudes and in distinct patches (Figure 1). The most common shrubs in exotic shrubland, as determined by vegetation sampling (see below and Appendix Table 3), were *E. umbellata*, *Lonicera* spp. (*L. tatarica*, *L. morrowii*, and *L. × bella* [*morrowii* × *tatarica*]), and *R. multiflora*, whereas in native shrubland, gray dogwood (*Cornus racemosa*), *I. verticillata*, and northern spicebush (*Lindera benzoin*) predominated.

In our study area, Swainson's Thrushes and Gray Catbirds are both commonly captured and highly frugivorous in fall (Parrish 1997). Swainson's Thrushes are intercontinental migrants that breed north of the study site and use it only for stopover during fall migration (Mack and Yong 2000). Gray Catbirds are intracontinental migrants, with some individuals breeding locally and others stopping over on their migration south (Smith et al. 2011). We excluded catbirds undergoing extensive prebasic molt and/or retaining juvenal undertail coverts from all analyses to avoid including birds of local origin.

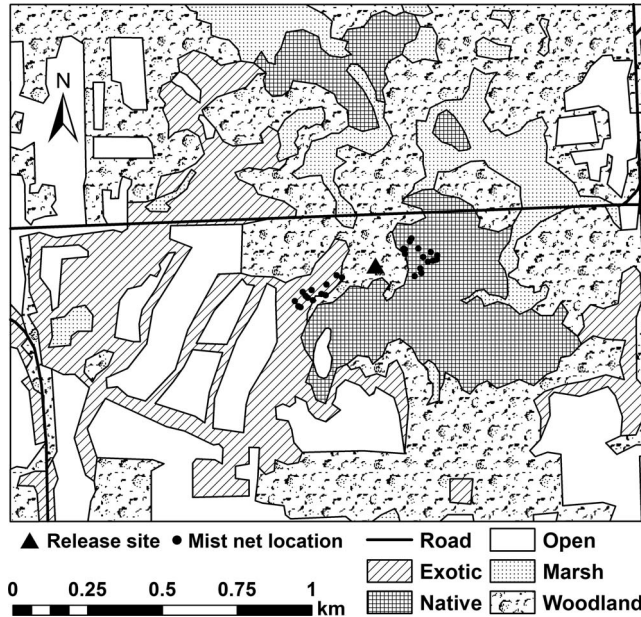


FIGURE 1. Map of the study area showing patches of exotic- and native-dominated shrublands and other habitat categories near East Lansing, Michigan, USA. Exotic and Native refer to exotic-dominated and native-dominated shrublands, respectively. The size of the study area was selected to match the spatial scale of these habitats. Dots indicate mist net locations and the triangle indicates the location of bird releases (banding site).

We passively captured birds using 15 mist nets (30-mm mesh, 12.0 m × 2.6 m) in each habitat type from August 14 to September 30, 2012, and from August 18 to September 30, 2013, as part of a long-term banding operation. Mist nets were opened daily (weather permitting) for 4–5 hr beginning 30 min before sunrise, with checks at 45 min intervals. Captured birds were held in individual cloth bags or bird boxes until processing, which included banding with uniquely numbered U.S. Geological Survey aluminum bands. In both years, >85% of Swainson's Thrushes and >90% of Gray Catbirds captured were hatch-year birds. Age ratio, wing chord length, and size-corrected mass were unrelated to habitat type for both species and years (Oguchi 2015).

Shrubland Habitat Sampling

Habitats (i.e. land cover categories) were delineated using an aerial photograph digitized into a vector layer (USDA-FSA-APFO 2010). We visited and assigned land cover (ground truthing) using a handheld Global Positioning System (GPS) unit wherever the habitat category or its boundary was unclear (Neatherlin and Marzluff 2004). Most shrubland areas required extensive ground truthing and were designated as exotic or native based on relative shrub stem density as estimated visually by a single observer from both the habitat edge and the interior. We

categorized land cover into the following 5 habitat classes (Figure 1): (1) Exotic: exotic-dominated shrubland with open canopy (i.e. tree) cover and closed shrub cover (>50% exotic by relative stem density and cover); (2) Native: native-dominated shrubland with open canopy cover and closed shrub cover (>50% native by relative stem density and cover); (3) Open: open water and anthropogenically created clearings of farmlands, fields (short grass <50 cm), clear-cuts, bare ground, and 9 individual homesteads with little to no shrub or canopy cover; (4) Marsh: wetland of primarily herbaceous vegetation (e.g., sedges [*Carex* spp.] and cattails [*Typha* spp.]) with sparse, open-cover low shrubs, if any (≤2 m height; e.g., willows [*Salix* spp.] and redosier dogwood [*Cornus sericea*]); and (5) Woodland: predominantly oak–maple (*Quercus*–*Acer*) upland deciduous woods with closed canopy cover and an open understory. Roads were mapped but ignored in analyses due to their width being smaller than the largest GPS error (~10 m) and because landbirds readily cross them during stopover (Seewagen et al. 2010).

In the summer of 2013, we used plot-based vegetation sampling (James and Shugart 1970) to determine shrub composition and habitat structure to validate our characterization as either native-dominated or exotic-dominated. Sampling circles (0.04 ha, radius = 11.3 m) were established around mist nets (midpoint at the net center) in both native ($n = 14$) and exotic ($n = 13$) shrublands. Where 2 nets were close enough that the circles overlapped, half-circles were sampled around the second net to avoid duplication. The half-circles were treated as one independent sampling unit in the analysis (counts multiplied by 2). In locations where 2 nets were connected ($n = 2$ in exotic and $n = 1$ in native habitat), we sampled habitat in one circle with the center at the point of the connected nets. Every tree of diameter at breast height (dbh, measured at 1.4 m) ≥8 cm within a plot was identified, counted, and assigned to a size class category. Next, the number of woody stems of <8 cm dbh intersecting a 2-arms-length (~1.6 m) transect across the circle in each cardinal direction was recorded by species. Along the same transect, presence or absence of ground cover, shrub cover, and canopy cover were recorded by sightings through an ocular tube at 20 locations (taken every 0.6 m). The heights of the 3 tallest trees and 3 tallest shrubs in each plot were estimated using an optical clinometer and triangulation, and the means were recorded as the canopy and shrub heights (m).

Radio-telemetry

We conducted radio-telemetry in 2013 on hatch-year Swainson's Thrushes and Gray Catbirds to verify the movement patterns inferred from capture–recapture data and to test for habitat selection. Very-high-frequency

(VHF: ~150 MHz) radio-transmitters (model BD-2, Holo-hill Systems, Carp, Ontario, Canada) for medium-sized passerines (~1.2 g; <5% of the body mass of birds) were attached to 13 Swainson's Thrushes (captured from September 10 to 27, with 7 initially captured in exotic habitat and 6 in native) and 14 Gray Catbirds (7 per habitat type, captured from September 8 to 24), all newly banded. Transmitters were attached dorsally using nontoxic, waterproof Duo A.I.I.063784 eyelash adhesive (American International Industries, Los Angeles, California, USA) and reinforced by applying cyanoacrylate glue SGH2J (Super Glue, Ontario, California, USA) where the transmitter contacted clipped feather tracts (Smolinsky et al. 2013). Radio-tagged individuals were released at the banding station located between native and exotic habitats to allow them access to both shrubland types (see Figure 1).

We tracked birds every morning using a hand-held, 2-point Yagi antenna connected to an AOR AR8200-Mk3 wide-range receiver (Authority On Radio Communications, Tokyo, Japan). Bird locations (1–4 per morning per individual) were triangulated or biangulated from fixed reference points set primarily outside shrublands to avoid disturbing birds by moving through dense shrub. Bird locations were resolved using the plugin Animove: Triangulation in QGIS 2.6.0 (QGIS Development Team 2014). Repeated tracking on the same day was performed at intervals of at least 45 min to ensure independence of relocation points (see Tietz and Johnson 2007, Seewagen et al. 2010). Maximum signal range was estimated to be ~500 m through woodlands and shrubs and ~1 km through open areas. Telemetry error (distance between estimated and true locations) was 24.90 ± 6.59 m ($n = 13$) based on trials performed with stationary transmitters. We excluded location estimates with error polygons larger than the smallest shrubland patch (0.98 ha). Birds were tracked until departure or prolonged inactivity that indicated the death of the bird or a dropped transmitter. We considered birds to have departed from the study area if they were not detected for 3 days from any fixed locations or by driving ~500 m from the site boundary. We also added locations of radio-tagged birds recaptured in mist nets (after confirming that the time of capture was separated by >45 min from their preceding and subsequent tracking records).

Fecal Sampling and Dietary Analysis

We assessed the diets of Swainson's Thrushes and Gray Catbirds using fecal samples collected from the first capture of each individual. Fecal samples were collected by placing white paper liners in the bird boxes in which captured birds waited to be processed. Samples were stored at -20°C until analysis. Fruits were identified by a combination of their seeds, color, and texture of the pulp and skin (Parrish 1997). We smeared fruits collected in the field on the same type of paper liner and stored them

under the same conditions to use as a guide for identification. Arthropod consumption was identified by the presence of exoskeleton remains. All fruits were identified by an observer blind to the habitat in which the bird was captured.

Statistical Analyses

All statistical computations were performed using R 3.1.2 (R Core Team 2014). All tests were 2-tailed with $\alpha = 0.05$. Values are presented as means \pm SE unless otherwise noted. Model assumptions were checked and verified using residual plots.

Validation of shrubland habitat categorization. We tested the expectation that exotic and native shrublands differed in shrub species composition (exotic-dominated vs. native-dominated), but not with respect to structural attributes. We compared shrub composition between habitats using function `manyglm` with the negative binomial error family in R package `mvabund` (Wang et al. 2012), which fits a separate generalized linear model (GLM) to each response variable within a multivariate framework (allowing for post hoc univariate tests adjusted for overall error rate) through resampling (set to 999 for bootstrapping). We ran `manyglm` on multivariate responses of (1) summarized total exotic shrub, total native shrub, and total sapling stem counts, and (2) stem counts of all shrub species (to detect species-level differences). For structural metrics, we performed permutational multivariate analysis of variance (PerMANOVA: function `adonis` in R package `vegan`; Oksanen et al. 2017), which uses distance matrices and obviates the necessity for distributional assumptions (Anderson 2001). Woody stem count, shrub height, canopy height, percent ground cover, percent shrub cover, percent canopy cover, total tree count, and total tree basal area were entered as one multivariate response (Cohen et al. 2012).

Indices of bird density and distribution. We compared capture rates (number of newly banded birds per net-hour) of Swainson's Thrushes and Gray Catbirds between habitats as an index of density (Smith and Hatch 2008, Akresh et al. 2009), which is generally positively correlated with habitat quality (reviewed by Johnson 2007). We used compound Poisson linear mixed models with a log link function fitted by Laplace approximation (function `cpglmm` in R package `cplm`; Zhang 2013), with habitat type specified as a fixed factor and ordinal date as a continuous random effect representing pseudoreplication within each individual net (sampling unit). The significance of the habitat effect was then determined via a single-term deletion chi-square-based test.

Movement and space use. Using birds with at least one recapture record, we compared the proportion of individual birds that transferred from one habitat type to the other (Akresh et al. 2009). We defined a bird as having

transferred habitats when the individual was recaptured in the other habitat relative to the one in which it was originally captured and was not recaptured again in the original habitat. Individuals that transferred back and forth were removed from the analysis. The proportion of birds that stayed in the same habitat vs. transferred to the other habitat was compared using Fisher's exact test for each species and year, and then for data pooled from the 2 yr after confirming that the proportions were similar between 2012 and 2013 within species (Fisher's exact test, $P > 0.05$).

We used the telemetry data to calculate the mean minimum stay length at our overall study site and the mean duration of continuous use of each habitat. Stay length was calculated as the difference between the date of initial capture and the last day of detection. Birds with truncated location records (suspected transmitter loss or death) were removed from this calculation. Similarly, duration of habitat use was calculated as the number of days (mornings) that a bird was continuously detected in that habitat before being found elsewhere or departing. As individuals typically used one habitat multiple times, we report the grand means of all use duration estimates. Additionally, we tested whether the mass of an individual at capture predicted stay length using simple linear regression.

To analyze the space use of radio-tagged birds, we calculated the 99% fixed kernel utilization distribution (UD) of each individual (Marzluff et al. 2004, Neatherlin and Marzluff 2004, Scarpignato and George 2013). Although we also report average areas within 50%, 90%, and 95% UD isopleths, we chose the 99% UD as the definition for foraging range because it is an objective estimate of the maximum extent of space use as inferred from relocation points (see Marzluff et al. 2004 for a detailed justification for using the 99% UD). We used the likelihood cross-validation method to select an individual-specific smoothing parameter (h ; in m) in program Animal Space Use 1.3 Beta (Horne and Garton 2006, 2009). Relocation data and the smoothing parameter were then entered into the Home Range Tool extension in ArcMap 10.4 (ESRI, Redlands, California, USA; Rodgers et al. 2015) to create the 99% foraging range and UD (10 m \times 10 m pixel size). The volume of the UD at the center of each pixel reflected the probability of the bird occurring in that location. We clipped UD's at the 99% isopleth. The minimum number of relocations per individual required for further UD analyses (8 for thrushes and 9 for catbirds) was determined by the lack of correlation between estimated range size and number of relocations (i.e. range size was not underestimated or inflated due to insufficient numbers of relocations). Individuals with truncated location records were included if they generated the required minimum number of

relocations. The average numbers of relocations generated by birds used for spatial analyses were 14.9 ± 1.7 (range: 8–23) for Swainson's Thrushes and 20.3 ± 4.2 (range: 9–42) for Gray Catbirds.

We examined habitat selection within each radio-tagged bird's foraging range (Neatherlin and Marzluff 2004, Long et al. 2008, Singleton et al. 2010), which corresponded to third-order selection by Johnson (1980). We calculated habitat-specific selection ratios (used/availability; Manly et al. 2002) of individuals within their 99% ranges so that a selection ratio >1 would suggest selection and a value <1 would suggest avoidance. The selection ratio was calculated from the bird's UD as Relative Concentration of Use (Neatherlin and Marzluff 2004, Long et al. 2008). Briefly, the proportion of a particular habitat within each individual's 99% foraging range was defined as that habitat's availability, and use was defined as the probability of the bird's occurrence in that habitat type within its foraging range (i.e. proportion of UD volume overlapping that habitat). This approach treated the individual as the sampling unit for both availability and use (design III in Manly et al. 2002), expressed use as a continuous random variable, incorporated the intensity of use, and was robust to telemetry error (Marzluff et al. 2004, Neatherlin and Marzluff 2004, Millsbaugh et al. 2006).

We compared within-foraging-range selection ratios of exotic, native, open, marsh, and woodland habitat types using one-way ANOVA (Neatherlin and Marzluff 2004) with post hoc pairwise t -tests (assuming unequal variance) with a Bonferroni correction with an overall $\alpha = 0.05$ (Manly et al. 2002). Simultaneous 95% Bonferroni CIs around mean selection ratios were calculated in order to determine whether each habitat was selected (selection ratio >1) or avoided (selection ratio <1) at the population level (Manly et al. 2002, Long et al. 2008, Singleton et al. 2010). For each species, we pooled individuals originally captured in exotic and native shrubs ($n = 9$ for both species).

Diet and fruit consumption. For each bird species, fecal samples from 2012 and 2013 were pooled by habitat type to increase sample size after confirming that the proportions of food items and their ranks were consistent between years within each habitat (Fisher's exact test, $P > 0.05$; Spearman's rank correlation test, $r_s > 0.65$, $P < 0.05$). We used Fisher's exact test to determine whether the proportions of fecal samples that contained fruits only, arthropods only, or both differed between habitat types. We then tested whether the proportion of fecal samples containing each food item differed between the 2 habitat types (Fisher's exact test; number of item present vs. number absent). Owing to the multiple comparisons performed, we used Bonferroni corrections in which critical $\alpha = 0.05$ was divided by the number of categories (i.e. food items; McDonald 2014).

TABLE 1. Movement of banded birds between exotic- and native-dominated shrublands near East Lansing, Michigan, USA, during fall migration in 2012 and 2013, based on individuals with at least one recapture record. An asterisk indicates significance ($P < 0.05$) based on Fisher's exact tests.

Species	Year	Habitat in which originally captured				P-value
		Exotic		Native		
		% Stayed ^b (n)	% Switched ^c (n)	% Stayed ^b (n)	% Switched ^c (n)	
Swainson's Thrush	2012	41.4 (12)	58.6 (17)	56.1 (37)	43.9 (29)	0.27
	2013	29.0 (9)	71.0 (22)	60.0 (18)	40.0 (12)	0.02*
	Pooled ^a	35.0 (21)	65.0 (39)	57.3 (55)	42.7 (41)	0.008*
Gray Catbird	2012	42.9 (3)	57.1 (4)	81.0 (34)	19.0 (8)	0.05
	2013	28.6 (2)	71.4 (5)	79.2 (19)	20.8 (5)	0.02*
	Pooled ^a	35.7 (5)	64.3 (9)	80.3 (53)	19.7 (13)	0.002*

^a Numbers were pooled from 2 yr after confirming lack of significant yearly difference in proportions of stayed vs. switched within each habitat type (Fisher's exact test: $P > 0.05$).

^b Represents individuals that were recaptured only in the same habitat type as the one in which they were originally captured in their entire recapture history.

^c Represents individuals recaptured in the other habitat relative to the habitat in which they were originally captured and never recorded again in their original habitat after the switch was recorded.

RESULTS

Characteristics of Shrubland Habitats

Exotic, native, and sapling stems differed between habitat types around nets (manyglm, deviance = 62.1, $P < 0.001$); exotic stems represented 73% (range: 63–93%) of all stems (<8 cm dbh) in exotic shrubland, and native stems represented 82% (range: 55–97%) of all stems in native shrubland. Univariate comparisons showed that the difference occurred in shrubs stems only (manyglm; total exotic: deviance = 34.8, $P < 0.001$; total native: deviance = 26.1, $P < 0.001$) and not in saplings (deviance = 1.3, $P = 0.31$), consistent with our habitat categorization as exotic-dominated or native-dominated. These results were replicated when the composition of individual shrub species was compared (manyglm, deviance = 334.1, $P < 0.001$; see Appendix Table 3 for univariate test results with stems ha^{-1} estimates). Habitat structure, on the other hand, was similar between habitat types around nets (PerMANOVA, pseudo- $F_{1,25} = 2.7$, $P = 0.08$). Estimated stem density was $7,381 \pm 805 \text{ ha}^{-1}$ and $7,559 \pm 554 \text{ ha}^{-1}$ in exotic and native shrubland, respectively.

Bird Density and Distribution

We captured 590 Swainson's Thrushes (exotic: $n = 247$; native: $n = 343$) and 389 Gray Catbirds (exotic: $n = 78$; native: $n = 311$) on 45 mornings in 2012, and 358 thrushes (exotic: $n = 163$; native: $n = 195$) and 237 catbirds (exotic: $n = 47$; native: $n = 190$) on 40 mornings in 2013. Median capture dates of thrushes were September 12 (2012) and September 14 (2013), and those of catbirds were September 5 (2012) and September 9 (2013). Swainson's Thrushes were 21% (cpplmm; 2012: $\chi^2_1 = 66.2$, $P < 0.001$) and 29% (2013: $\chi^2_1 = 9.8$, $P = 0.002$)

more likely to be captured in native shrubland than in exotic shrubland. Similarly, captures of Gray Catbirds in native shrubland were 3.74 times (274%; cpplmm, $\chi^2_1 = 70.7$, $P < 0.001$) and 4.32 times (332%; $\chi^2_1 = 118.4$, $P < 0.001$) greater than in exotic shrubland in 2012 and 2013, respectively.

In both years, >85% of Swainson's Thrushes and >90% of Gray Catbirds captured were hatch-year birds, with neither species showing age-specific differences in capture rate between habitats (Fisher's exact tests; Swainson's Thrush, 2012: $P = 0.61$, 2013: $P = 1.00$; Gray Catbird, 2012: $P = 1.00$, 2013: $P = 1.00$). Likewise, wing chord (2-sample t -tests; Swainson's Thrush, 2012: $t_{513.3} = -1.1$, $P = 0.27$, 2013: $t_{341.6} = -1.6$, $P = 0.11$; Gray Catbird, 2012: $t_{133.7} = 1.2$, $P = 0.25$, 2013: $t_{68.2} = 1.2$, $P = 0.22$) and date- and size-corrected mass (GLMs; Swainson's Thrush, 2012: $F_{1,578} = 3.5$, $P = 0.06$, 2013: $F_{1,352} = 0.6$, $P = 0.43$; Gray Catbird, 2012: $F_{1,384} = 1.3$, $P = 0.26$, 2013: $F_{1,229} = 1.2$, $P = 0.28$) were unrelated to the habitat type in which birds were captured.

Movement and Space Use

Birds that were recaptured were more likely to be recaptured in native habitat than in exotic habitat, regardless of where they were initially captured. In 2012, this difference was not significant for Swainson's Thrushes and neared significance for catbirds (Table 1). In 2013 and when both years were combined, the difference was significant for both species (Table 1). Multiple transfers between habitats (resulting in removal from analysis) were rarely detected; of the 6 thrushes and 32 catbirds captured more than twice, no thrushes and 2 catbirds (1 in each year) moved back and forth between shrubland habitats over the course of their stopover.

TABLE 2. Estimated foraging range, stay length, and continuous use duration of shrublands (exotic-dominated or native-dominated) and other habitats of 12 Swainson's Thrushes and 13 Gray Catbirds radio-tagged near East Lansing, Michigan, USA, during fall migration in 2013. Individuals were tracked every morning; hence, values here are assumed to primarily reflect foraging behavior.

	Swainson's Thrush			Gray Catbird		
	Mean \pm SE	Range	No. indiv (<i>n</i>) ^a	Mean \pm SE	Range	No. indiv (<i>n</i>) ^a
Kernel foraging range (ha) ^b						
99%	34.1 \pm 8.0	6.4–71.0	9	39.3 \pm 9.4	8.6–89.7	9
95%	23.3 \pm 5.4	4.6–48.5	9	27.4 \pm 6.5	6.0–62.4	9
90%	18.1 \pm 4.1	3.5–38.0	9	21.7 \pm 5.2	4.3–49.7	9
50%	5.4 \pm 1.2	1.1–11.2	9	6.5 \pm 1.6	1.1–15.8	9
Minimum stay length (day) ^c						
Site	10.4 \pm 2.3	1.0–24.0	12	18.3 \pm 4.7	1.0–50.0	12
Habitat use duration (day) ^d						
Exotic	2.4 \pm 1.2	0.5–7.0	3 (5)	2.5 \pm 0.9	0.5–5.0	3 (5)
Native	2.9 \pm 0.5	0.5–11.5	11 (29)	4.7 \pm 0.7	0.5–18.5	13 (37)
Open	—	—	0	0.6 \pm 0.2	0.3–1.0	3
Marsh	1.0	—	1	—	—	0
Woodland	0.9 \pm 0.1	0.3–3.5	11 (22)	1.1 \pm 0.2	0.5–3.5	10 (26)

^a Sample size in parentheses represents the number of observed durations used for calculation if that number differs from the number of individuals (No. indiv).

^b Estimated as areas within the isopleth of fixed kernel utilization distribution using a likelihood cross-validation smoothing parameter.

^c Estimated as the difference between the initial capture date and the final date of signal reception.

^d Estimated as the number of days (mornings) of being continuously detected in the given habitat before being detected in another habitat or departure.

We attempted a total of 408 triangulations or biangulations to locate radio-tagged birds and estimated 341 locations (success rate: 84%). Adding recapture locations of tagged birds, we obtained 141 thrush and 203 catbird locations. Summary statistics for minimum stay length and duration of use of each habitat type were obtained from 12 thrushes and 13 catbirds (Table 2). Three thrushes and 1 catbird departed on the evening of the capture day. All remaining individuals showed a similar pattern of occupying native shrubland for multiple days and occasionally making brief (≤ 1 day) visits to woodland (Table 2). Only 3 tagged birds of each species were relocated in exotic shrubland, but their use lasted for a few days on average, and transfer between exotic and native shrublands on the same morning was detected only once per species. The last thrush departed the study site on October 6 and the last catbird on October 30. The longest minimum observed stay length was 24 days (September 10–October 3) for Swainson's Thrushes and 50 days (September 11–October 30) for Gray Catbirds. The mass of radio-tagged birds at capture ranged from 28.5 g to 37.4 g for thrushes and from 32.3 g to 42.0 g for catbirds, but was not correlated with the stay length of either species (linear regressions; Swainson's Thrush: $r^2 = 0.02$, $F_{1,10} = 0.2$, $P = 0.63$; Gray Catbird: $r^2 = 0.07$, $F_{1,10} = 0.7$, $P = 0.42$).

Nine Swainson's Thrushes (5 originally captured in exotic shrubland and 4 in native shrubland) and 9 Gray Catbirds (4 originally captured in exotic shrubland and 5 in native shrubland) generated enough relocation points for

foraging range estimates (Table 2) and further analyses of habitat selection. These included 1 individual per species with truncated relocation data (1 Swainson's Thrush that lost its transmitter and 1 Gray Catbird from which tag recovery failed). Another catbird individual with truncated data (failed tag recovery) did not provide sufficient relocation points. On average, tagged thrushes and catbirds used in further analyses generated 15 and 20 relocation points, respectively.

Based on data from radio-tagged individuals, we found that habitat use was not random at the within-foraging-range scale, both by Swainson's Thrushes (one-way ANOVA, $F_{4,36} = 27.6$, $P < 0.001$) and Gray Catbirds ($F_{4,36} = 19.4$, $P < 0.001$). For both species, the selection ratio of native shrubland was greater than that of all other habitat types (all $P \leq 0.001$; Figure 2); native shrubland was on average 39% (thrushes) and 32% (catbirds) more likely to be used than expected by land cover proportion (selection ratio > 1 , $P < 0.005$; Figure 2). Thrushes avoided exotic shrubland within their foraging ranges (selection ratio < 1 , $P < 0.005$, although 1 individual showed a ratio > 1), and exotic shrubland was on average 44% less likely to be used than expected (Figure 2). This ratio did not differ when compared with the other habitat types of open area, marsh, or woodland (Figure 2). We did not find significant evidence of Gray Catbirds selecting or avoiding exotic shrubland within their foraging ranges at the population level (due to 2 individuals with ratios > 1), and the selection ratio of exotic shrubland was similar to

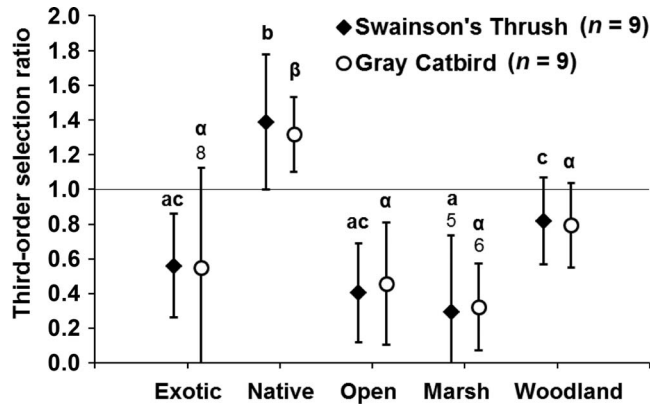


FIGURE 2. Selection ratios (used/availability) of habitats at the within-foraging-range (third-order) spatial scale for Swainson's Thrushes and Gray Catbirds near East Lansing, Michigan, USA, during fall migration stopover in 2013. Data are shown as means \pm simultaneous 95% Bonferroni CIs (truncated at zero as necessary). 95% CIs that do not intersect 1 indicate significant selection by populations (values >1 = selection; values <1 = avoidance). Unshared letters (Latin for Swainson's Thrushes and Greek for Gray Catbirds) indicate significant differences between means as detected by post hoc pairwise tests with Bonferroni correction. Sample size is denoted above the error bar if not $n=9$.

that of other habitat types, except for native shrubland (Figure 2).

Diet and Fruit Consumption

We identified food items in 255 (exotic: $n=89$; native: $n=166$) fecal samples from thrushes and in 138 (exotic: $n=22$; native: $n=116$) samples from catbirds. Across both native and exotic shrubland habitats, 97% and 99% of thrush and catbird fecal samples contained fruits, whereas only 15% and 11% of these samples, respectively, contained arthropods. Proportions of samples containing fruits only, arthropods only, or both did not differ by habitat type for either species (Fisher's exact tests; Swainson's Thrush: $P=0.67$; Gray Catbird: $P=0.79$). The proportions of presence vs. absence of each food item revealed that both bird species consumed *L. benzoin* $>50\%$ more frequently in native shrubland than in exotic shrubland (Fisher's exact test; Swainson's Thrush: $P<0.001$; Gray Catbird: $P<0.001$; Figure 3). *R. cathartica* ($P<0.001$) and *E. umbellata* ($P=0.004$) were consumed at greater frequencies in exotic vs. native habitat by thrushes but not by catbirds (Figure 3). The frequency of arthropods in fecal samples did not vary by habitat type for either species (Fisher's exact test; Swainson's Thrush: $P=1.00$; Gray Catbird: $P=1.00$; Figure 3).

DISCUSSION

Characteristics of Shrubland Habitats

Exotic and native shrublands were characterized by differences in shrub species composition but not in

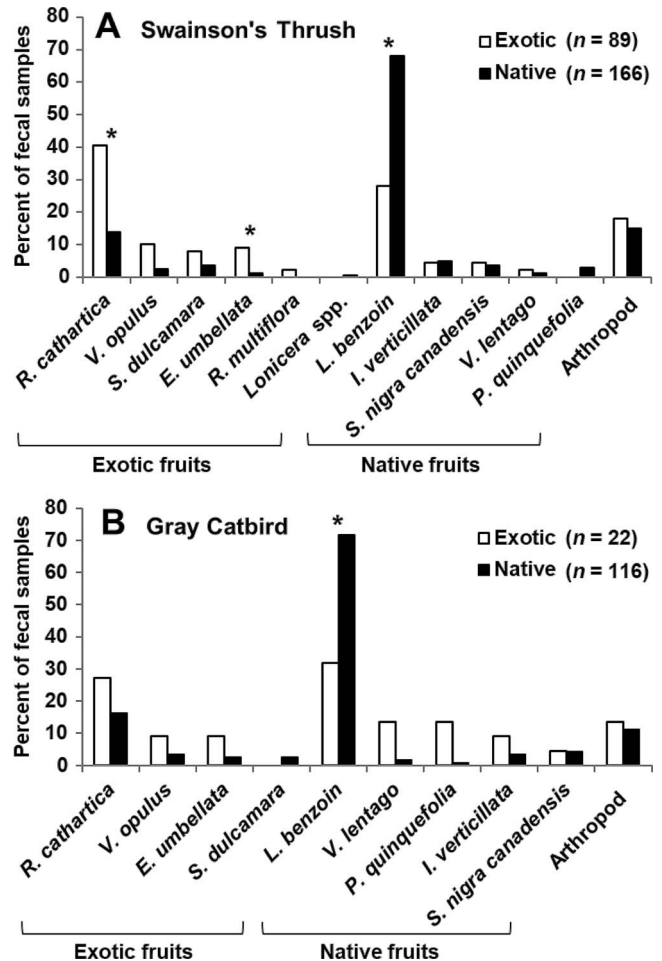


FIGURE 3. Frequency of food items found in fecal samples of (A) Swainson's Thrushes and (B) Gray Catbirds captured in exotic-dominated and native-dominated shrublands near East Lansing, Michigan, USA, during fall migration. An asterisk indicates a significant difference between habitat types based on binomial comparisons (number of samples present vs. number absent) of each item with Bonferroni correction. Values do not sum to 100% due to some fecal samples containing multiple items. For full fruit species names, see Appendix Table 3.

structure. While our sampling was limited to mist net locations, differences in vegetation composition between exotic- and native-dominated plots were large and we have no reason to expect these differences to be present only at our net locations. The importance of shelter from predators and weather is well established (Moore et al. 1995, 2005, Ktitorov et al. 2008). Early-successional shrublands characterized by an open canopy and structurally complex understory have been suggested to provide important shelter during spring migration (Smith and Hatch 2008), postbreeding (Akresh et al. 2009), and fall migration (Cimprich et al. 2005). With respect to cover, our results suggest that the quality of exotic shrublands as stopover habitat is similar to that of native counterparts.

Additionally, the overall abundance of potential food items was similar between shrublands based on crude estimates of fruit density (in 2012 only) and flying arthropod biomass taken concomitantly with this study (Oguchi 2015). Hence, we conclude that the composition of fruiting shrub species was the key difference between habitats.

Bird Density and Distribution

Capture rates of Swainson's Thrushes and Gray Catbirds were higher in native than in exotic shrubland, irrespective of sampling year, and this skewed distribution did not appear to be driven by metrics of condition, age, or size (Oguchi 2015). Catbirds in particular showed ~3- to 4-fold higher capture rates in native shrubland. These results are unlikely to have been confounded by vegetation density immediately surrounding the mist nets, given the similarities in habitat structure, and hence can be interpreted as a proxy for density. Previous studies have found food abundance and availability of suitable cover to be likely factors explaining high migrant densities in predominantly exotic shrublands compared with nonshrubland areas during migration (Smith and Hatch 2008, Gleditsch and Carlo 2011). Our study suggests that when shrublands that offer similar cover and food abundance are compared, fall migrant density will be higher in native-dominated than in exotic-dominated habitat.

Movement, Space Use, and Habitat Selection

Higher capture rates of Swainson's Thrushes and Gray Catbirds in native compared with exotic shrubland may have been due to their net movement into native shrubland and concentrated use of this habitat type. We found a greater habitat transfer rate from exotic to native shrubland than vice versa, and these results were supported by radio-telemetry data. Native shrubland was the only habitat type that was selected (selection ratio >1) by all radio-tagged birds within their foraging ranges, regardless of where they were initially captured. On the other hand, the selection ratio of exotic shrubland did not differ significantly compared with that of woodlands, open areas, and marshes, which were generally avoided. Likewise, exotic shrubland was avoided at the population level by thrushes, but not by catbirds, within their foraging ranges. These results were similar when we analyzed the same data using 95% kernel foraging ranges, except that the selection for native shrubland by thrushes was no longer significant (Y. Oguchi personal observation). Net immigration from other adjacent habitats and a high selection ratio are expected characteristics of better-quality habitat because migrants during stopover tend to move into and concentrate their foraging efforts within habitats where food resources are more abundant or where more shelter is available (Moore et al. 1995, Cohen et al. 2012).

Diet and Patterns of Fruit Consumption

Swainson's Thrushes and Gray Catbirds captured during our study were highly frugivorous, with >97% of fecal samples containing fruits. We found no relationship between habitat and arthropod content in fecal samples. Hence, arthropod abundance does not seem to limit the use of exotic shrubs by either species. Both bird species consumed a range of fruit species that differed between habitat types. The native *L. benzoin* was the predominant food item in native shrubland and was found in ~70% of samples from both bird species. *L. benzoin* was also commonly found (~30%) in fecal samples from birds caught in exotic shrubland, despite its low abundance in that habitat. This observation may have been the result of birds preferring *L. benzoin* and captures of birds that had recently transferred from native shrubland. These observations suggest that the birds' selection for *L. benzoin* may account for the high density of thrushes and catbirds in native shrubland. *L. benzoin* is among the fruits with the highest lipid content found in our study site (based on White 1989, Smith et al. 2013), and our results are consistent with previous findings showing that fall migrants generally prefer lipid- and energy-rich fruits (White and Stiles 1992, Stiles 1993, Bairlein 2002). We also found that the exotic *R. cathartica* fruits appeared in ~40% and ~30% of fecal samples from thrushes and catbirds captured in exotic shrubland. For thrushes, this frequency was greater than that for conspecifics captured in native shrubland. *R. cathartica* fruits contain more energy than many other exotic fruits found in our study site (White 1989, Smith et al. 2013, Oguchi et al. 2017) and may be consumed as an alternative when more energy-rich native fruits are uncommon. Other exotic fruits, such as those of *E. umbellata* and *Lonicera* spp., that were abundant in exotic shrubland (Oguchi 2015) were rarely found in the fecal samples of either species, suggesting their low value relative to other fruits.

Conclusions and Management Implications

Our results suggest that native-dominated shrubland is more important for fall frugivorous migrants than exotic-dominated shrubland, probably because birds prefer certain native fruits, notably *L. benzoin*. Landbird migrants are thought to select certain native fruits within shrublands that offer both exotic and native fruits (e.g., White and Stiles 1992, Parrish 1997, Suthers et al. 2000, Smith et al. 2007, 2013). Our study adds to these findings by showing that fruit selection follows a comparable pattern at larger spatial scales when exotic- and native-dominated shrublands occur as distinct patches across the landscape. The relative value of exotic shrubs and their fruits for migrating landbirds will depend on what other food resources are present at a given stopover site. Exotic fruits may be of high importance when a stopover site is set in a landscape

where few other fruiting species are present (Gleditsch and Carlo 2011) or for late migrants arriving after native fruits have been depleted (White and Stiles 1992, Craves 2009). In our study site, the possibility remains, therefore, that heavily consumed native fruits (e.g., *L. benzoin*) could have been depleted after the termination of our field season (end of October), in which case the relative importance of exotic shrubland might have increased. Nevertheless, our results support the view that exotic shrubs and fruits are of limited value to fall frugivorous migrants in the presence of native counterparts (Smith et al. 2013) and are used as an alternative when density is high in native shrublands. Furthermore, our concomitant study showed that catbirds (but not thrushes) using exotic shrubland experienced lower immune and antioxidant status compared with conspecifics using native shrubland, depending on the year (Oguchi et al. 2017). This pattern may have been related to the nutritional attributes of fruits and species-level fruit preferences and consumption, suggesting that there may be subtle but important health consequences of using exotic vs. native habitats for certain species (Oguchi et al. 2017). We thus recommend efforts to prevent encroachment of exotic shrubs into native-dominated shrubland if the management objective is to improve habitat quality for fall frugivorous migrants. Supplanting exotic shrubs in a predominantly exotic shrubland with native shrubs such as *L. benzoin* that produce preferred high-energy fruits (Smith et al. 2013, Oguchi 2015) may also be effective, as birds seem to be able to selectively consume native fruits even in predominantly exotic shrublands.

We point out that our study was limited to fall frugivorous migrants. Whether and how exotic-dominated shrublands affect birds may be contingent on the stage in a bird's annual cycle and the composition of the avian and vegetation communities that an individual experiences. Such impacts may be indirect, subtle, and dependent on both plant and avian species (Rodewald 2012, Meyer et al. 2015). We encourage studies to take a community ecology approach when investigating bird species assemblages that vary in dietary preference in a similar system to ours. Studies that associate food and habitat selection with seasonally dependent nutritional opportunities and predation risks in exotic and native shrublands over the entire annual cycle will also likely enhance our understanding of the impact of exotic shrubs on landbird populations and communities.

ACKNOWLEDGMENTS

We thank many field assistants and volunteers for their hard work, particularly C. Gesmundo, L. Theile, C. Gawne, H. Matsumura, K. Johnson, K. Clark, D. Boston, K. Wilson, N. Martineau, and J. Caton. D. Williams, M. Quigley, H. Kim, R. Tempelman, S. Kravchenko, E. Cohen, J. Craves, S. McWil-

liams, and M. Hatch provided advice for data analyses and interpretation. F. Moore and R. Campa lent us valuable equipment. We thank the Michigan Department of Natural Resources for permitting us to use the Rose Lake State Wildlife Research Area and The University of Scranton and Michigan State University for providing logistical support.

Funding statement: We thank the U.S. Fish and Wildlife Service (USFWS) Avian Health and Disease Program (USFWS Migratory Bird Conservation in the Upper Midwest), the Hal and Jean Glassen Memorial Foundation, and Michigan State University Undergraduate Research Fund for their financial support. No funder provided input to the manuscript or requested their approval prior to submission or publication.

Ethics statement: We performed all work under the following permits: U.S. Geological Survey (USGS) Master Banding permit #23629 to J.C.O., USFWS Scientific Collection permit #MB19470, MI Scientific Collection permit #SC1386, Rose Lake Special Use permit, and Michigan State University Institutional Animal Care and Use Committee (IACUC) protocol #07/11-145-00.

Author contributions: Y.O., R.J.S., and J.C.O. conceived and designed the research and wrote the paper; Y.O., Z.P., and J.C.O. conducted the study; Y.O. and Z.P. analyzed the data; and R.J.S. and J.C.O. provided substantial materials, resources, and funding.

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APPENDIX TABLE 3. Estimated shrub stem densities (stems ha⁻¹) in exotic- and native-dominated shrublands near East Lansing, Michigan, USA. Data (mean ± SE) are presented in decreasing order of stem density in exotic shrubland and in increasing order in native shrubland to highlight the difference in composition between the 2 shrublands. Exotic species regarded as invasive in Michigan (based on Borland et al. 2009) are indicated by superscript “I” in U.S. status. Deviances and *P*-values were derived from post hoc multiple comparisons controlled for family-wise error rate across species, and an asterisk denotes significance (*P* < 0.05).

Scientific name	Common name	U.S. status	Exotic shrubland	Native shrubland	Deviance	<i>P</i> -value
<i>Elaeagnus umbellata</i>	Autumn olive	Exotic ^I	1,575.8 ± 221.5	30.0 ± 22.3	24.5	0.001*
<i>Lonicera</i> spp.	Honeysuckle	Exotic ^I	1,459.8 ± 324.6	0.0	57.1	0.001*
<i>Rosa multiflora</i>	Multiflora rose	Exotic ^I	902.9 ± 299.7	409.5 ± 115.6	3.1	0.77
<i>Vitis riparia</i>	Riverbank grape	Native	722.3 ± 250.1	157.1 ± 42.7	10.8	0.04*
<i>Akebia quinata</i>	Chocolate vine	Exotic	600.7 ± 455.6	0.0	4.9	0.40
<i>Rhamnus cathartica</i>	Common buckthorn	Exotic ^I	357.4 ± 83.9	171.2 ± 70.2	2.7	0.81
<i>Rubus occidentalis</i>	Black raspberry	Native	146.4 ± 96.3	7.1 ± 4.8	3.6	0.63
<i>Parthenocissus quinquefolia</i>	Virginia creeper	Native	114.0 ± 24.2	75.9 ± 26.7	0.8	0.96
<i>Rubus allegheniensis</i>	Allegheny blackberry	Native	57.0 ± 53.0	0.0	3.1	0.77
<i>Rhamnus alnifolia</i>	Alderleaf buckthorn	Native	51.3 ± 33.9	1.8 ± 1.8	5.9	0.29
<i>Rhus typhina</i>	Staghorn sumac	Native	34.2 ± 34.2	0.0	1.5	0.91
<i>Cornus alternifolia</i>	Alternateleaf dogwood	Native	34.2 ± 19.9	0.0	6.8	0.20
<i>Malus</i> spp.	Crab apple	Native	32.3 ± 19.7	1.8 ± 1.8	3.1	0.77
<i>Toxicodendron radicans</i>	Eastern poison ivy	Native	26.6 ± 15.2	14.1 ± 9.2	0.6	0.96
<i>Viburnum opulus</i> L. var. <i>americanum</i>	American cranberrybush	Native	26.6 ± 26.6	35.3 ± 31.5	0.0	0.96
<i>Rubus idaeus</i>	American red raspberry	Native	22.8 ± 22.8	47.7 ± 20.6	0.6	0.96
<i>Viburnum opulus</i>	European cranberrybush	Exotic	17.1 ± 10.2	42.4 ± 20.5	0.8	0.96
<i>Rubus flagellaris</i>	Northern dewberry	Native	13.3 ± 13.3	0.0	1.5	0.94
<i>Sambucus nigra canadensis</i>	American black elderberry	Native	7.6 ± 7.6	455.4 ± 240.2	9.1	0.05
<i>Amelanchier</i> spp.	Serviceberry	Native	5.7 ± 5.7	28.2 ± 19.9	0.6	0.96
<i>Vaccinium angustifolium</i>	Lowbush blueberry	Native	0.0	1.8 ± 1.8	1.3	0.96
<i>Prunus virginiana</i>	Chokecherry	Native	0.0	10.6 ± 7.6	2.9	0.81
<i>Betula pumila</i>	Bog birch	Native	0.0	12.4 ± 12.4	1.4	0.96
<i>Crataegus</i> spp.	Hawthorn	Native	0.0	21.2 ± 21.2	1.4	0.96
<i>Berberis thunbergii</i>	Japanese barberry	Exotic	0.0	30.0 ± 30.0	1.4	0.95
<i>Physocarpus opulifolius</i>	Common ninebark	Native	0.0	130.6 ± 74.2	6.2	0.27
<i>Solanum dulcamara</i>	Climbing nightshade	Exotic	0.0	169.4 ± 58.8	20.6	0.001*
<i>Cornus sericea</i>	Redosier dogwood	Native	0.0	176.5 ± 161.9	2.8	0.81
<i>Viburnum lentago</i>	Nannyberry	Native	0.0	194.2 ± 82.8	14.3	0.007*
<i>Corylus americana</i>	American hazelnut	Native	0.0	356.5 ± 130.2	15.4	0.004*
<i>Toxicodendron vernix</i>	Poison sumac	Native	0.0	656.6 ± 121.9	35.6	0.001*
<i>Lindera benzoin</i>	Northern spicebush	Native	0.0	806.6 ± 167.1	32.7	0.001*
<i>Ilex verticillata</i>	Common winterberry	Native	0.0	1,163.2 ± 284.4	36.4	0.001*
<i>Cornus racemosa</i>	Gray dogwood	Native	19.0 ± 19.0	1,350.3 ± 422.6	20.5	0.001*