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Scale-dependent effects of nonnative plant invasion on host-seeking tick abundance

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Abstract

Nonnative, invasive shrubs can affect human disease risk through direct and indirect effects on vector populations. Multiflora rose (*Rosa multiflora*) is a common invader within eastern deciduous forests where tick-borne disease (e.g. Lyme disease) rates are high. We tested whether *R. multiflora* invasion affects blacklegged tick (*Ixodes scapularis*) abundance, and at what scale. We sampled host-seeking ticks at two spatial scales: fine-scale, within *R. multiflora*-invaded forest fragments; and patch scale, among *R. multiflora*-invaded and *R. multiflora*-free forest fragments. At a fine scale, we trapped 2.3 times more ticks under *R. multiflora* compared to paired traps 25 m away from *R. multiflora*. At the patch scale, we trapped 3.2 times as many ticks in *R. multiflora*-free forests compared to *R. multiflora*-invaded forests. Thus, ticks are concentrated beneath *R. multiflora* within invaded forests, but uninvaded forests support significantly more ticks. Among all covariates tested, leaf litter volume was the best predictor of tick abundance; at the patch scale, *R. multiflora*-invaded forests had less leaf litter than uninvaded forests. We suggest that leaf litter availability at the patch-scale plays a greater role in constraining tick abundance than the fine-scale, positive effect of invasive shrubs.

Keywords

forest fragmentation; invasive species; *Ixodes scapularis*; nonnative plant; *Rosa multiflora*; scale

Introduction

Altered ecosystems can produce cascading effects. For example, nonnative, invasive species impact a range of abiotic and biotic ecosystem components from soil chemistry (Howard et al. 2004) to biodiversity (Wilcove et al. 1986, Coblentz 1990), and even human health (Juliano and Lounibos 2005, Allan et al. 2010, Morlando et al. 2012). On the east coast of the United States, multiflora rose (*Rosa multiflora*) is an ubiquitous invader in forest

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understories (Huebner et al. 2014), with documented ecosystem effects including accelerated litter nitrogen loss (Ashton et al. 2005) and reduced avian nest success (Borgmann and Rodewald 2004). Herein, we investigate whether *R. multiflora* may also affect human health by increasing tick-borne disease risk.

Blacklegged ticks (*Ixodes scapularis* Say) are an important vector of zoonotic pathogens, including *Borrelia burgdorferi*, *Anaplasma phagocytophilum*, *Babesia microti*, *Borrelia miyamotoi*, and Powassan virus (Centers for Disease Control and Prevention 2015). *Borrelia burgdorferi* causes Lyme disease, the most commonly reported vector-borne disease in North America (Bacon et al. 2008). Recent work in forest ecosystems suggests that the abundance of host-seeking *I. scapularis* (nymphs and adults) is positively associated with invasion by nonnative shrubs (Lubelczyk et al. 2004, Elias et al. 2006, Williams et al. 2009, Williams and Ward 2010). *Ixodes scapularis* abundance is a key factor in predicting human Lyme disease cases (Mather et al. 1996, Khatchikian et al. 2012); thus, nonnative plant invasion potentially increases human disease risk.

The dense understory structure created by nonnative plants can increase humidity and protection from extreme temperature fluctuations, thereby creating a more favorable microclimate for ticks (Williams et al. 2009). Dense understory structure is also used preferentially by host animals (e.g. white-tailed deer, *Odocoileus virginianus*) that are important to tick reproduction and survival (Allan et al. 2010). Both of these mechanisms (improved microclimate and increased host use) support a potential positive association between *I. scapularis* abundance and the presence of nonnative, invasive shrubs.

There is a critical need to determine whether fine-scale habitat associations between invasive shrubs and ticks create larger vector populations at broad enough scales to increase human disease risk (Allan et al. 2010). Ecological processes are often scale-dependent (Wiens 1989). Many biotic and abiotic factors affect *I. scapularis* density and distribution (Ostfeld et al. 1995) and likely operate at different scales. Nonnative plant invasion may increase tick abundance at a fine scale within a given forest patch, but it is unclear whether this would produce a larger vector population at a landscape scale relevant to human disease risk.

We assessed the effects of *R. multiflora* invasion at two spatial scales: at a fine scale within forest fragments and at a patch scale among different forest fragments. We tested the following: 1. whether *I. scapularis* abundance differs under *R. multiflora* compared to other shrub species or open understory within the same forest patch; and 2. whether *I. scapularis* abundance differs among *R. multiflora*-invaded forest fragments compared to forest fragments without *R. multiflora* invasion.

Methods

Study area

Delaware has one of the highest per capita rates of human Lyme disease cases in the United States (Bacon et al. 2008). This, combined with fragmented forests containing significant nonnative plant invasion, makes Delaware an ideal location to examine the effects of nonnative plants on *I. scapularis* populations. We trapped ticks in forest fragments (Figure 1) composed of mixed deciduous hardwood stands in New Castle County, DE (Rega 2012).

Tick trapping

In 2013 and 2014, we selected eight forest fragments ranging from 6 to 16 ha for trapping–four "uninvaded fragments" with <1% *R. multiflora* cover in the understory and four "invaded fragments" with >10% *R. multiflora* cover in the understory. We used dry-ice (CO_2) baited traps (Kensinger and Allan 2011) to target host-seeking *I. scapularis* nymphs because they pose the greatest disease risk to humans (Centers for Disease Control and Prevention 2015). Although dragging or flagging methods are often preferred for capturing *I. scapularis* nymphs (Falco and Fish 1992), CO_2 traps avoid sampling bias due to vegetation structure (Falco and Fish 1992, Schulze et al. 1995, 1997, Daniels et al. 2000, Kensinger and Allan 2011). Drag cloths become snagged on *R. multiflora* thorns, making tick habitat beneath it inaccessible for dragging or flagging.

Within invaded fragments, we deployed traps in a paired design, with each pair consisting of one trap under *R. multiflora* and one trap 25 meters away, not under *R. multiflora*. We chose four pairs (8 traps total) in each invaded fragment. Trap locations beneath *R. multiflora* were randomly selected within previously mapped and digitized patches of *R. multiflora* in ArcGIS v10 (ESRI 2012); paired trap locations not under *R. multiflora* were designated 25 meters away in a random cardinal direction, with the only selection criterion being that they could not be under *R. multiflora*. As a result, we set up these paired traps beneath a variety of understory structures and plant species. Within each uninvaded forest fragment, we randomly chose four points as trap locations using ArcGIS. Each year, we deployed 16 pairs of traps (32 total) across four *R. multiflora*-invaded fragments and 16 traps across four uninvaded fragments. Over the two years of the study, we used a total of 64 trap locations (Figure 1). On any given trap night, half of the traps were active. To eliminate biases associated with weather, we always deployed trap pairs together and in equal numbers of invaded and uninvaded fragments on the same nights. Each trap was baited with 1.4 kg of pelleted dry ice, and we lined the edges of the plywood base with double-sided carpet tape (3M brand). We checked traps after 24h and collected all ticks with forceps and deposited them into individual microcentrifuge tubes. Ticks were transported live, frozen at −80°C, and later identified to species and life stage using dichotomous keys (Keirans and Litwak 1989, Durden and Keirans 1996, Keirans and Durden 1998). Between April and July of 2013 and 2014, we trapped up to two nights per week, avoiding rain, for a total of 671 trap nights.

Vegetation surveys

We measured understory vegetation at several scales surrounding each trap during June and July. Within a 12.5 m radius surrounding the trap, we identified the dominant four understory plant species and estimated the percent of the ground that each covered, the percent of ground covered by *R. multiflora*, the percent of ground covered by coarse woody debris, and we measured understory vegetation density using 2.0 m high Nudds boards divided into four 0.5 m sections (Nudds 1977). The 12.5 m radius area was chosen to represent the approximate size of *Peromyscus leucopus* (an important larval tick host) home ranges (Wolff 1985) that could influence immature tick abundance, while avoiding overlap with paired traps. Within a 2.5 m radius around the trap, we estimated the percent of ground covered by *R. multiflora* to more closely represent the effective trapping area (Falco and Fish 1991). We identified the plant species immediately over the trap, and we quantified leaf litter volume by gathering up all litter within a $0.5\mathrm{m}^2$ quadrat next to the trap and measuring its volume in a 19L bucket.

We calculated landscape variables for each trap location in ArcGIS using 2007 Delaware Land Use Land Cover layer (State of Delaware 2008). We quantified landscape variables that might influence habitat suitability for ticks and/or host animals and that represent the human-dominated landscape context of the study sites (Nicholson and Mather 1996, Bunnell et al. 2003). These variables included distance to nearest stream, distance to nearest road, distance to nearest agriculture, distance to nearest human development, distance to nearest impervious surface, distance to nearest residential development, and distance to nearest forest edge from each trap location.

We included vegetation variables that characterized vegetation at the patch scale (Rega 2012). These variables included proportion of *Fagus grandifolia, Acer spp*, *Quercus spp*, *Liriodendron tulipifera*, or *Liquidambar styraciflua* as dominant canopy trees, percent of ground covered by *R. multiflora*, average leaf litter volume, tree basal area, average diameter at breast height (dbh) of trees, percent of ground covered by understory plants (all spp.), proportion of understory woody stems that were nonnative, year of canopy closure.

Statistical analyses

We standardized total *I. scapularis* nymphs captured at each trap by effort (number of trap nights) to get a daily mean tick capture rate, which we used as an index of host-seeking *I. scapularis* abundance (hereafter: tick abundance) at each location. Prior to analyses, we log-transformed the response, tick abundance, to satisfy parametric test assumptions. At the fine scale, we used a paired t-test to determine if tick abundance differed between paired traps under *R. multiflora* and not under *R. multiflora*. At the patch scale we used an analysis of variance (ANOVA), blocking on site, to test for a difference in tick abundance between invaded and uninvaded forest patches.

Tick abundance models

Because forest fragments differed in additional characteristics beyond presence/absence of *R. multiflora* invasion, we assessed which vegetation and landscape variables influenced tick abundance at the landscape scale. We used boosted regression trees (BRT) to assess relative variable importance (Friedman and Meulman 2003, Elith et al. 2008) using packages gbm (Ridgeway 2015) and dismo (Hijmans et al. 2015) to run BRTs in R v 3.1.1 (R Development Core Team 2014); we set the error distribution for the response variable as gaussian, and specified the learning rate as 0.005, bag fraction as 0.5, and tree complexity at 2. Using the top four predictor variables according to BRT rankings, we built several generalized additive models (GAM) to compare for the best fit using package mgcv (Wood 2015) in R.

Results

Tick captures

We captured 282 total *I. scapularis* individuals (275 nymphs, 7 adults) over 671 trap nights. At traps deployed in *R. multiflora*-invaded fragments, we captured a total of 79 and 33 *I. scapularis* nymphs in *R. multiflora* and not in *R. multiflora*, respectively. We caught a total of 163 *I. scapularis* nymphs in uninvaded forest fragments. Forty-seven of the 64 traps (73%) captured at least one *I. scapularis* nymph, and tick abundance ranged from 0 to 2.33 (nymphs/day). At the fine scale within invaded forest fragments, tick abundance under *R. multiflora* was 2.3 times greater than not under *R. multiflora* (t_{19}=2.37, $P = 0.03$) (Figure 2). At the patch scale, we detected the opposite pattern; tick abundance in uninvaded forest fragments was 3.2 times greater than in *R. multiflora*-invaded fragments ($F_{(1,53)}$=30.27, $P <$ 0.01) (Figure 2). To verify that patch-level differences were not driven by the low capture rates in the invaded patches at the traps not under *R. multiflora*, we confirmed that tick abundance at traps in uninvaded patches was greater than at traps under *R. multiflora* ($t_{=42}$=2.75, $P < 0.01$).

Tick models

Several vegetation variables were correlated (coefficients ≥ 0.6), so we reduced the candidate set of local vegetation and landscape predictor variables to include only those listed in Table 1. Boosted regression trees (BRT) achieved a cross validation correlation 0.731 after fitting 1,350 trees. Of all potential predictor variables, leaf litter volume at the trap location had the highest relative influence (17% of total deviance explained) on tick abundance, followed by several variables with similar relative influence (11.7–11.9%): distance to nearest road, average tree dbh, and distance to nearest stream.

We log-transformed certain predictor variables to improve their distributions along the x-axis. Our best GAM (61% deviance explained) based on Akaike's information criterion adjusted for small sample size (Burnham and Anderson 2002) included log-transformed litter volume, distance to nearest road, log-transformed distance to nearest stream, and average tree dbh (Figure 3, Table 2). Tick abundance responded to leaf litter volume nonlinearly. Increase in leaf litter volume at low levels (<10 L/m^2) had little effect on tick abundance. Between 12 L/m^2 and 20 L/m^2 there was a strong positive change in tick abundance with increasing leaf litter volume, which then leveled out around 30 L/m^2. We saw a similar non-linear response with the distance to stream. Close to a stream, there were very few ticks captured, but this response increased rapidly up to a certain distance from the stream, beyond which there is little effect of the stream on tick abundance. Distance to nearest road had a positive effect on tick abundance at low and high values, and average tree dbh was inversely related to tick abundance.

Discussion

At a fine scale, we trapped 2.3 times more nymphal blacklegged ticks under *R. multiflora* compared to areas without *R. multiflora* within the same forest fragments. However, we trapped over 3 times as many ticks in uninvaded forest fragments compared to *R. multiflora*-

invaded forest fragments. Host-seeking ticks were concentrated beneath *R. multiflora* within invaded forests, but they were more abundant in uninvaded forests. Thus, although at fine scales *R. multiflora* appears to increase tick abundance, *R. multiflora* invasion actually suppresses tick abundance at the patch scale. Our results suggest that reduced leaf litter volume constrains tick abundance (Schulze et al. 1995, Burtis et al. 2014). The lack of leaf litter in *R. multiflora*-invaded forest fragments creates an inhospitable environment for ticks, from which they are rescued by invasive shrubs with dense growth forms (e.g. Williams et al. 2009).

Within invaded forests, our results are consistent with prior studies that show a positive relationship between nonnative, invasive shrubs (e.g. *B. thunbergii*) and questing nymphal and adult *I. scapularis* abundance (Williams et al. 2009, Lubelczyk et al. 2004, Elias et al. 2006). Densities of nymphal and adult lone star ticks (*Amblyomma americanum*) were also higher in invasive honeysuckle (*Lonicera maackii*)-dominated plots compared to uninvaded, adjacent plots (Allan et al. 2010). At a landscape scale, however, we found ticks were more abundant in uninvaded forest fragments than invaded fragments. We captured more than three times as many *I. scapularis* nymphs in uninvaded forest fragments compared to *R. multiflora*-invaded forest fragments. *Rosa multiflora* invasion was associated with habitat changes at the forest-fragment scale that create an aggregation of ticks around *R. multiflora* within invaded forests. However, uninvaded habitats appear to be more suitable for ticks than invaded habitats, seemingly due to the greater volume of leaf litter in uninvaded forest fragments.

Of all vegetation and landscape covariates tested, leaf litter volume was the best predictor of tick abundance. Leaf litter is an important component of *I. scapularis* habitat (Schulze et al. 1995, 2002, Lubelczyk et al. 2004, Elias et al. 2006). In the forests investigated, leaf litter volume was negatively correlated with invasion by nonnative plants at the patch scale. We found more than four times the volume of leaf litter in *R. multiflora*-free forest fragments compared to *R. multiflora*-invaded forest fragments ($P < 0.01$), and there was no difference in leaf litter volume between paired points within invaded forests. The widespread relationship between leaf litter and invasive plants is ultimately driven by nonnative, invasive earthworms (Nuzzo et al. 2009). These earthworms lead the nonnative plant invasion front by devouring leaf litter and disrupting mycorrhizal networks, inhibiting native plant growth and regeneration (Lawrence et al. 2003, Suárez et al. 2006, Hale et al. 2006). This reduction in habitat quality for native plants, combined with high densities of white-tailed deer over-browsing native plants, helps nonnative plants to invade. Therefore, at a patch scale, the forest fragments with significant nonnative plant invasion are lacking the layer of leaf litter that comprises favorable tick habitat.

The presence or absence of earthworm invasion and subsequent nonnative plant invasion are determined by numerous factors including soil chemistry (Moore et al. 2013), litter composition (Belote and Jones 2009), and historical land use patterns (Beauséjour et al. 2015). With increasing disturbance and propagule pressure in human-dominated landscapes, currently uninvaded forest fragments may eventually host high densities of earthworms and nonnative plants, with implications for tick and litter arthropod survival. On the other hand, uninvaded forest fragments may possess certain characteristics, such as high soil acidity

(Bernard et al. 2009), that make them more resistant to earthworm invasion. In either scenario, we suggest continued monitoring at multiple spatial scales to understand the impacts of invasion on tick population dynamics.

Conclusions and Future Directions

Our results suggest that while *R. multiflora* invasion concentrates host-seeking *I. scapularis* nymphs at a fine scale, the loss of leaf litter associated with *R. multiflora* invasion reduces tick habitat quality at the patch scale. We found the greatest abundance of host-seeking *I. scapularis* nymphs in uninvaded forests with deep litter layers. Thus, while removal of invasive plants may reduce tick abundance within certain forests, management actions toward reducing host-seeking tick abundance may have a greater impact in forests with deep litter layers.

Future work should test potential mechanisms influencing tick abundance in invaded and uninvaded forest fragments. Furthermore, we should implement broader scale studies using multiple landscapes within the temperate deciduous forest biome to test our hypotheses about invasive earthworms, leaf litter, and invasive shrub effects on host-seeking *I. scapularis* abundance.

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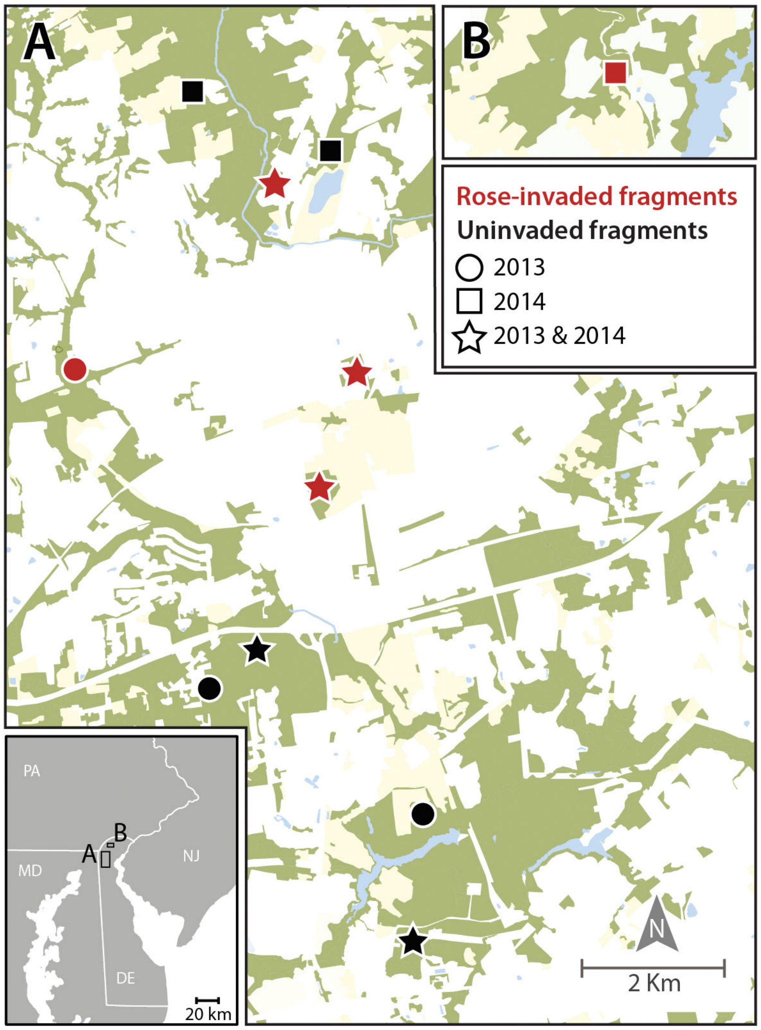

Figure 1.

Study area in New Castle County, Delaware. Green represents forest cover; pale yellow is agriculture; blue is water; and white is any type of human development. “Rose-invaded” and “uninvaded” fragments refer to forest fragments with and without *R. multiflora* invasion.

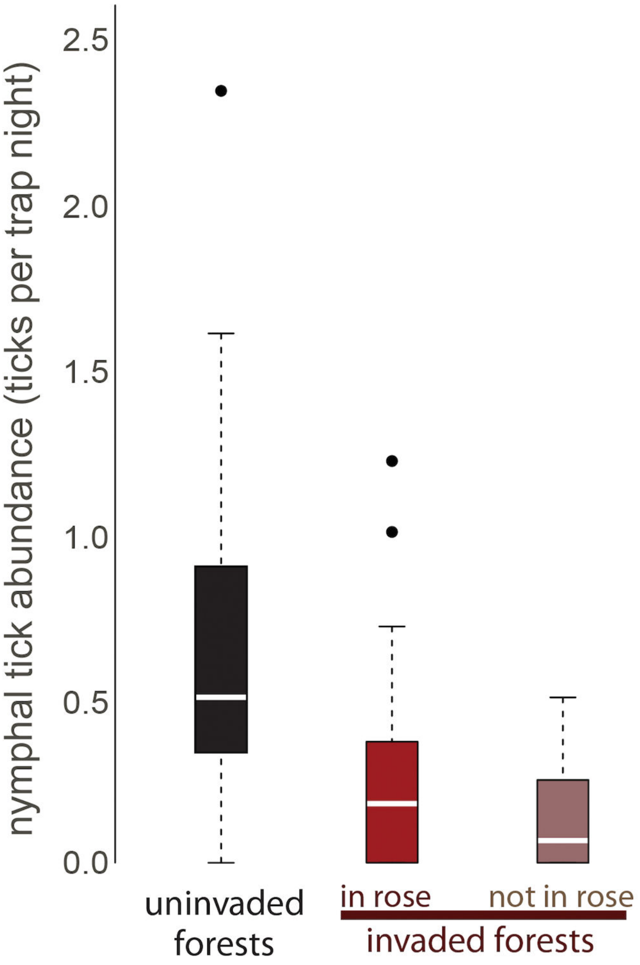

Figure 2.

Boxplot of tick abundance measured at traps in uninvaded forests, at traps under *R. multiflora* in invaded forests ("in rose"), and at traps not under *R. multiflora* ("not in rose") in invaded forests. Horizontal white lines represent medians and boxes demonstrate the interquartile range.

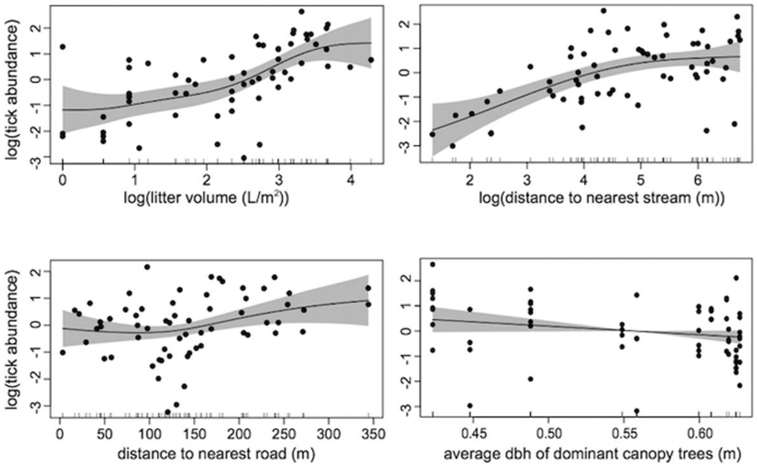

Figure 3.

Generalized additive model (GAM) partial dependence plot of top-ranked model. Lines display the best fit for the relationship between log-transformed tick abundance and predictor variables. Gray bars represent 95% confidence interval and black dots show actual data points.

Table 1

Summary of vegetation and landscape covariates measured at the trap and patch scale.

Trap and patch level covariates	**Uninvaded forests**	**Invaded forests**	
Trap-level covariates	**traps**	**traps in *R. multiflora***	**traps not in *R. multiflora***
Nudds at 0.5–1.0 m (%)	**18.0**^{A} ± 3.9	**73.9**^{B} ± 4.5	**53.3**^{C} ± 5.9
Leaf litter volume (L/m^{2})	**28.0**^{A} ± 2.8	**6.1**^{B} ± 1.4	**6.7**^{B} ± 1.2
Coarse woody debris (%)	**6.5**^{A} ± 0.9	**3.4**^{B} ± 0.7	**4.2**^{B} ± 0.7
Distance to agriculture (m)	**288.3**^{A} ± 54.7	**156.7**^{B} ± 24.6	**159.6**^{B} ± 24.6
Distance to edge (m)	**67.8**^{A} ± 9.1	**39.8**^{B} ± 8.8	**41.9**^{B} ± 8.4
Distance to road (m)	**154.7** ± 16.7	**135** ± 18.1	**133.4** ± 15.4
Distance to residential (m)	**716.9** ± 377.6	**186.2** ± 31.5	**174.4** ± 32.9
Distance to stream (m)	**371.8**^{A} ± 62.7	**148.4**^{B} ± 35.7	**134.1**^{B} ± 35.6
Patch-level covariates			
***Fagus grandifolia* (%)**	**8.5**^{A} ± 2.8	**0.7**^{B} ± 0.2	
***Acer spp.* (%)**	**0.7**^{A} ± 0.1	**21.2**^{B} ± 1.2	
Year of canopy closure	**1916.7**^{A} ± 4.9	**1963**^{B} ± 5.1	
Nonnative stems (%)	**9.1**^{A} ± 2.7	**40.0**^{B} ± 3.3	
***Liriodendron tulipifera* (%)**	**21.2** ± 2.4	**22.9** ± 2.8	
Average tree dbh (m)	**0.6** ± 0.0	**0.6** ± 0.0	

Notes: Covariates are summarized as mean ± standard error. Letters (A,B,C) denote significant differences among groups ($P < 0.05$) detected using analysis of variance (ANOVA), blocking on site, followed up with Tukey post-hoc comparison when there were more than two groups. “Nudds” refers to Nudds board (Nudds 1977) measurements, and “dbh” stands for diameter at breast height.

Table 2

Summary of candidate generalized additive models including number of parameters (K), AIC$_c$, differences (ΔAIC$_c$), and Akaike weights (w_i).

Predictor variable(s)	***K***	**AIC$_c$**	**ΔAIC$_c$**	**w_i**
litter, road, stream, dbh	6	209.47	0	0.59
litter, dbh, stream	5	211.65	2.18	0.20
litter, road, stream	5	212.66	3.19	0.12
litter, stream	4	213.26	3.79	0.09
litter, road, dbh	5	224.19	14.72	0.00
litter, road	4	231.72	22.25	<0.001
stream, road, dbh	5	232.41	22.93	<0.001
litter, dbh	4	233.07	23.60	<0.001
road, stream	4	233.74	24.27	<0.001
stream, dbh	4	237.33	27.86	<0.001
stream	3	237.84	28.37	<0.001
litter	3	238.47	28.99	<0.001
dbh	3	239.15	29.68	<0.001
road, dbh	4	239.64	30.17	<0.001
road	3	249.95	40.48	<0.001
null	2	258.45	48.98	<0.001

Notes: The variable “litter” is the volume of leaf litter (L/m^2) at each trap. The variables “road,” and “stream” refer to the distance between these features and the trap; “dbh” is the average diameter at breast height of dominant canopy trees in each forest fragment. The response (tick abundance) and two predictors (litter and stream) were log-transformed prior to analysis.