






Features in and around residential gardens affecting the presence and abundance of questing *Ixodes ricinus* ticks

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ABSTRACT

People may be exposed to questing *Ixodes ricinus* ticks in urban settings, e.g. residential gardens. Little is known about the garden characteristics that support a tick population. To determine which features in and around residential gardens support or limit the occurrence and abundance of questing *I. ricinus* ticks, we sampled them in residential gardens in the Braunschweig region that differed in various intrinsic and extrinsic parameters. We recorded the number of questing nymphal and adult ticks on transects, and by using mixed-effects generalized linear regression models, we related their occurrence and abundance to garden characteristics, meteorological covariates, and landscape features in the vicinity. We detected questing *I. ricinus* ticks in about 90% of the 103 surveyed gardens. Our occurrence model (marginal $R^2=0.31$) predicted the highest probability of questing ticks on transects with hedges or groundcover in gardens, which are located in neighborhoods with large proportions of forest. The abundance of questing ticks was similarly influenced. We conclude that *I. ricinus* ticks are frequent in residential gardens in Northern Germany and likely associated with intrinsic garden characteristics on a small scale, such as hedges, as well as extrinsic factors on a local scale, such as the proportion of nearby woodland.

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Introduction

In Central Europe, the wood tick *Ixodes ricinus* Linnaeus, 1758 serves as a vector of several pathogenic agents, causing, e.g. Lyme disease, neorhlichiosis, and tick-borne encephalitis [1]. For people, the risk of infection with tick-borne pathogens depends on the pathogens' prevalence in the tick population, but also on the abundance of questing ticks and the probability of contact. An optimal habitat for *I. ricinus* ticks must provide sufficient humidity to prevent desiccation during the host-seeking and developing phases as well as abundant and accessible hosts for the subadult and adult stages [2]. The abundance of questing *I. ricinus* ticks in rural European sites is driven by various habitat-, landscape-, and climate-related predictor variables reflecting its complex ecology [3]. The larger the proportion of forest and the higher the abundance of trees and shrubs, the more questing *I. ricinus* nymphs appear abundant in these sites. The ecotone at the woodland edge seems to be the preferred habitat of these ticks [4,5]. There, the risk of contact may be greatest during recreational activities of people.

In addition, people may also be exposed to questing ticks in urban settings, such as parks, cemeteries, and private gardens [6–10]. Indeed, contact rates may be substantial in residential settings. Almost one-third of 8,043 Dutch study participants reported having acquired a tick bite in a private garden when gardening or playing [11]. This contact rate with ticks was second to that in the sylvatic setting. Most reports on ticks in residential gardens are anecdotal [12], and systematic studies on this kind of exposure site are scarce. In a study comparing public parks, periurban forests, and private gardens in the area of the city of Bonn, Germany, questing *I. ricinus* ticks were detected in 7 of 20 gardens; however, tick densities and details on particular garden features were not recorded [13]. Although people acquire tick bites in residential gardens, little is known about the characteristics that may support a tick population and whether these are features that may be actively modified with the intention to decrease the contact risk in this type of cultivated urban landscapes.

To determine whether particular features in and around private gardens support or limit the occurrence and abundance of questing *I. ricinus* ticks, we

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sampled ticks in residential gardens that differed in various intrinsic and extrinsic parameters. In particular, we recorded the number of questing nymphal and adult ticks on transects and related their occurrence and abundance to various garden characteristics, meteorological covariates, and landscape features in the vicinity of each garden.

Methods

Study site and sampling

Garden owners interested in having their garden sampled for ticks contacted us after an announcement in a local newspaper. Thus, the selection of gardens was biased by their owners' interest in ticks. We sampled questing *I. ricinus* ticks in 103 private gardens in the greater region of the city of Braunschweig, Germany, during the daytime hours from 8 April through 16 July 2015 (Figure 1). Within each garden, we identified transects to be sampled by aiming to include the variety of different structures present, such as lawns, patches of

other ground vegetation (e.g. ivy), flowerbeds and vegetable patches, hedges and aggregated shrubs, compost heaps, and accumulated deadwood. The transects were linear but followed the natural shape of the vegetation structure to allow for uniform sampling. For each transect, we recorded the length, the type of vegetation (lawn, groundcover, hedge or shrubs, flowerbed or vegetable patch, no vegetation), the density of vegetation (i.e. dense, sparse, no vegetation), the type of ground (i.e. bare soil, litter, or vegetated), the type of compost (i.e. open, closed, used for deadwood only, or no compost), and whether the transect was shaded (Figure 2). Each garden was sampled once. We sampled for ticks only when the vegetation was dry. Questing ticks were collected using a white flannel flag ($1.0 \times 1.5 \text{ m}^2$) attached to a rod, which was slowly drawn over the vegetation. At intervals of 20 steps, if the transect was longer than 20 steps, the flag was inspected and all ticks were collected. For each transect, ticks were counted and gathered into an individual tube containing tissue soaked with 70% ethanol. Ticks were

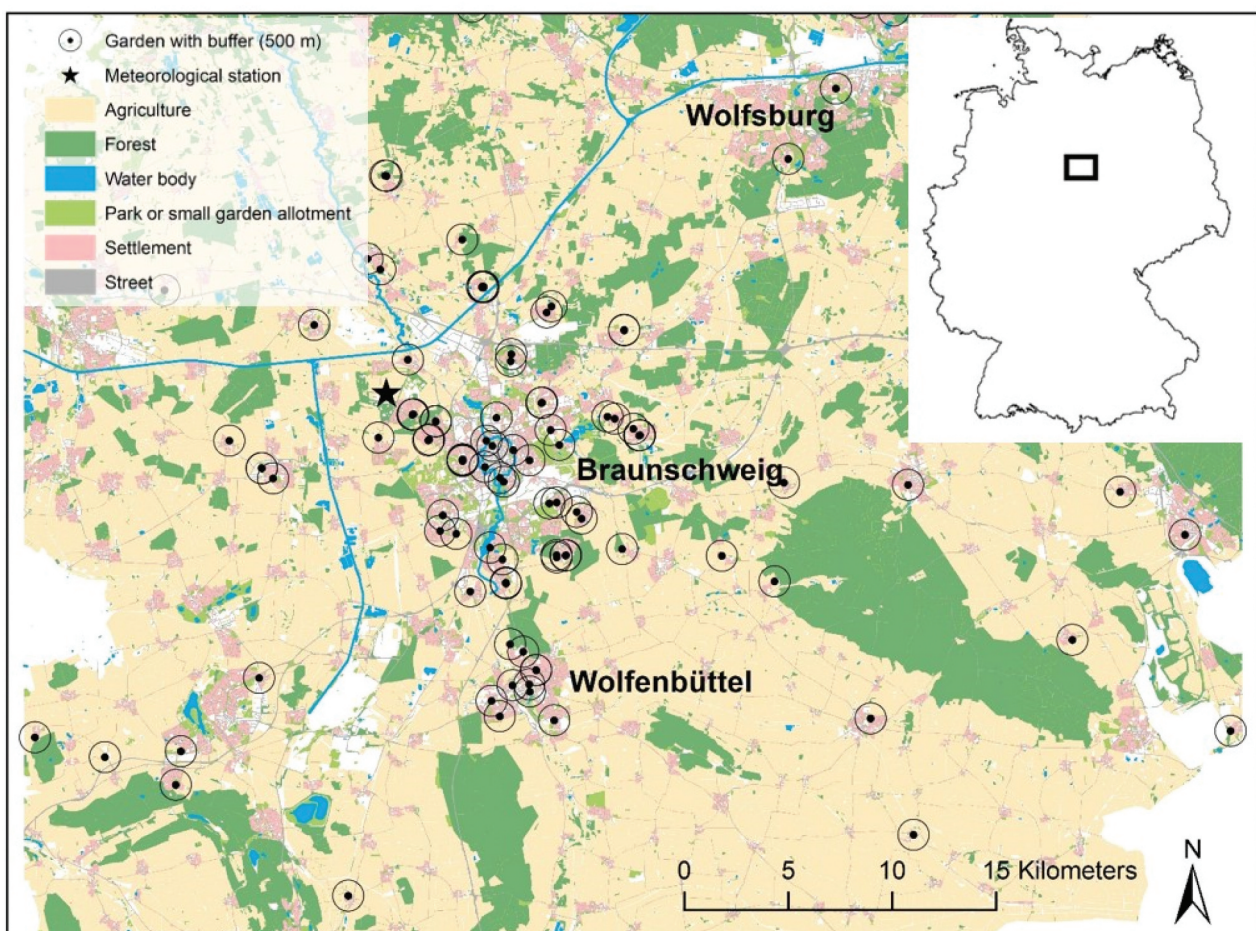


Figure 1. Study area with the 103 individual gardens (points with 500 m buffers) and land use units, such as agriculture, forest, water body, park or garden allotment, settlement, and street, which may affect the occurrence and abundance of questing *Ixodes ricinus* ticks. Source of land use data: German Authoritative Real Estate Cadastre Information System ALKIS® (LGLN - Landesamt für Geoinformation und Landesvermessung Niedersachsen, 2014).



Figure 2. Examples of the predictor variables on the garden level: vegetation type (a–e) including no vegetation (a), lawn (b), groundcover (c), hedge (d), and flower bed (e); vegetation density (f–h) including no vegetation (f), sparse vegetation (g), and dense vegetation (h); and ground type (i–k) including bare soil (i), litter (j), and vegetated ground (k).

identified to species and stage under the microscope; we did not differentiate *I. ricinus* from *I. inopinatus* which may be present in the Braunschweig region. The presence of larval ticks was noted but not included in the analysis.

Statistical modelling

We used mixed-effects generalized linear regression models to link potential predictor variables with either the occurrence of questing ticks (i.e. presence of at least one tick in a garden) or their abundance (i.e. sum of all ticks sampled in a garden). Although evidence suggests that nymphs and adult ticks respond somewhat differently to environmental predictors [14,15], we decided to combine both stages in our analyses, because the number of collected adult ticks did not justify a stage-specific consideration.

We chose a binomial error distribution (logit link) for the occurrence data. For the abundance analysis, we standardized the tick counts to a 5-m-transect length and chose a negative binomial error distribution and an observation-level random effect to account for overdispersion [16]. Since both, the occurrence and abundance data, were gathered in an unbalanced, nested sampling design (number of

Table 1. Characteristics of potential predictor variables, covariates, and their distribution in and around 103 private gardens in the Braunschweig region. Garden-level predictor variables (In Figure 2 are several examples) characterizing the sample transects ($n = 2,666$).

Predictor variable	Factor levels	No. transects
Vegetation type	no vegetation	141
	lawn	697
	groundcover	316
	hedge	744
	flower/vegetable bed	768
Vegetation density	no vegetation	189
	sparse	1,033
	dense	1,444
Ground type	bare soil	114
	litter	224
	vegetated	2,328
Compost type	no compost	2,471
	open	100
	closed	14
	deadwood	81
Shade	shaded	817
	not shaded	1,849

transects per garden ranged between 7 and 70, median number of transects was 22), we added the gardens as random intercept (block effect).

Potential predictor variables were divided into three thematic subsets (Tables 1–3): 1) garden level, 2) landscape level, and 3) meteorological variables. Predictors on the garden level characterized the transects by

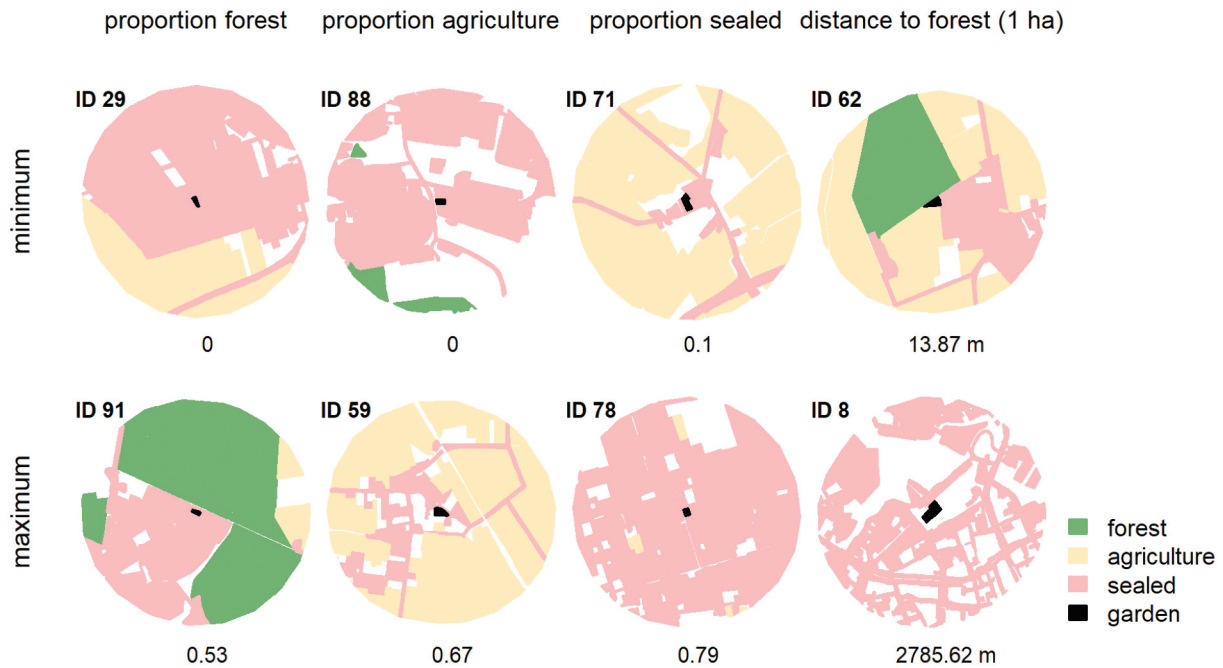


Figure 3. Sampled gardens with minimum and maximum values of the landscape predictor variables, such as forest, agriculture, and sealed area, in their 500 m buffers. Source of land use data: German Authoritative Real Estate Cadastre Information System ALKIS® (LGLN - Landesamt für Geoinformation und Landesvermessung Niedersachsen, 2014).

a classification of vegetation type, vegetation density, ground property, compost type, and shading (Table 1). Variables on the landscape level included the distance to or proportions of particular land use types considered relevant for the spatial distribution of questing *I. ricinus* [3,15]. We, therefore, included the proportion of the land use types forest, agricultural land, and sealed area surrounding the garden within a 500 m buffer (Figures 1, 3) and Euclidean distances to forest patches of at least 1 ha size, measured from the garden's centroid to the nearest edge of a forest polygon (Table 2, Figure 1). Vectorial land use data were derived from the German Authoritative Real Estate Cadastre Information System ALKIS® (LGLN – Landesamt für Geoinformation und Landesvermessung Niedersachsen, 2014). To account for the temporal variability of meteorological conditions during the sampling period spanning 14 weeks, we added meteorological variables as potential covariates (Table 3, Figure 4). Hourly meteorological data were obtained from the Climate Data Center (CDC, <https://cdc.dwd.de/portal/>) of the German National Meteorological Service (Deutscher Wetterdienst, DWD) for a station in the northwest of our study area (52°

17°29'N, 10°26'47'E, 81 m a.s.l.) and aggregated according to Kiewra et al. [14]. All numeric predictor variables were standardised (z-transformed) before entering the variable selection process.

We applied a multi-step variable and model selection procedure due to the high number of potential predictor variable combinations (Tables 1–3). In the first stage, we selected the best models within each of the three predictor variable subsets (Tables 1–3), and in the second stage, we combined the predictors of the best models from each subset into the final model. In both stages (i.e. within and across variable subsets), we applied the following three-step model-building procedure: (i) we avoided collinearity biasing the model estimates [17] by building alternative models for highly correlated predictor variables. To assess correlations between two numeric variables, we used Spearman's rank correlation coefficient (critical threshold = 0.5); for a numeric and a binary or multifactorial predictor variable, we used biserial or polyserial correlation (critical threshold = 0.5); and for associations between two factorial variables, we either used the χ^2 -test or Barnard testing if any expected

Table 2. Characteristics of potential predictor variables, covariates, and their distribution in and around 103 private gardens in the Braunschweig region. Landscape-level predictor variables. Proportions were determined within a 500 m buffer around the garden perimeter (see Figure 3 for gardens with minimum and maximum values of these variables).

Predictor variable	Proportion or distance		
	Minimum	Maximum	Median
Proportion of			
forest (ALKIS class 43,002)	0.00	0.53	0.01
agriculture (ALKIS class 43,001)	0.00	0.67	0.21
sealed area, i.e. building area (ALKIS class 41,001) and traffic area (ALKIS class 42,001)	0.10	0.79	0.38
Euclidean distance (m) to nearest forest patch >1 ha	13.8	2,785.6	609.6

Table 3. Characteristics of potential predictor variables, covariates, and their distribution in and around 103 private gardens in the Braunschweig region. Meteorological covariates observed at various times on or before the sampling day. Predictor variables were selected and aggregated according to Kiewra et al. [14].

Condition measured	Air temperature ¹ (°C)	Relative humidity ¹ (%)	Precipitation ² (mm)	Cumulative number of hours with	
				Air temperature >8°C	>8°C + relative humidity >60%
on same day					
minimum	6.0	53.5	0.0	7	1
maximum	21.9	83.5	6.3	24	23
median	13.7	65.4	0.0	23	11
2 days prior					
minimum	6.2	59.0	0.0	21	2
maximum	22.1	88.9	15.9	48	48
median	13.0	68.1	0.2	46	28
7 days prior					
minimum	4.3	58.3	0.0	28	8
maximum	23.6	80.5	24.1	168	152
median	12.9	69.3	9.6	155	86

¹measured at 2 m height; ² measured at 1 m height.

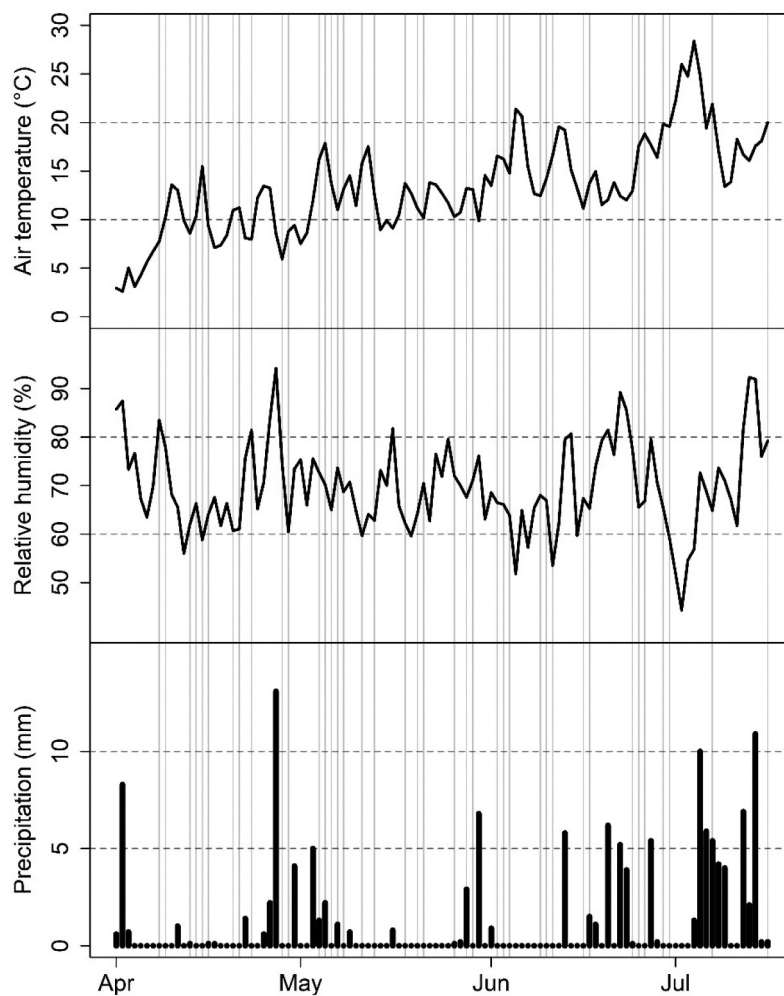


Figure 4. Time series of meteorological covariates during the sampling period in 2015: daily mean air temperature, daily mean relative humidity, and daily precipitation sum. Sampling dates are given as vertical grey lines.

value in the χ^2 -test was <5 (p -value threshold = 0.05), following Dormann [18]. (ii) For the resulting full model candidates, we applied a backwards variable selection using the Akaike information criterion (AIC [19]). And (iii), we ranked the reduced models according to their marginal R^2 [20] which depicts the explained variance of the fixed effects in the

mixed effects model. The predictors of the best models from each variable subset in stage 1 entered the three-step model-building procedure of stage 2. After these fully automated first two stages, we finally assessed the ecological plausibility of the resulting few best models by drawing partial dependence plots, and model parsimony by taking the number

of predictor variables into account. For occurrence models, we additionally calculated the ROC-AUC (area under the receiver operating characteristic curve) to account for the models' discriminatory performance. All analyses were performed in R (version 3.6.2) [21], using packages rgeos (version 0.4-2) [22], for geodata processing, psych (version 1.9.12.31) [23], polycor (version, 0.7-10) [24], and Barnard (version 1.8) [25] for detecting correlations and associations, as well as lme4 (version 1.1–21) [26], for mixed-effects modelling.

Results

In 103 private gardens, we flagged the vegetation on 2,666 transects spanning a total length of 26,872.4 m. The sampled transects varied in length (1–39 m) to cover the entire extent of each uniform vegetation type. We collected a total of 3,193 questing ticks on 956 transects harboring at least one tick, spanning a total length of 9,716.2 m (Table 4). Of these ticks, the majority (77.5%) were in the nymphal stage. Males constituted 46.4% of the adult ticks. Only *I. ricinus*-like ticks were found. Besides *I. ricinus* ticks, our collection may have included *I. inopinatus* which are hardly distinguishable from the former. One transect of 22.2 m harbored as many as 60 questing nymphs, as well as one male and one female adult. In one garden, we detected questing ticks on

Table 4. Distribution of questing *Ixodes ricinus* ticks on transects on which at least one tick was found, when sampling 2,666 transects in 103 private gardens in the Braunschweig region.

Stage	Number of questing ticks		Number of transects with at least one questing tick
	Total	Maximum per transect	
Nymphs	2,475	60	791
Males	334	16	217
Females	384	11	251
Total adults	718	27	371
Total ticks	3,193	62	956

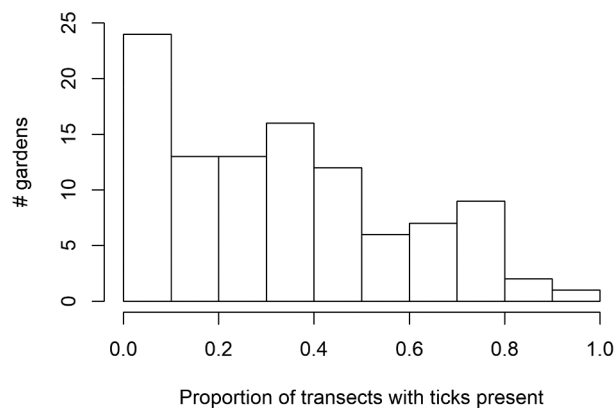


Figure 5. Proportion of transects with ticks present in the 103 sampled gardens.

30 of 32 transects. In another garden, ticks were found only on 1 of 27 transects. Ticks quested on more than 50% of the transects in 25 gardens (Figure 5). In contrast, we did not detect any questing ticks during our visit to 10 gardens with a total of 170 transects spanning a combined length of 1,769.3 m. On 24 transects, we noticed the presence of larval ticks (data not shown and not included in the analysis). Overall, we detected questing *I. ricinus* ticks in about 90% of the surveyed residential gardens.

According to the final model, the occurrence of questing nymphal and adult *I. ricinus* ticks on transects in residential gardens was affected by the vegetation type, proportion of forest in a 500 m buffer and the cumulative hours above 8°C on the day of sampling. The model yielded an explained variance of 0.31 (marginal R^2) with these three predictor variables and an ROC-AUC of 0.83, i.e. good discrimination. On transects at hedges, the relative risk of encountering a questing tick was four times that of a lawn transect (cf. odds ratio in Table 5, Figures 6a, 7). Groundcover or lacking vegetation doubled the relative risk compared to lawn (cf. odds ratios in Table 5). The effect of vegetable or flower beds on tick occurrence did not differ significantly from the effect of lawn, which was used as reference category. With an increasing proportion of forest in a 500-m vicinity of a garden, the relative risk of encountering ticks there increased by a factor of 1.2 for every 25% increment of forest. Cumulative hours of air temperatures above 8°C on the day of sampling decreased the relative risk by 0.8 per added hour (Figure 7b). Analysing solely nymphal ticks supported the same variables and only slightly modified the models' outcome (Table S1). Taken together, our occurrence model predicted the highest probability of questing ticks on transects with hedges or groundcover in gardens that are located in a neighborhood with large proportions of forest.

The final model for the abundance of nymphal and adult *I. ricinus* ticks questing in residential gardens identified the same set of predictors as the occurrence model, i.e. vegetation type, proportion of forest, and the cumulative number of hours above 8°C (Table 5). This model yielded a marginal R^2 of 0.23. Most ticks were collected on hedge transects, amounting to one tick questing on average every 10 m at this type of vegetation. Although this description of the effect of garden features on tick abundance may help to discern the differences, it is important to consider that questing ticks are not evenly distributed, but rather clumped. Transects characterized by groundcover or not covered by vegetation harbored on average a questing tick every 15 or 12 m, respectively. In contrast, ticks were rarest on lawn transects, a tick would quest there only every 32 m on average. The number of ticks questing per 5 m transect increased with an

Table 5. Occurrence and abundance of questing nymphal and adult *Ixodes ricinus* ticks in 103 private gardens in the Braunschweig region in the final generalized linear mixed-effects models and their performance. Reference for comparisons was lawn as vegetation type (intercept), $n = 2,666$ transects.

Variables	Occurrence model				Abundance model			
	Coefficient	SE	Significance ¹	Odds ratio (95% CI) ²	Coefficient	SE	Significance	1 tick per x meter ³
Intercept	-1.52	0.16	***	0.22 (0.16–0.30)	-1.87	0.13	***	32.1
Vegetation type:								
hedge	1.46	0.14	***	4.33 (3.32–5.65)	1.20	0.10	***	9.8
groundcover	0.87	0.17	***	2.40 (1.71–3.35)	0.77	0.12	***	15.0
no vegetation	0.77	0.23	***	2.17 (1.38–3.39)	0.99	0.16	***	12.1
flower/vegetable bed	0.19	0.14		1.21 (0.92–1.59)	0.11	0.11		29.2
Proportion of forest	0.73	0.12	***	1.07 ⁴ (1.05–1.08)	0.59	0.10	***	NA ⁵
Hours >8°C on sampling day	-0.22	0.11	*	0.81 (0.65–0.99)	-0.21	0.08	*	NA
R ² with fixed effects only			0.31		0.23			
R ² with fixed and random effects			0.68		0.67			
ROC-AUC			0.83		-			

¹Levels of significance: *** <0.001; ** <0.01; * <0.05; ² CI – Confidence interval; ³ Estimate analogous to odds ratio; ⁴ with each 10% increase; ⁵ NA – not applicable.

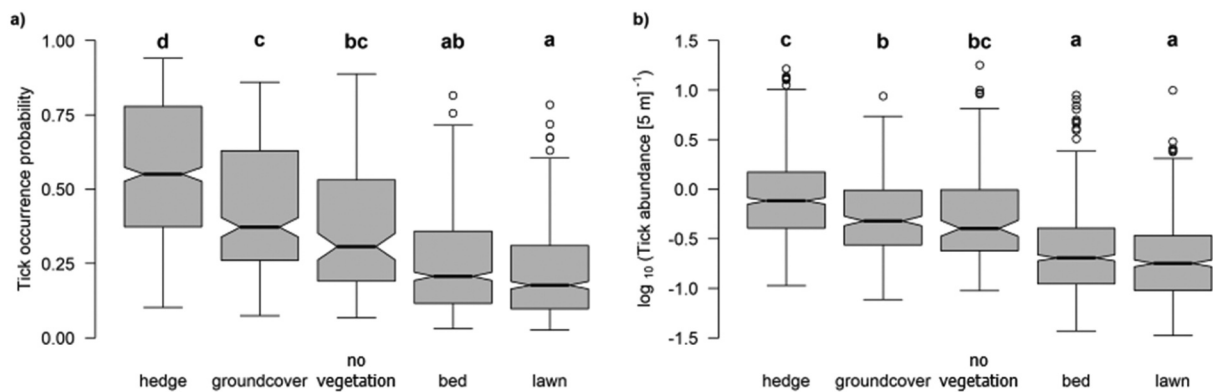


Figure 6. Comparison of the effects of various vegetation types on the occurrence probability (a) and abundance (b) of questing *Ixodes ricinus* ticks in private gardens in the Braunschweig region. The letters above the boxes denote effects that differ significantly from all other effects with different letters.

increasing proportion of forest surrounding the garden (Figure 8a, partial dependency plots based on model predictions). The cumulative hours of air temperature above 8°C on the sampling day negatively affected the number of questing ticks collected during our study period (Table 5, Figure 8b). Taken together, the abundance of questing ticks in a garden was positively influenced by hedges and groundcover as well as an increasing proportion of nearby forest, but negatively by the presence of lawn.

Discussion

Garden-specific predictors

The type of vegetation that characterized a transect appeared to affect the occurrence and abundance of questing wood ticks in residential gardens in Northern Germany. Hedges, in particular, increased

the likelihood of encountering a tick. Our definition of hedge included not only hedgerows but also non-linear clusters of shrubs, i.e. wooden perennial plants. The structural and functional properties of hedges and larger shrubs directly enhance the survival of ticks during phases of questing and development by providing a supportive microclimate [27]. Such vegetation structures may also indirectly affect the tick population by providing shelter and food for hosts of the subadult tick stages, such as rodents and birds [3]. The effect of hedges and shrubs on ticks is also observed in sylvatic and agricultural landscapes. Abundance of questing *I. ricinus* ticks increased with increasing shrub cover in oak stands [28]. When comparing the presence and abundance of *I. ricinus* ticks among structures adjacent to farmland in southern England, questing ticks were more likely and more abundant at hedges than on transects at arable land [5]. Hedges would, thus, constitute

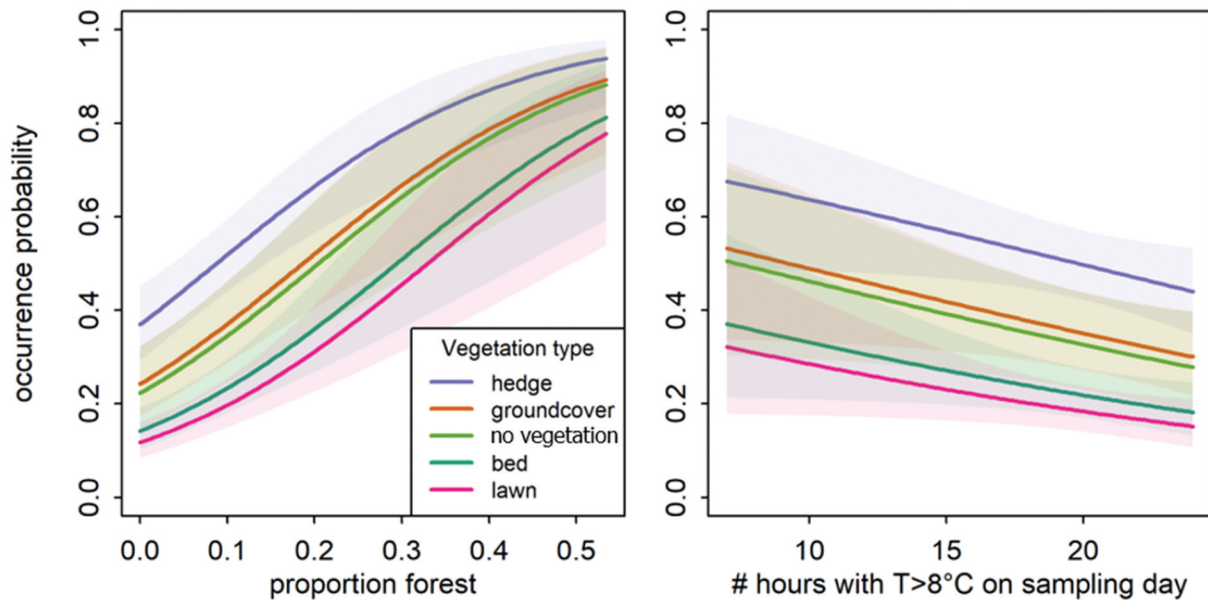


Figure 7. Modeled occurrence probabilities of questing *Ixodes ricinus* ticks in private gardens in the Braunschweig region, characterized by the vegetation type on the sampled transects, related to varying proportions of forest in a 500 m buffer around the garden (left) or related to varying numbers of cumulative hours of air temperatures $>8^{\circ}\text{C}$ on sampling day (right). Shaded areas around the lines display the 95% confidence interval.

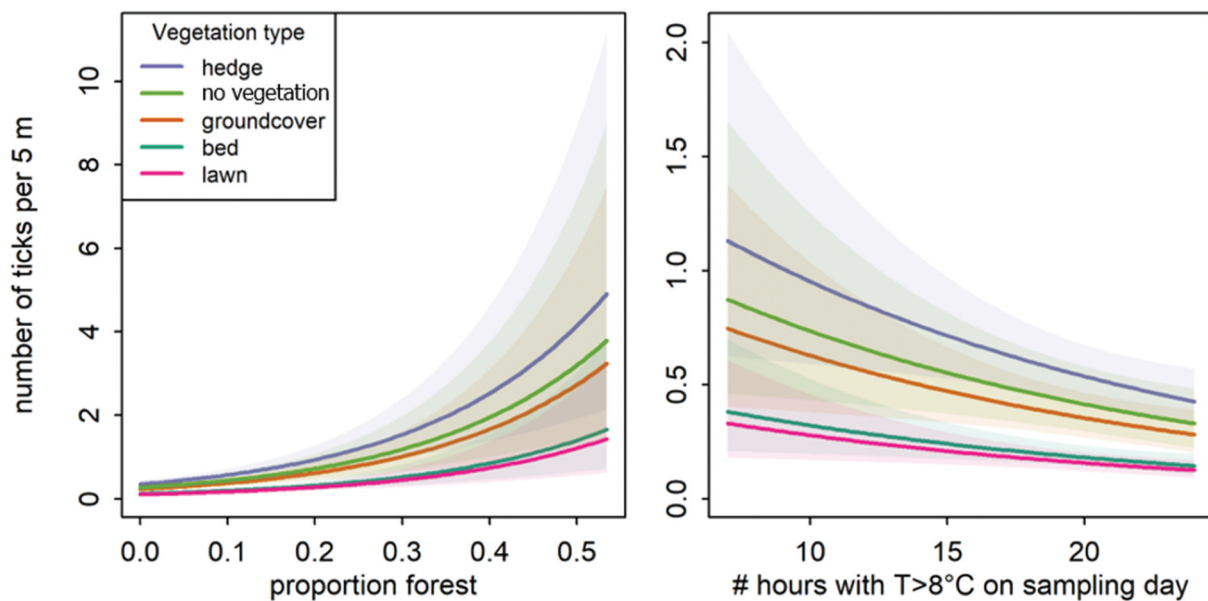


Figure 8. Modeled abundance of questing nymphal and adult *Ixodes ricinus* ticks on transects, characterized by the vegetation type, in private gardens in the Braunschweig region, related to varying proportions of forest in a 500 m buffer around the garden (left), or related to varying numbers of cumulative hours of air temperatures $>8^{\circ}\text{C}$ (right). Shaded areas around the lines display the 95% confidence interval.

dispersules for tick hosts [3] and ticks may be dispersed from these sites by frequenting hosts. In contrast to hedges, lawns were the most unlikely of all vegetation types in private gardens to harbor ticks. Similarly, nymphal and adult *Ixodes dammini* (= now also called *I. scapularis*) ticks are the least abundant on lawns when compared to ornamental vegetation, unmaintained ecotonal edges, and woodlots on residential properties in Westchester County, NY, USA [29,30]. In the rural landscape, too, significantly fewer questing ticks were observed on a sun-exposed

meadow and a pasture than on densely vegetated fallow land [31]. Because ticks are likely more intensely exposed to desiccating conditions on a well-maintained lawn than in the shade of hedges and shrubs, they are more likely to be encountered in densely vegetated parts of private gardens.

Somewhat unexpectedly, we noticed that questing ticks on transects not covered by vegetation were as likely as on transects with short groundcover, such as ivy. Of the 141 transects without vegetation, 51 transects harbored ticks, adding to a total of 177 ticks. Interestingly,

80% of these tick-infested transects (41 of 51) were covered by leaf litter and 84% of all ticks collected on transects without vegetation (149 of 177) were sampled from transects with leaf litter. The predictor 'ground type', which included litter, had been eliminated during the stepwise model generation due to collinearity between the categorical garden predictors, as inclusion of this predictor would have resulted in a loss of model performance. Nevertheless, leaf litter appeared to affect the occurrence and abundance of ticks in non-vegetated areas of gardens. *Ixodes ricinus* ticks intersperse periods of questing in an exposed position on the vegetation with those on the ground near the soil to reconstitute their water balance [32,33]. Thus, they retreat into the leaf litter, especially during desiccating weather conditions. The composition and condition of this humus layer also affects the nymphal density, because the moder type, consisting of fragmented leaves, is associated with more ticks than the mull type, consisting mainly of whole leaves [34]. The presence of leaf litter may also support the overwintering survival of ticks, as has been demonstrated for nymphs of the related tick species, *Ixodes scapularis*, prevalent in northeastern America [35]. In addition, sylvatic study plots with deeper layers of leaf litter or residential study plots with artificially accumulated leaf litter harbor significantly augmented numbers of these ticks [27,36]. Thus, particular intrinsic characteristics of residential gardens, such as hedges, ground-cover, and litter as well as combinations thereof, appeared to support questing ticks.

Surrounding landscape

Characteristics of the surrounding landscape affected whether questing ticks were present and abundant in a garden. The likelihood of encountering ticks in a garden as well as their abundance increased with the proportion of forest in the immediate garden's neighbourhood of 500 m. A garden's distance to a forest may likely also affect questing ticks, but the Euclidean distance to the nearest forest as predictor has been eliminated in our models due to collinearity. In a study comparing public parks, periurban forests, and private gardens in the area of the city of Bonn, Germany, questing *I. ricinus* ticks were detected in only 7 of 20 gardens, and all of these properties were in suburban settings with a neighboring forest [13]. Similarly, more forest cover in the surroundings increased tick abundance when environmental drivers were examined in rural European sites [3]. On a gradient of urban parks to suburban forests, the level of urbanization lowers the density of questing ticks, as does the cost distance for potential tick hosts, but cost was calculated for the relatively large roe deer [37]. Other synurbanized animals potentially serving as hosts to adult ticks, such as cats, hedgehogs, or foxes, with their various life-history traits were not examined. However, any suitable tick host that

frequently moves between these habitats, such as birds, rodents, hedgehogs, or cats, would be likely to introduce these generalist ticks into gardens. With an increasing proportion of sylvatic habitat in the vicinity, this transport likelihood ought to increase [38]. Woodland may be considered a source of ticks and more open landscape types, such as meadow [39] or even a garden's lawn, as sink. Gardens are rarely isolated but are connected to the surrounding habitat and serve, themselves, as a connecting element. Particularly in the urban landscape, the green infrastructure realized on residential property may increase the connectivity between suitable habitats for animals [40,41] that serve as tick hosts and may support dispersion of ticks by host-mediated movement. In addition, due to behavioral adaptation and anthropogenic resource subsidies, synurbanized animals may be somewhat less sensitive to particular barriers than individuals of the same species in the rural landscape [42], thus efficiently transporting ticks within the urban landscape. The influx and efflux of ticks during their blood meal on agile hosts would be considered constant and may also be affected by behavioral preference of particular host species to garden-specific characteristics. On a local scale, a garden appeared to be more suitable for ticks with an increasing proportion of forest in the immediate vicinity.

Meteorological covariates

We considered various meteorological covariates in our models, because our survey was not conducted simultaneously at the various sites. We sampled ticks throughout a period of 100 days during their main period of activity. Therefore, meteorological covariates may have exerted a confounding effect on our sampling [43]. We did not consider the spatial variability in microclimatic meteorological data, as it was not feasible to measure micrometeorological conditions before or during our visit to each garden. Instead, we explored the effect of meteorological condition depicting the general weather situation in our models. Of the covariates included, such as air temperature, relative humidity, precipitation, and cumulative numbers of hours above 8°C as well as those above 8°C and above 60% relative humidity at various time points before sampling (similar to [14]), sums of hours above 8°C on the day of sampling negatively affected the occurrence and abundance of questing ticks. Thus, it may be that we slightly underestimated the presence and abundance of questing ticks in those gardens that were sampled on warmer days. Although the macroclimate may explain only a small fraction of the variation, temperature sums seem to be macroclimatic drivers for tick abundance at local scales in combination with habitat and landscape predictors [3]. Micrometeorological conditions, in contrast, may be more favorable for ticks in sites that are cooled by a nearby forest than those in urban heat islands. An

ideal macrohabitat, such as a forest in the vicinity, and a particular microhabitat, such as a shrub layer, may serve as buffers moderating the microclimate experienced by questing ticks and increasing the habitat suitability [3,27]. The general weather situation, particularly cumulative hours above 8°C, affected the sampling effort and should be considered in the sampling design.

Anthropogenic influence and recommendations

Similar to results from a Europe-wide study in rural settings [3], predictors related to the macro- and microhabitat, i.e. extrinsic and intrinsic features of the garden, seemed to drive the occurrence and abundance of questing ticks in the residential urban setting in our Northern German site. Some gardening practices, especially frequent watering, may support habitat conditions – particularly microclimatic conditions – for ticks. Accumulating leaf litter or neglected areas in the garden may similarly enhance the risk of encountering ticks there [6,36]. In contrast, keeping the vegetation height of lawn areas short by frequent mowing may substantially reduce the habitat suitability for ticks. We did not evaluate whether a garden was well maintained or contained numerous semi-natural elements because these are somewhat subjective criteria. Residential gardens, as part of the green urban infrastructure, are of great importance for ecosystem services [44,45]. Less intensely managed or even neglected areas in gardens, composts, leaf litter, etc., serve as habitat for a variety of vertebrates and invertebrates and, thereby, contribute to urban biodiversity. The overlap of habitat suitability for beneficial and harmful organisms constitutes a considerable tradeoff between the benefits of urban ecosystem services and the potential or perceived health risks associated with the presence of questing ticks [46,47]. Thus, it is important to raise awareness that particular areas in a garden may be more likely to harbor ticks than others and that garden owners are well advised to check themselves routinely for ticks. Those garden owners interested in determining the presence of questing ticks on their property may drag a white cloth over the vegetation in various areas to detect ticks. Garden owners who strive to reduce the number of ticks on their premises may purposefully limit the amount of litter, groundcover, and vegetation height in highly frequented areas. Whether particular characteristics of hedges affect the presence of ticks is a focus of another current study. We conclude that *I. ricinus* ticks are frequent in residential gardens in Northern Germany and likely associated with intrinsic garden characteristics on a small scale, such as hedges and groundcover, as well as extrinsic factors on a local scale, such as the proportion of nearby sylvatic landscape.

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References

- [1] Richter D, Matuschka F-R. “*Candidatus* Neoehrlichia mikurensis”, *Anaplasma phagocytophilum*, and Lyme disease spirochetes in questing European vector ticks and in feeding ticks removed from people. *J Clin Microbiol.* 2012;50:943–947.
- [2] Matuschka F-R, Spielman A. The emergence of Lyme disease in a changing environment in North America and Central Europe. *Exp Appl Acarol.* 1986;2:337–353.
- [3] Ehrmann S, Liira J, Gärtner S, et al. Environmental drivers of *Ixodes ricinus* abundance in forest fragments of rural European landscapes. *BMC Ecol.* 2017;17:31.
- [4] Hansford KM, Fonville M, Gillingham EL, et al. Ticks and *Borrelia* in urban and peri-urban green space habitats in a city in southern England. *Ticks Tick-Borne Dis.* 2016;8:352–361.
- [5] Medlock JM, Vaux AGC, Hansford KM, et al. Ticks in the ecotone: the impact of agri-environment field margins on the presence and intensity of *Ixodes ricinus* ticks (Acari: Ixodidae) in farmland in southern England. *Med Vet Entomol.* 2020;34:175–183.
- [6] Hornok S, Meli ML, Gönczi E, et al. Occurrence of ticks and prevalence of *Anaplasma phagocytophilum* and *Borrelia burgdorferi* s.l. in three types of urban biotopes: forests, parks and cemeteries. *Ticks Tick-Borne Dis.* 2014;5:785–789.
- [7] Jore S, Vanwambeke SO, Slunge D, et al. Spatial tick bite exposure and associated factors in Scandinavia. *Infect Ecol Epidemiol.* 2020;10:1764693.

- [8] Matuschka F-R, Endepols S, Richter D, et al. Risk of urban Lyme disease enhanced by the presence of rats. *J Infect Dis.* 1996;174:1108–1111.
- [9] Nelson C, Banks S, Jeffries CL, et al. Tick abundance in South London parks and the potential risk for Lyme borreliosis to the general public. *Med Vet Entomol.* 2015;29:448–452.
- [10] Vollack K, Sodoudi S, Névir P, et al. Influence of meteorological parameters during the preceding fall and winter on the questing activity of nymphal *Ixodes ricinus* ticks. *Int J Biometeorol.* 2017;61:1787–1795.
- [11] Mulder S, van Vliet AJH, Bron WA, et al. High risk of tick bites in Dutch gardens. *Vector Borne Zoonotic Dis.* 2013;13:865–871.
- [12] Petney TN, Skuballa J, Pfäffle M, et al. The role of European starlings (*Sturnus vulgaris* L.) in the dissemination of ticks and tick-borne pathogens in Germany. *Syst App Acarol.* 2010;15:31–35.
- [13] Maetzel D, Maier WA, Kampen H. *Borrelia burgdorferi* infection prevalences in questing *Ixodes ricinus* ticks (Acari: Ixodidae) in urban and suburban Bonn, western Germany. *Parasitol Res.* 2005;95:5–12.
- [14] Kiewra D, Kryza M, Szymanowski M. Influence of selected meteorological variables on the questing activity of *Ixodes ricinus* ticks in Lower Silesia, SW Poland. *J Vector Ecol.* 2014;39:138–145.
- [15] Li S, Heyman P, Cochez C, et al. A multi-level analysis of the relationship between environmental factors and questing *Ixodes ricinus* dynamics in Belgium. *Parasites Vectors.* 2012;5:149.
- [16] Browne WJ, Subramanian SV, Jones K, et al. Variance partitioning in multilevel logistic models that exhibit overdispersion. *J R Stat Soc Ser A Stat Soc.* 2005;168:599–613.
- [17] Dormann CF, Elith J, Bacher S, et al. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography.* 2013;36:27–46.
- [18] Dormann CF. *Parametrische Statistik. Verteilungen, maximum likelihood und GLM in R.* 2nd ed. Berlin: Springer Verlag; 2017. p. 363 pp.
- [19] Akaike H. A new look at statistical model identification. *IEEE Trans Automat Contr.* 1973;19:716–723.
- [20] Nakagawa S, Johnson PCD, Schielzeth H. The coefficient of determination R^2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *J Roy Soc Interface.* 2017;14:20170213.
- [21] R Core Team. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing; 2019. URL <https://www.R-project.org/>
- [22] Bivand R, Rundel C (2018) Rgeos: interface to Geometry Engine - Open Source ("GEOS"): r package version 0.4-2, <https://CRAN.R-project.org/package=rgeos>.
- [23] Revelle W. 2019. Psych: procedures for psychological, psychometric, and personality research. Evanston, Illinois: Northwestern University. R package version 1.9.12: <https://CRAN.R-project.org/package=psych>
- [24] Fox J (2019). Polycor: polychoric and Polyserial Correlations, R package version 0.7-10, <https://r-forge.r-project.org/projects/polycor/>
- [25] Erguler K, Smith-Unna SE, Waldock J. Barnard: Barnard's Unconditional Test. R package version 1.8. PLoS ONE. 2016;11: <https://github.com/kerguler/Barnard>
- [26] Bates D, Maechler M, Bolker B, et al. Fitting linear mixed-effects models using lme4. *J Stat Softw.* 2015;67:1–48.
- [27] Schulze TL, Jordan RA. Influence of meso- and micro-scale habitat structure on focal distribution of sympatric *Ixodes scapularis* and *Amblyomma americanum*. *J Med Entomol.* 2005;42:285–294.
- [28] Tack W, Madder M, Baeten L, et al. The abundance of *Ixodes ricinus* ticks depends on tree species composition and shrub cover. *Parasitol.* 2012;139:1273–1281.
- [29] Frank DH, Fish D, Moy FH. Landscape features associated with Lyme diseases risk in a suburban residential environment. *Landscape Ecol.* 1998;13:27–36.
- [30] Maupin GO, Fish D, Zultowsky J, et al. Landscape ecology of Lyme disease in a residential area of Westchester County, New York. *Am J Epidemiol.* 1991;133:1105–1113.
- [31] Richter D, Matuschka F-R. Differential risk of Lyme disease along hiking trail, Germany. *Emerg Infect Dis.* 2011;17:1704–1706.
- [32] Lees AD, Milne A. The seasonal and diurnal activities of individual sheep ticks (*Ixodes ricinus*). *Parasitol.* 1951;41:180–209.
- [33] Randolph SE, Storey K. Impact of microclimate on immature tick-rodent host interactions (Acari: Ixodidae): implications for parasite transmission. *J Med Entomol.* 1999;36:741–748.
- [34] Goldstein V, Boulanger N, Schwartz D, et al. Factors responsible for *Ixodes ricinus* nymph abundance: are soil features indicators of tick abundance in a French region where Lyme borreliosis is endemic? *Ticks Tick-Borne Dis.* 2018;9:938–944.
- [35] Linske MA, Stafford KC III, Williams SC, et al. Impacts of deciduous leaf litter and snow presence on nymphal *Ixodes scapularis* (Acari: Ixodidae) overwintering survival in coastal New England, USA. *Insects.* 2019;10:227.
- [36] Jordan RA, Schulze TL. Artificial accumulation of leaf litter in forest edges on residential properties via leaf blowing is associated with increased numbers of host-seeking *Ixodes scapularis* (Acari: Ixodidae) nymphs. *J Med Entomol.* 2020;57:1193–1198.
- [37] Heylen D, Lasters R, Adriaenssens F, et al. Ticks and tick-borne diseases in the city: role of landscape connectivity and green space characteristics in a metropolitan area. *Sci Total Environ.* 2019;671:941–949.
- [38] Diuk-Wasser M A, VanAcker M C, Fernandez M P. Impact of land use changes and habitat fragmentation on the eco-epidemiology of tick-borne diseases. *Journal of Medical Entomology.* 2021;58(4):1546–1564. DOI:10.1093/jme/tjaa209
- [39] Hoch T, Monnet Y, Agoulon A. Influence of host migration between woodland and pasture on the population dynamics of the tick *Ixodes ricinus*: a modelling approach. *Ecol Mod.* 2010;221:1798–1806.
- [40] App M, Strohbach MW, Schneider A-K, et al. Making the case for gardens: estimating the contribution of urban gardens to habitat provision and connectivity based on hedgehogs (*Erinaceus europaeus*). *Landsc Urban Plan.* 2022;220:104347.
- [41] Goddard MA, Dougill AJ, Benton TG. Scaling up from gardens: biodiversity conservation in urban environments. *Trends Ecol Evol.* 2010;25:90–98.
- [42] Kimmig SE, Beninde J, Brandt M, et al. Beyond the landscape: resistance modelling infers physical and behavioural gene flow barriers to a mobile carnivore

- across a metropolitan area. *Mol Ecol.* **2020**;29:466–484. DOI:[10.1111/mec.15345](https://doi.org/10.1111/mec.15345).
- [43] Daniel M, Maly M, Danielovaa V, et al. Abiotic predictors and annual seasonal dynamics of *Ixodes ricinus*, the major disease vector of Central Europe. *Parasites Vectors.* **2015**;8:478.
- [44] Lepczyk CA, Aronson MFJ, Evans KL, et al. Biodiversity in the city: fundamental questions for understanding the ecology of urban green spaces for biodiversity conservation. *BioScience.* **2017**;67:799–807.
- [45] Löhmus M, Balbus J. Making green infrastructure healthier infrastructure. *Infect Ecol Epidemiol.* **2015**;5:30082.
- [46] Fischer LK, Neuenkamp L, Lampinen J, et al. Public attitudes toward biodiversity-friendly greenspace management in Europe. *Conserv Let.* **2020**;2020:e12718.
- [47] Lerman SB, D’Amico V. Lawn mowing frequency in suburban areas has no detectable effect on *Borrelia* spp. vector *Ixodes scapularis* (Acari: Ixodidae). *PLoS ONE.* **2019**;14(4):e0214615. DOI:[10.1371/journal.pone.0214615](https://doi.org/10.1371/journal.pone.0214615)