Forest classes and tree cover gradient: tick habitat in encroached areas of southern Norway

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Abstract

Forest, in particular deciduous forest, is a key element in determining areas with a high probability of tick presence. The way forest is generally monitored may be ill suited to some landscapes where *Ixodes ricinus* is found, as forest is usually characterised using crisp land cover classes. However, tree vegetation can be found outside of forests and continuous gradations of tree density can be found a variety of landscapes. In this paper we investigate the probability of tick presence in southern Norway using landscape description based both on land cover classes and continuous data describing the tree cover fraction. Both perspectives on the landscape are significant in the logistic model, indicating that the usual approach based solely on land cover classes may not be comprehensive enough in capturing tick habitat, and characterising the landscape with variables focused on single specific elements may be insufficient.

Keywords

Ixodes ricinus, forest land cover, landscape structure, forest gradient

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Introduction

The main landscape features of *Ixodes ricinus* habitat have been studied with diverse tools and in diverse environments (e.g., De Keukeleire et al., 2015; Dobson et al., 2011; Li et al., 2012). One recurrent element is the importance of forests. Woodlands are the natural habitat for *I. ricinus* (Barandika et al., 2006; Pietzsch et al., 2005; Tack et al., 2012) as they provide a favourable environment for questing and off-host survival, and a range of hosts. The litter, particularly in deciduous forests, provides an appropriately moist environment for ticks when they are off the host and not questing (Gassner et al., 2011; Randolph and Storey, 1999). *Ixodes ricinus* ticks have also been found in other vegetated areas, such as pasture, meadows, and fallow land (Richter and Matuschka, 2011). Small mammals and wild cervids circulate between woodlands, ecotones and pasture areas and this movement of animals affects the distribution of *I. ricinus* (Boyard et al., 2008; Hoch et al., 2010; Li et al., 2014; Ruiz-Fons and Gilbert, 2010). Still, forest is often seen as the primary habitat, and many studies view forests as discrete elements of the landscape that can be clearly delineated. This is, however, not always the case in locations where *I. ricinus* has been recorded.

In many areas of Europe, including Norway, there is a continuous gradation of tree density ranging from dense forest to sparse woody vegetation with areas of rough grazing. Many of these areas would often not be classified as forest, neither formally nor through remote sensing approaches. However, the presence of hosts and of sufficiently developed vegetation, including woody vegetation, can make those areas suitable for ticks. This can lead to identifying both 'forest' and 'non-forest' as suitable tick habitat, leading therefore to somewhat confusing results. Adding to that, in various areas of Europe, including Norway, the decreasing intensity of grazing by livestock, abandonment of grazed areas, bush encroachment and afforestation (Austrheim et al., 2011; Ericsson et al., 2000; Estel et al., 2015; Meyfroidt and Lambin, 2011; Navarro and Pereira, 2015) mean that the limit between forests (as a dense arrangement of trees) and other areas with woody vegetation is increasingly blurred, and that tick-suitable areas may be found outside of fully fledged forests, in places with a well-developed vegetation that may not be recorded as forest. Wild animals may consume some of the vegetation no longer consumed by livestock, but cervids tend to browse on woody fodder, rather than graze on graminoids, therefore they do not necessarily maintain the vegetation in the same way (Austrheim et al., 2011). Such changes have been identified as a driving force for tick expansion in Europe (Medlock et al., 2013; Jore et al. 2014). Rough grazing, heather and other grassy or bushy vegetation have also been found suitable in some areas (Medlock et al., 2013; Tack et al., 2011). In Norway, grazing by sheep was found to reduce tick abundance, probably by keeping vegetation lower and sparser (Steigedal et al., 2013), and landscapes characteristics describing encroachment were associated to tick presence in our study area (Jore et al., 2014) and to the presence of tick-borne encephalitis in Latvia (Vanwambeke et al., 2010).

This calls for a more complete perspective of the landscape, which is able to describe habitats suitable for ticks in a more comprehensive and nuanced fashion. The human perspective on landscapes tends to be categorised, using discrete land cover classes. This is useful for many purposes but adopting a more functional perspective of the landscape, which accounts for the organisms' functions, might improve the understanding of the role of the landscape environmental features on the vector presence or absence (Hartemink et al., 2014). In the case of ticks, it is not the presence of forest itself that makes the habitat suitable, but rather an assemblage of resources that allows ticks to fulfil their functions: from reproduction and egg-laying to questing, feeding and diapause. The resources associated with these functions would be, litter, low vegetation (grassy or bushy), and hosts. Identifying tick habitat therefore requires, ideally, identifying these resources in the landscape.

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In this study, we investigated the landscape determinants of tick presence in an area of Norway where forests are not clearly separated from other landscape features, such as rough grazing or abandoned grazing land. For this purpose, we processed remotely sensed data in two ways: characterising the landscape in discrete elements corresponding to land cover classes, and mapping tree cover by pixel as a continuous variable. It is known that factors other than the landscape, such as climate and host availability, influence tick habitat suitability (Randolph, 2008; Jore et al., 2014), particularly at northern latitudes close to the limit of the niche of the tick (Jaenson et al., 2012; Jore et al., 2014). This study covers three ecologically diverse areas which differ with respect to historical tick presence, topography, demography, bush encroachment, presence of cervids and degree of climate change.

Material and methods

Study area

Ticks were collected from municipalities in Hordaland (Etne and Vindafjord), Rogaland (Time, Hå, Bjerkeim and Sandnes), Aust-Agder (Bygland), and Telemark (Fyresdal, Vinje and Kviteseid) (Figure 1). This area is at the northern fringe of the distribution of *I. ricinus* in Europe and tick presence has been expanding there. The topography in Telemark and Aust-Agder is more pronounced, and more intensive farming is concentrated at the valley bottoms, with some extensive pastures and rough grazing in areas of higher elevation. The valley sides are often covered by dense boreal forest, mostly consisting of spruce, with pine at higher altitudes, but there are also large areas of bare rock. Previously published tick distribution maps showed tick absence for the study area in the 1980s, but a recent tick distribution map indicated tick presence. Historical serological evidence indicates that ticks may have been present in those less-surveyed areas as far back as the 1970s in some areas (Jore et al., 2014). The coastal municipalities in southwest Rogaland are intensively used for agriculture and have undergone little land abandonment over the past decades, except in the foothills where some bush encroachment can be noted. Ticks also used to be absent from most of these municipalities, but have recently been reported (Jore et al., 2011, 2014; Mehl, 1983; Tambs-Lyche, 1943). The municipalities in northern Rogaland and Hordaland have a rugged and moist landscape with agriculture and pastures in the fertile bottoms of valleys, and broadleaf forest on the slopes. The two municipalities in Hordaland present a more sheltered fjord and valley districts where *I. ricinus* has been common since the first surveys back in 1940s (Tambs-Lyche, 1943).

Remotely sensed land cover and forest cover

The entire archive of Landsat 4/5 TM and Landsat ETM+ (30-m resolution) taken in June, July or August was acquired for the year 2010 from the GLOVIS portal (Path/row combinations 197/19, 198/18, 198/19, 198/20, 199/18, 199/19, 200/18, 200/19 and 201/19). Digital numbers were converted to top of the atmosphere reflectance. All images were resampled to a common coordinate system (WGS UTM Zone 32N). Clouds and their shadows, snow and water were masked out and the images were topographically corrected. Finally, images were mosaicked and radiometrically normalised (relatively). The mosaic image of 2010 was subsequently processed in two ways: first using a supervised hard-classifier and secondly a soft classification on the percentage of forest.

The hard classification relied on Support Vector Machine (Huang et al., 2002). A hierarchical approach was used in which the pixels were first classified in forest/non-forest, and then a more

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detailed classification was carried out on each set of pixels. The hard classification resulted in three groups of classes (Table 1), (I) non-forest vegetation, (II) artificial areas, and (III) forest vegetation. Class I was further divided into (1) alpine vegetation and non-vegetated land, (2) non-forested land below the forest limit (i.e. at altitudes low enough for forest growth; it includes heath, thicket, meadows, pioneer vegetation), (3) wetlands, (4) cultivated land, and (5) pastures. Class III was subdivided into (7) deciduous forest, (8) pine forest, and (9) spruce forest. The classification used the Landsat bands, as well as the Normalized Difference Vegetation Index and four additional layers: elevation and slope extracted from a digital elevation model, a layer indicating wetlands (both datasets from the Norwegian Mapping Authority, Digital Norway, www.geonorge.no), and the soil type (Norwegian Geological Survey, www.ngu.no). The classifications were trained using the 'Norwegian area frame surface of land cover and outfield land resources' conducted by the Norwegian Forest and Landscape Institute (AR18X18). Details of this survey are provided in Strand (2013).

The percentage of each pixel occupied by tree vegetation was estimated with Random Forest (Breiman, 2001), also trained using the AR18X18 data as training data and the Landsat bands as explanatory variables. The result is a continuous variable, indicating for each image pixel, the fraction that is covered by trees. With most ligneous vegetation being small and shrub-like trees, this fraction provides a more gradual representation of the landscape compared to the crisp land cover classes.

Buffers of 500-m radius were constructed around each tick collection point (see below) and landscape variables were extracted for each buffer. The landscape composition was described using the proportion of each land cover class (detailed legend). The landscape structure was described using the aggregated level of the land cover legend (Table 1). For classes I and III, the mean patch area, and the mean patch Shape Index were computed. The Shape Index compares a patch to a compact form, in the case of raster data, to a square(McGarical et al., 2012). Finally, the mean and standard deviation of the tree cover were computed within each buffer. All variables tested are listed in Table 2.

Field collections of ticks

Two field collections of ticks took place in June and September 2013 in south-western Norway, which match observed tick phenology at low altitudes in south-western Norway (no peaks were observed at higher altitudes) (Qviller et al., 2014), all life-stages considered. Sites were selected to match the study area of a previous study (Jore et al., 2014) in which three districts were selected to cover a range of environments with regard to historical tick presence, topography, landscape, human and livestock presence. Not all farms included in Jore et al. (2014) could be covered, but the field missions intended also to validate the satellite data processing and therefore covered the range of conditions encountered in the study area. The number of sites covered was determined by time constraints. Coordinates at the sampling locations were recorded using a hand held GPS. Questing ticks were collected by dragging a 1x1m cotton cloth on the vegetation (flagging). Each drag extended over 2.5 m before the underside of the blanket was examined and repeated 40x to give a total sampled area of 100 m^2. Larvae, nymphs and adults were collected. During field work, collected ticks were stored in freezer bags on crushed ice, and later a normal freezer (-18°C), and eventually transferred to -70°C in the National Veterinary Institute's freezer after the field mission, to allow for future identification of pathogens. Ticks were identified by species and life stage using reference keys, based on morphological characteristics of the coxae, palp, scutum and genital and anal grooves (Arthur, 1963).

Statistical analysis

The effects of each environmental variable on the probability of tick presence were first tested individually using bivariate logistic regression. Multivariable models were built for land cover class

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variables, tree cover variables, and for land cover class variables and tree cover variables together. Models were built by introducing each variable significant at the 0.15 level in a stepwise backward model, in which only the variables significant at the 0.05 level were kept. Each environmental variable that came out not significant after testing was then introduced in the multivariable model in order to check for interaction and confounding. All models were compared using Akaike's Information Criterion (AIC), in particular the difference between the AIC values, with values <2 indicating equivalent models. The final model was also evaluated using Nagelkerke's pseudo-R^2. The correlations between the variables significant in the multivariable model and the other independent variables were examined using Spearman's rho. All analyses were run using SPSS.

Results

Tick collections

A total of 1586 *I. ricinus* ticks (larvae, nymphs and adults) was collected in 22 locations. Twenty-one locations were visited in September and 18 in June (17 were visited twice). In June, ticks were sampled from seven locations and an average of 31.4 larvae (range 0-129), 8.9 nymphs (0-23), and 2.2 adults (0-8) were found in places where ticks were present. In September, ticks were sampled from eight locations, and an average of 14.4 larvae (0-60), 25.4 nymphs (0-119) and 0.2 adults (0-1) were found. Overall, 17 sites were sampled during both field campaigns (June and September) and in only five locations ticks were present on both occasions. Accounting for all sites and all visits, ticks were recorded in 10 out of 22 locations (45%), and in only one of those presence sites were larvae only collected.

Landscape characteristics

The sampling sites cover a range of conditions in terms of composition and configuration (Table 2). Forest can dominate (up to over 60% of pine forests), but is generally found at intermediate levels, averaging proportions of 0.17 (deciduous forest) to 0.20 (pine forest). In other areas, cultivated areas dominate (average proportion: 0.19, with a maximum of 0.51). Some vegetation classes are less well represented, such as the proportion of non-forested land below the forest limit and the proportion of wetlands. Built-up areas are present at very small fractions, as sampling focused on vegetated land. In terms of landscape configuration, the Shape Index and mean area of patches, both for classes I and III, also indicate that a diverse set of conditions were sampled. Conditions regarding the forest fraction indicate, like the proportion of forest that no area is found without any tree cover. A broad range of mean tree cover fraction (20 to over 80%) is found, with a mean at 53%.

Environmental determinants of tick presence

The analysis of environmental determinants of tick presence was based on the 22 locations for which there were samples in June and/or September. The AIC on an empty model was 32.31. In bivariate analyses, the proportion of deciduous forest was positively associated with the probability of tick presence. The variables that were negatively associated with tick presence were the mean area of forest patches, the mean Shape Index of forest patches, the proportion of cultivated land, and the standard deviation of the tree cover fraction. However, the reductions in AIC for the bivariate models including mean area of forest patches, the mean Shape Index or the proportion of cultivated land were very modest and much lower than two. The proportion of deciduous forest and the standard deviation of tree cover result in AIC reductions higher than five.

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The multivariable model using only land cover class variables included only the proportion of deciduous forest, and the multivariable model using tree cover variables included only the standard deviation of tree cover fraction. Their results can therefore be seen in the bivariate column of Table 2. The multivariable model with all variables included the proportion of deciduous forest and the standard deviation of the tree cover fraction, with a positive and negative sign, respectively. The AIC was 21.67, a reduction of AIC of 10.64, which strongly supports the multivariable model. Nagelkerke's pseudo-R^2 was 0.65 indicating a reduction in unexplained variance and a good model fit.

Correlation between the multivariable model variables and other independent variables

The proportion of deciduous forests was significantly negatively associated ($p < 0.05$) with the mean area of forest patches (class III) and Shape Index of forest patches (class III), the proportions of pine (class 8) and spruce forests (class 9), and positively with the amount of pasture (class 4). The standard deviation of the tree cover fraction was significantly negatively associated with the mean area of non-forest vegetation patches (class I), the proportion of non-forested land below the forest limit (class 2), and positively with the mean area and mean Shape Index of forest patches, and the proportion of spruce forest.

Discussion

The amount of deciduous forest, as mapped using discrete landscape classes, was a significant predictor of tick presence in south-western Norway, but the best model and predictive performance is obtained by adding the standard deviation of the tree cover fraction per pixel within a buffer surrounding the collection point. This indicates that discrete representations of the landscape miss complexities of landscape composition and configuration that have an impact on tick habitat. In this study, we explored a new perspective of the landscape, away from the focus on individual, specific landscape factors, which may allow taking a more complete perspective on the landscape as a tick habitat.

Bivariate analyses indicated that tick collection locations surrounded by smaller forest patches (variable 'Mean area of patches, class III'), of a more regular, simpler shape (Mean Shape Index, class III) had a higher likelihood of having ticks. A large fraction of cultivated land decreased the probability of finding ticks. However, these variables only contributed very modestly to variance reduction, as per the reduction in AIC. Only the other significant variables, proportion of deciduous forest, and standard deviation of tree cover fraction were included in the multivariable model. The results of the multivariable model indicated that although forest was indeed a significant element determining tick presence, the standard deviation of the tree cover fraction also had a significant additional influence. The standard deviation of the tree cover fraction was negatively associated with the outcome, indicating that ticks were more likely to be found in areas where this standard deviation, effectively the extent to which the tree vegetation fraction of each pixel varied around the collection point, was lower. The standard deviation of tree cover fraction is significantly (Spearman's rho $p<0.05$) positively associated to the amount of cultivated land, the structure of forest (mean area and Shape Index), and the amount of spruce, and negatively to the amount of non-vegetated land below the forest limit. These correlations were not strong enough to interfere with regression models (all <0.65). The correlations between the standard deviation of tree cover fraction and those variables were consistent with the effect on tick habitat that could be hypothesised for them, e.g., cultivated land positively related to the standard deviation of tree cover fraction would be hypothesised to relate in a negative way to tick presence due to its lack of a protective, moist cover; it is indeed negatively related to tick presence in the bivariate analysis. However, the variables were not significantly related to tick

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presence in the multivariable model. Possibly, it is the combination of these variables that results in an unsuitable tick habitat. Other indicators, which focus on combinations rather than on single factors, may be necessary to identify tick-suitable environments in transition areas where biotopes other than forest may gather the resources necessary for ticks. The role of internal characteristics of forest patches and of the landscape features surrounding the forest (whether and where its edge can be crisply identified) in determining the suitability of landscape is poorly known, despite evidence that ticks are found in diverse environments (Dobson et al., 2011). Other studies have pointed also to forest as a consistent element favourable to ticks across sites and times (Boyard et al., 2011). Beyond the forest itself, the structure of the landscape, in particular forest ecotones, has been identified in diverse studies as a favourable element (De Keukeleire et al., 2015; L'Hostis et al., 1995, (Richter and Matuschka, 2011). The present study, however, indicated that some aspects of the landscape that can be managed may be relevant to identify, such as the structure of forest and tree cover in the vicinity of cultivated land.

Characterising further those areas where the standard deviation in tree cover fraction was higher, including their recent land use history, would improve our understanding of the role of this variable in determining tick habitat suitability.

It may be relevant to elaborate on the Resource-Based Habitat Concept (Hartemink et al., 2014) to further understand these results. Questing and feeding ticks require resources such as grassy or bushy vegetation and hosts, and these can be found, potentially, in both forested and non-forested environments. Egg laying and diapause would require a protective cover on the ground which may only be available in forests with a well-developed layer of litter, making deciduous forests the more suitable habitat. Understanding of how these resources for ticks relate to land cover classes or specific combination of land covers remains poor.

This study focused on landscape determinants with the specific purpose of confronting two perspectives on the landscape, the categorical one made of land cover classes, and the continuous one considering the tree cover fraction. Other variables that deserve consideration in a model of the probability of tick presence are weather, climate and hosts, but due to the small size of the sample, we focused on landscape and on presence and absence of ticks. These variables would be most relevant to a model investigating tick abundance, but our tick data were too sparse to investigate this.

Conclusion

Our results open interesting new perspectives on how to represent and monitor tick-infested landscapes. The significance of tree cover fraction may relate to complex composition and configuration of the landscape that transcend a single land cover class perspective, or relate to whether a low-density tree cover provide all the resources necessary for ticks. A patch-based monitoring of landscapes relying on discrete land cover classes may be insufficient to get a holistic perspective on tick habitat.

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Tables

Table 1: Land cover classes

Land cover classes, aggregated level	Land cover classes, detailed level
I. Non-forest vegetation	1) Alpine vegetation and non-vegetated land
	2) Non-forested land below the forest limit
	3) Wetlands
	4) Cultivated land
	5) Pastures
II. Artificial areas	6) Artificial (built up) areas
III. Forest vegetation	7) Deciduous forests
	8) Pine forests
	9) Spruce forests

Table 2: Land cover variables: descriptive statistics

Variable°	Mean ±SD	Range
Mean area of patches, class I (ha)	16.72±31.72	0.0003-81.30
Mean Shape Index of patches, class I	15.89±24.87	1.34-68.39
Mean area of patches, class III (ha)	60.80±56.78	0.0001-136.67
Mean Shape Index of patches, class III	123.46±102.31	1.69-262.27
Proportion of alpine vegetation and non-vegetated land	0.04 ±0.06	0-0.26
Proportion of non-forested land below the forest limit	0.03±0.05	0-0.18
Proportion of wetlands	0.06±0.09	0-0.35
Proportion of cultivated land	0.19±0.15	0-0.51
Proportion of pastures	0.13 ±0.11	0.01-0.37
Proportion of built up areas	0.003 ±0.009	0-0.04
Proportion of deciduous forest	0.17 ±0.16	0.01-0.49

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Proportion of pine forest	0.16 ±0.16	0.01-0.61
Proportion of spruce forest	0.20 ±0.18	0-0.54
Mean tree cover fraction	52.69 ±16.48	19.84-83.30
Standard deviation of the tree cover fraction	32.26 ±5.49	19.33-38.77

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Table 3: list of variables tested and results of the statistical analysis

	Bivariate analysis			Multivariable model	
Variable[1]	Estimate ±SD	P	AIC	Estimate ± SD	P
Mean area of patches, class I (ha)		>0.15			
Mean Shape Index of patches, class I		>0.15			
Mean area of patches, class III (ha)	-1.44e-6±8.85e-7	<0.15	31.38		
Mean Shape Index of patches, class III	-0.007±0.005	<0.15	32.03		
Proportion of alpine vegetation and non-vegetated land		>0.15			
Proportion of non-forested land below the forest limit		>0.15			
Proportion of wetlands		>0.15			
Proportion of cultivated land	-5.83±3.84	<0.15	31.62		
Proportion of pastures		>0.15			
Proportion of built up areas		>0.15			
Proportion of deciduous forest	10.78±5.21	<0.05	26.76	10.58±6.53	<0.10
Proportion of pine forest		>0.15			
Proportion of spruce forest		>0.15			
Mean tree cover fraction		>0.15			
Standard deviation of the tree cover fraction	-0.33±0.14	<0.05	25.16	-0.27±0.13	<0.05

[1]*All variables refer to the proportion or average within a 500-m buffer around the collection point. NS= Not significant at the p<0.15 level; * = p<0.15, **= p<0.10, ***=p<0.05*

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Figures

Fig 1 Tick data collection points and presence

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