



Mapping parasite transmission risk from white-tailed deer to a declining moose population

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Abstract

White-tailed deer (WTD; *Odocoileus virginianus*) are the definitive hosts of meningeal worm (*Parelaphostrongylus tenuis*) and liver fluke (*Fascioloides magna*); two parasites implicated in the decline of moose populations (*Alces alces*) in northern USA. Understanding which areas pose transmission risk may contribute to effective mitigation of these parasites in imperiled moose populations. Our objective was to predict areas of potential *P. tenuis* and *F. magna* transmission risk in terms of landscape features and deer density. Analyses were based on biogeographic and ecological factors related to both parasites. Using ecological niche modeling tools, remote sensing satellite data, field sampling, and estimated densities of WTD in Minnesota, we characterized current suitable environmental conditions for *F. magna* and *P. tenuis* across the historical range of moose in the state and identified potential areas for the occurrence of these parasites in unsampled areas. Our results help elucidate risky landscapes for *F. magna* and *P. tenuis* transmission by identifying geographic locations where WTD occur at high densities and with the landscape features suitable for the parasites. High-risk areas identified by our models may guide future surveillance, conservation, and management plans by identifying hotspots of potential infection of these parasites from WTD to moose populations. Our study shows the applicability of ecological niche modeling tools for investigating disease transmission risks of complex parasite systems for conservation purposes.

Keywords *Fascioloides magna* · Niche modeling · Maxent · *Parelaphostrongylus tenuis* · Spillover

Introduction

Infectious diseases are a serious threat for animal conservation worldwide. The impact of parasites on wildlife population dynamics has been increasingly recognized, both in terms of

direct regulation through effects on mortality and fecundity or through interactions with other immunological and ecological factors (Hudson 1986; Stien et al. 2002; Joseph et al. 2013; Ezenwa and Jolles 2015). While many populations appear to tolerate parasites with little apparent effects at the population level, parasites can have detrimental health impacts in accidental or “dead end” host species that are not part of the natural life cycle of the parasite (Tompkins et al. 2002). Such transmission of parasites between different host species is a type of pathogen spillover (Smith et al. 2009). Empirical evidence shows that spillover events may generate parasite-mediated apparent competition among host species (Cleaveland et al. 2000; Sainsbury et al. 2000; Tompkins et al. 2002; Lembo et al. 2008; Vanak and Gompper 2009; Acosta-Jamett et al. 2011; Soto-Azat et al. 2013). Such competition can result in the extinction of one host population, with the persisting species being the one that can support higher infestations of parasites or that has a longer co-evolutionary history with the parasite.

White-tailed deer (WTD; *Odocoileus virginianus*) populations have been steadily expanding in the north-central part of North America in the last decades due to a combination of

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suitable climate and anthropogenic land use changes and extirpation of natural predators (Thomson et al. 1998; Pickles et al. 2013). White-tailed deer are the definitive host for the meningeal worm (*Parelaphostrongylus tenuis*) and liver fluke (*Fascioloides magna*), which cause mortality when incidentally infecting moose (*Alces alces*) (Lankester and Samuel 1998). Moose populations in the state of MN, USA, have experienced steep declines over the past decade, and recent population estimates from Minnesota indicate that the population has declined by > 50% from 2005 to 2017 (DelGiudice 2017). Moose are susceptible to spillover events of parasites carried by WTD, and field investigations suggest that *P. tenuis* and *F. magna* parasites are substantial contributors to moose mortality (Murray et al. 2006; Wünschmann et al. 2015; Carstensen et al. 2017). Indeed, higher densities of WTD are associated with high presence of these parasite species in the landscape, and moose have decreased in areas with highest intensity of parasite larva in WTD feces, large WTD populations, higher WTD density, and higher parasite prevalence in WTD supporting the role of WTD in parasite spillover to moose (Karns 1967; Saunders 1973; Gilbert 1974; Whitlaw and Lankester 1994; Slomke et al. 1995; Lankester 2010, 2018; Peterson et al. 2013).

Parelaphostrongylus tenuis is a protostrongylid nematode parasite that requires terrestrial gastropods as an intermediate host (Lankester and Samuel 1998). An infected WTD sheds larvae in its feces; larvae must then survive in the environment until they can infect an intermediate host. Potential mechanisms for larvae survival in the environment may include reduction of free water and increase of bound water in the cells to reduce dehydration during the summer and protein denaturation during the winter and accumulation of the carbohydrates glycerol, sorbitol, and trehalose as cryoprotectants (Storey and Storey 1986). *Parelaphostrongylus tenuis* prevalence in most WTD populations where landscape is suitable for gastropod survival is 50–80%, and the parasite does not appear to negatively impact WTD populations (Murray et al. 2006). Symptoms in moose include circling, blindness, lack of fear, ataxia, and other neurological symptoms (Lankester and Samuel 1998). In Minnesota, > 10% of moose mortalities are attributed directly to *P. tenuis* (Lenarz 2009; Carstensen et al. 2017), but the percentage may be even higher (> 40%; Carstensen et al. 2017) as infected individuals with neurological symptoms would be more vulnerable to wolf predation or road kills (indirect mortality). For example, Wünschmann et al. (2015) found *P. tenuis* in 45% of necropsies of free-ranging moose in Minnesota, although sampling was biased because moose carcasses were opportunistically submitted for necropsy. The actual mortality rate from *P. tenuis* is probably between 10 and 45%.

The life cycle of the trematode parasite *F. magna* also relies on an intermediate gastropod host. The parasite has been implicated as a major factor in the decline of moose populations in

northwestern Minnesota (Murray et al. 2006). In moose, juvenile flukes migrate within the liver, potentially damaging 50–90% of the tissue; infection may lead to lower physical condition and death if accompanied by malnutrition (Pybus 2001; Murray et al. 2006; Lankester and Foreyt 2010). This parasite species is also gaining international attention given that it is invasive in Europe (Demiaszkiewicz et al. 2015; Juhásová et al. 2016).

Parasite prevalence in moose has been linked with WTD densities (Whitlaw and Lankester 1994; Slomke et al. 1995; Wasel et al. 2003; Peterson et al. 2013) but the relative importance of deer density as compared with other environmental factors facilitating exposure remains unclear (Lenarz 2009). For example, landscape could play a role in determining the probability of infection of *P. tenuis* (Jacques et al. 2016). Indeed, transmission between animals does not rely on contact with infected individuals, but rather on ingesting infective stages of the parasites from a gastropod intermediate host. Because both parasite species are driven by complex life cycles, favorable landscape conditions are crucial for the free-living parasitic stages and intermediate gastropod hosts to complete their life cycles (Lankester and Samuel 1998; Pybus 2001; VanderWaal et al. 2015). In addition, climate and anthropogenic changes can lead to shifting geographic distributions of WTD. This may affect parasite transmission dynamics, which in turn can impact the population status of host animal populations (Douda et al. 2012). Thus, to understand infection risk to imperiled moose populations, a greater understanding of environmental factors affecting the life cycle of these parasites outside the host is needed.

Ecological niche modeling (ENM) provides a useful approach to identify the environmental factors shaping parasite distributions (Peterson 2008, 2014). Here, we used an ENM approach to generate information on the ecology and geography of *F. magna* and *P. tenuis* to understand where these species currently occur or have the potential to occur. Our objective was to model the potential geographic distribution of *P. tenuis* and *F. magna* within the range of an imperiled moose population to generate maps of transmission risk. Such maps could be a significant advancement in the study of infectious diseases as a causative factor in regional declines of moose and may help to identify long-term moose population management objectives. We explored (i) the association of landscape features and parasite occurrence (i.e., locations where parasites were detected) and (ii) WTD density to identify areas of plausible parasite transmission risk to moose populations. This allowed us to calibrate an ecological niche model to forecast parasite potential occurrence at a landscape level coupled with deer density across the moose range in Minnesota as a proxy of the parasites realized niche. Identifying potential areas for the distribution of these two parasites may be a key tool for identifying critical areas for surveillance and designing evidence-based interventions for moose conservation.

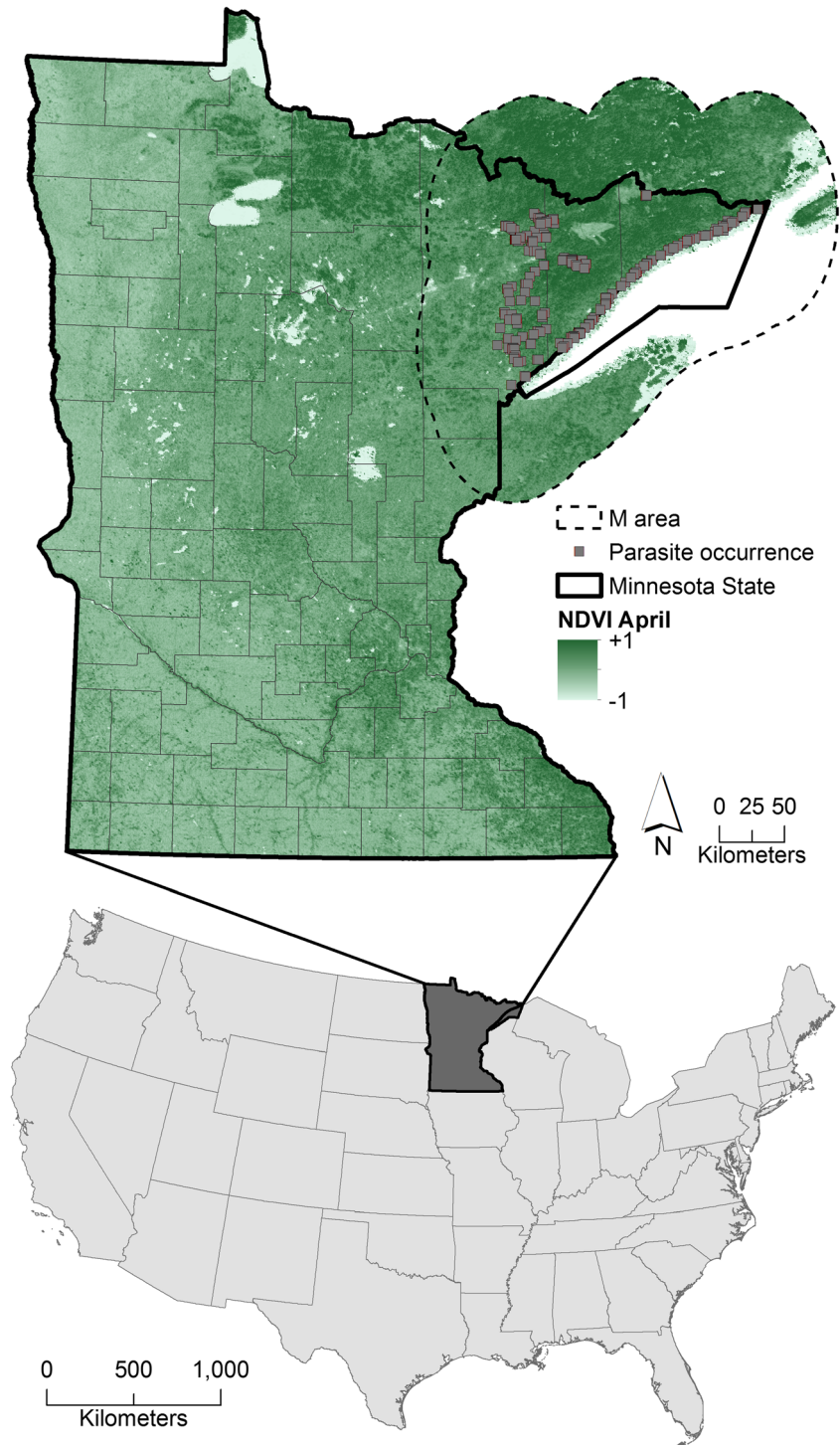
Materials and methods

Study area

This study was conducted in northeastern Minnesota, in the boreal forest ecoregion where moose have historically occurred (Fig. 1). The boundary of the study area was within the current geographic range of moose populations in this state

(MNDNR 2011), which included Cook, Lake, and the eastern part of St. Louis counties (east of State highway 53 and south of Ely). Dominant vegetation included upland conifer, upland deciduous, and mixed conifer-deciduous forests (Lillesand et al. 1998), with a north-south gradient between northern hardwoods in the south and boreal forest in the north (Pastor and Mladenoff 1992). The study area has a continental climate with severe winters and warm summers. Pre-fawn WTD

Fig. 1 Parasite occurrence used for the ecological niche modeling. Top: occurrence points for both parasite species (gray squares) were used to delimitate the calibration area M (dashed black line). Background is a NDVI original raster showing areas of high (+1; dark green) and low vegetation (-1; light green). Bottom: location of Minnesota (dark gray) in the USA (light gray)



densities in the study region were estimated to be 0.76–3.80 deer/km² in 2014, with higher densities found in southern and western portions of the study area (Grund 2014).

Deer pellet collection

We developed latitudinal and longitudinal sampling transects in areas where animals have been reported infected. Transects allowed including the diversity of landscapes and environmental conditions in the study area (Fig. 1). To determine parasite occurrence, deer fecal samples ($n = 602$) were collected between January and April 2014, a time period coinciding with peak fecal shedding of *F. magna* eggs and *P. tenuis* larvae in WTD (Lankester and Samuel 1998). A set of fecal samples ($n = 28$) were collected directly from WTD that were trapped and chemically immobilized as part of a GPS collaring project. Additionally, fecal samples ($n = 574$) were also collected off the top of the snowpack. To collect pellets, deer trails were identified during surveys conducted from roads, snowmobile trails, and cross-country ski trails. Trails were followed on foot or snowshoe until pellets were found. We sampled pellet groups that differed in size, shape, and color and were at least 20 m apart to avoid collecting multiple samples from the same individual (VanderWaal et al. 2015). We collected 10–20 individual pellets per pellet group. GPS coordinates of each pellet group were recorded. Samples were kept frozen until laboratory analysis. A modified Baermann technique was used to extract *P. tenuis* larvae from fecal samples (Forrester and Lankester 1997). To determine the presence of *F. magna*, we examined fecal samples for fluke eggs via the FlukeFinder® technique (FlukeFinder, Soda Springs, ID). Presence of eggs was recorded for each sample. Approval for data collection was obtained from the Minnesota Department of Natural Resources, as well as animal care and use approvals from University of Minnesota, Duluth, and the Minnesota Zoo. Animal capture and handling protocols met American Society of Mammalogists recommended guidelines and were approved by the University of Minnesota Animal Care and Use committee (Protocol Number 1309-30915A for deer).

Ecological niche modeling

According to ecological theories, ecological niches are the set of environmental conditions in which species can maintain populations in the long term without need of immigration (Peterson et al. 2011). Thus, ecological niche modeling (ENM) aims to reconstruct such environmental conditions via correlative analyses between sites where organisms are found and the environmental conditions available in such sites. These models can be calibrated using landscape variables (Escobar and Craft 2016) and have been recently applied

to parasites (Peterson 2014). The first step in the ENM process is to calibrate the models in a specific area supported by the sampling effort (Barve et al. 2011). The model calibration area, here termed M (sensu Soberón and Peterson 2005) was defined based on previous data-driven protocols (Poo-Muñoz et al. 2014) (Fig. S1). Briefly, we measured the distance between sampled areas and a central point among them and selected the average of the most marginal sites to generate buffers among all sites (four marginal points across northern-southern Saint Louis County and two points in northern Cook County; Fig. S1). Previous experiments have showed that smaller M areas are more critical to develop significant ENM (Barve et al. 2011). Thus, to avoid biased results produced by an arbitrary delimitation of M and consider constrained areas, we calibrated models based on 100%, 50%, and 25% of the buffer distance, resembling potential dispersal of host individuals, a constrained M region, and sampled sites, respectively (Fig. S1). These buffered areas were used for model calibration and included northeastern MN, USA, and southwestern Ontario, Canada (Fig. 1). Based on this area, we obtained Terra MODIS satellite imagery to represent the landscape structure in the region. We used 16-day intervals of normalized difference vegetation index (NDVI) rasters at 500-m spatial resolution from January to December following the protocol in (Escobar et al. 2015) (Supplementary data S1). NDVI captures variation in vegetation type, climate, and soil conditions (Nemani and Running 1997), and these data are associated with primary productivity. Because NDVI correlates with precipitation and temperature (Pettorelli 2013), associations of NDVI with animal populations have been well documented (Pettorelli et al. 2005), and NDVI has been considered the next-generation data source for ecological niche modeling (He et al. 2015). We developed a principal components analysis (PCA) on the NDVI rasters in ArcGIS 10.4 (ESRI 2017) to reduce the number and correlation of the 23 original rasters retaining most of their information (Hornung et al. 2010). The new uncorrelated components were used during model calibration instead of the original rasters. For model calibration, we used all first components that summarized > 90% of the original information.

To reduce model overfitting due to autocorrelation, clustered parasite occurrence locations were filtered by removing occurrences so that there was only one occurrence every 500 m. We employed a type of logistic regression that considers densities of available occurrences and density of the environmental background in the calibration area M to generate the ENMs (Elith et al. 2011; Merow et al. 2013). Due to the imperfect detection of the species from the diagnostic methods employed (i.e., limited sensitivity), we avoided model calibration and evaluation based on presence-absence ENM. Analyses were performed using Maxent software version 3.3.3k (Phillips et al. 2006). Maxent is a present-background ENM method that reconstructs landscape conditions where

parasites occur and allows model fit to landscape conditions where parasites are more frequently found as a proxy of the species realized niche, and allows model transference to other areas with and without extrapolation and clamping, which is a versatile model feature not available in most present-only methods (e.g., Bioclim (Peterson et al. 2011), minimum-volume ellipsoids (Qiao et al. 2016), Marble (Qiao et al. 2015)). We tuned the regularization coefficient in Maxent from 0.5 to 2.0 by increments of 0.5 and assessed different feature combinations employed by the community—i.e., linear (L), linear + quadratic (LQ), hinge (H), linear + quadratic + hinge (LQH), and linear + quadratic + hinge + threshold + product (LQHTP). This detailed assessment allowed us to identify optimal model complexity while reducing overfitting (Radosavljevic and Anderson 2014) based on Akaike's information criterion (AIC) values (Warren and Seifert 2011; Radosavljevic and Anderson 2014). Additionally, ENMs were assessed to ensure that the algorithm, available occurrences, and environmental variables generated robust predictions of independent data based on AUC ROC and omission rate metrics (see Muscarella et al. 2014). We used the omission rate as evaluation metric using occurrences and areas independent to those used during calibration (Muscarella et al. 2014), prioritizing models with low Type II error equivalent false negatives or omission error (Peterson et al. 2008), which is critical when modeling infectious diseases where neglecting an infected site may have dramatic consequences compared with neglecting a healthy site. To obtain independent data for model evaluation, we followed the protocol of Muscarella et al. (2014) to split the data available in calibration and evaluation datasets using the block method.

Once the best model fit was determined and evaluated in each calibration area (100%, 50%, and 25% buffer), we developed final Maxent models with the feature combination and regularization coefficients with best performance by study area (Elith et al. 2011). Final models for both parasite species were converted from the original continuous format to binary (suitable = 1, unsuitable = 0), considering a threshold model including 95% of calibration occurrences predicted correctly—a calibration error of 5% (Jiménez-Valverde and Lobo 2007; Peterson et al. 2011). Final models were transferred to the historical range of moose in Minnesota (Owens et al. 2013; Anderson 2013), as this region has historical records of moose but limited parasite surveillance coverage (Geist et al. 2008). The model transference restricts model predictions only to environmental conditions contained in the calibration area, avoiding predictions beyond observed environmental values (Owens et al. 2013). Model transference was done using Maxent without clamping or extrapolation (Anderson 2013). Final binary models of the three calibration areas M (100%, 50%, and 25% buffer) were multiplied to generate an ensemble summarizing areas with agreement among models.

We assumed that combining landscape features from NDVI values with deer density adds more information regarding transmission risk of these parasites as reported elsewhere (Karns 1967; Saunders 1973; Gilbert 1974; Whitlaw and Lankester 1994; Slomke et al. 1995; Peterson et al. 2013). Thus, the final binary model denoting suitable and unsuitable areas for parasite occurrence was then categorized based on WTD density estimations. We used deer harvest data between 1993 and 2014 (Minnesota Department of Natural Resources 2014) as a proxy of WTD density. We estimated mean values of deer harvest density by deer management unit (DMU) across this time period to generate a continuous surface based on a kernel density estimation using the Heat Map tool in QGIS and used standard deviation of the annual density values as a proxy of uncertainty. We denoted areas with parasite suitability and high deer density as high risk.

Results

Prevalence for *F. magna* and *P. tenuis* in WTD fecal samples was 30.1% and 66.3%, respectively. After resampling positive samples one-per-cell, we obtained 121 and 203 single occurrences of positive samples for *F. magna* and *P. tenuis*, respectively (Fig. 2). The first ten principal components from NDVI layers summarized 91.3% of the overall variance contained in the original NDVI rasters (Fig. 2), thus capturing the environmental variability across the entire study area, reducing the correlation among the original variables as visualized in a correlation matrix (Table S1). Our model evaluation for tuning the Maxent regularization coefficients and feature combinations across three different M extents revealed that best fit models (AICc = 0) showed robustness for the algorithm, environmental variables, and predictive performance for *F. magna* and *P. tenuis* in each M area (original 100% buffer, 50%, and 25%) (Figs. S2 and S3; Table S2). Feature combination of selected models for *F. magna* were LQ in all study area extents—i.e., original 100% buffer, 50%, and 25%, but with regularization coefficients of 2, 1, and 2 for each M area, respectively; features for *P. tenuis* included LQ, LQHTP, and LQHTP with regularization coefficients of 2, 2, and 0.5 for the original 100%, 50%, and 25% buffers, respectively. Selected parameters were used to develop final predictive models of the potential distribution of *F. magna* and *P. tenuis* in each M area (original 100% buffer, 50%, and 25%; Fig. S3) and transfer models beyond the study area to historic range of moose in Minnesota. The ensemble of the final binary models revealed broader suitable areas for *F. magna* (Fig. S4).

We predict that areas along the shores of Lake Superior and northwest of Lower Red Lake and Upper Red Lake are particularly suitable for *F. magna*. The predictions from the ENM for *P. tenuis* were less widespread compared with *F. magna*. Suitable areas predicted for *P. tenuis* generally included

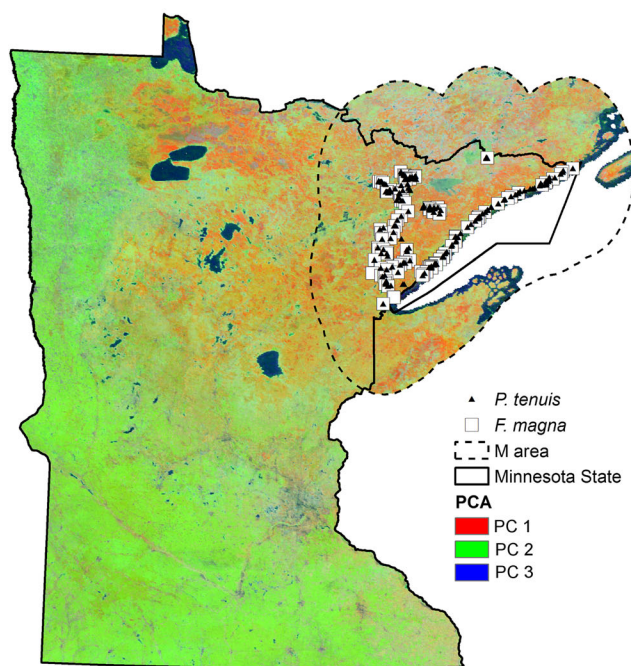
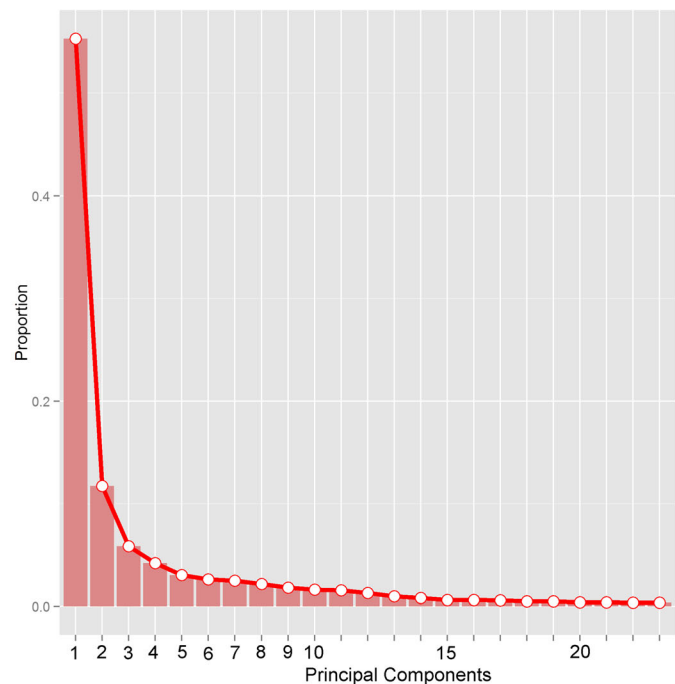


Fig. 2 Environmental data used during the ecological niche modeling. Left: occurrence points for *Fasciolooides magna* (white squares) and *Parelaphostrongylus tenuis* (black triangles). Models were calibrated in the M area (dashed line). The figure background is a composite image showing principal components 1 (red), 2 (green), and 3 (blue)



summarizing 72% of the total environmental variability from the 23 vegetation variables. Right: histogram of the proportion of variance provided by each principal component. Models were developed based on the first ten components summarizing >90% of variable information

shoreline and riverine zones (colored areas in Fig. 3). Incorporation of deer density (Figs. S5 and S6; Supplementary data S2) into the suitability maps revealed two main foci of high WTD density in the central and southern regions of historical moose range in turn suggesting high risk for parasite transmission (intensity of colors in Fig. 3). Uncertainty of WTD density estimates was found in the western and eastern regions of the study area (Fig. S6).

Discussion

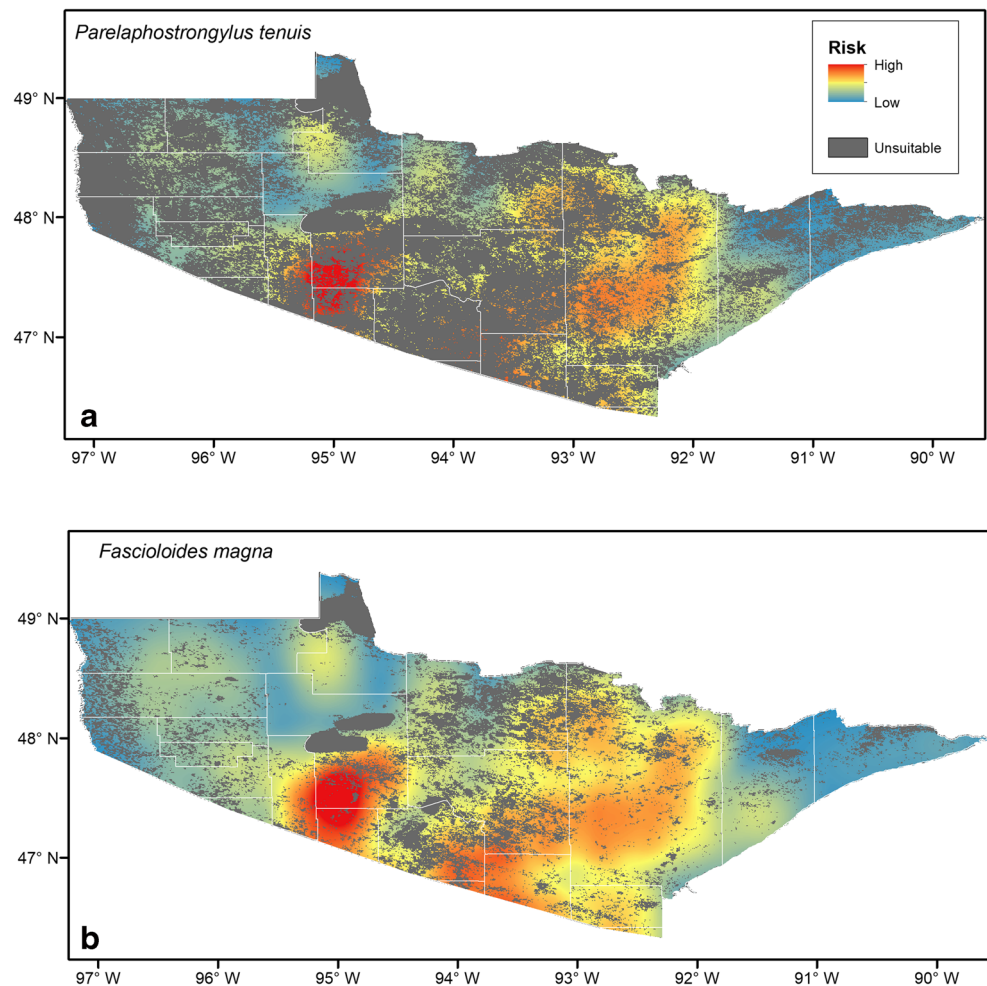
We applied ecological niche modeling methods to map the potential occurrence of two WTD parasites, *F. magna* and *P. tenuis*, and identified areas of potential transmission risk to imperiled moose populations (Geist et al. 2008). Ecological niche modeling predictions have been shown to be an effective guide for field surveillance (Rebelo and Jones 2010; Dicko et al. 2014), suggesting that our risk maps could be informative for effective control interventions and to guide targeted parasite surveillance (Fig. 3).

By incorporating deer density into the suitability maps (Fig. 3), we accounted for the fact that environmental risk may be mediated by deer densities (Karns 1967; Saunders 1973; Gilbert 1974; Whitlaw and Lankester 1994; Slomke et al. 1995; Peterson et al. 2013). This highlights that although landscape may be suitable for these parasites to exist, other

factors, like deer presence and snail availability (Maskey 2008), may reduce the ability of parasites to complete their life cycle in some areas. Indeed, because infected moose do not shed either parasite, the parasite burden is linked to deer presence, which then translates to transmission risk. Notably, we found that broad swaths of moose landscape in northeastern Minnesota are suitable for both parasites (Fig. 3), supporting previous empirical findings for *F. magna* (Karns 1972). The former range of the northwestern moose population, which declined during the 2000s (Murray et al. 2006), was also identified as suitable for both parasite species though deer densities were not particularly high (e.g., northwestern Red Lakes; Fig. 3). We note that coarse patterns of WTD density described in this study were generated from deer harvest data; however, accurate data on deer population density may be more informative at finer scales. Additionally, while we assessed transmission risk by including deer abundance based on a post-processing modeling approach (Anderson 2017), other ENM protocols may instead include these biotic variables directly into the model (Anderson 2017). ENMs calibrated with biotic variables, however, require careful descriptions of the assumptions and detailed interpretation of what is being modeled (Soberón and Peterson 2005).

Although WTD density has often been considered the primary metric of infection risk to moose, here, we show that the occurrence of *F. magna* and *P. tenuis* may be influenced by spatial variation in ecological conditions. That

Fig. 3 Risk maps of *Fascioloides magna* (top) and *Parelaphostrongylus tenuis* (bottom) across moose range in Minnesota. Colored areas are suitable for parasites in terms of landscape condition. Gradations in color are based on overlaying with deer densities: areas with high (red) and low (blue) risk were defined in terms of high and low deer density, respectively. Map restricted to the moose range in Minnesota. Areas predicted unsuitable for parasites based on satellite-derived data resembling landscape features are denoted as gray and are expressed as areas where transmission risk is not priority



is, we estimated high transmission risk in areas with high density of WTD but also with suitable landscape for the parasites as denoted by the satellite derived data. However, the heterogeneity in risk estimated by our model is not extreme, suggesting that parasites may be somewhat more uniformly distributed than expected. The moderate amount of heterogeneity in the availability of suitable landscape for *F. magna* and *P. tenuis* has not been previously demonstrated and may inform future study designs and management efforts related to these parasites. Indeed, moose management plans often target WTD densities to be maintained < 4 deer/km² in order to minimize transmission risk (Aho and Hendrickson 1989; Whitlaw and Lankester 1994; MNDNR 2011). However, management could also be informed by maps showing areas where landscapes are suitable for parasites (Soberón and Peterson 2005). Given that our approach captured course-scale heterogeneity, comprehensive studies on the ecological requirements at finer spatial scales are warranted to provide additional clarity on the distribution of snails in the region.

Regarding intermediate hosts, Lymnaeid snails required by *F. magna* appear to be broadly distributed in wet areas within grass

landscapes found in the Great Plains (Maskey 2008, 2011). Terrestrial gastropods required by *P. tenuis*, which thrive in shaded and damp microclimates, prefer forests (Lankester and Anderson 1968; Kearney and Gilbert 1978). These highlight the need for more research in the ecological and physiological requirements of these parasites at a fine scale and the need for updated parasite surveys in areas that our models predict to be of risk in the southern range of moose. Other research suggests that the prevalence of *P. tenuis* in WTD is higher in forested areas with colder winters (Lankester and Peterson 1996), further substantiating the higher suitability for this parasite in areas of the Upper Midwest (Wasel et al. 2003). In this context, past research showed that woodlands provide suitable landscape for intermediate hosts and larval survival (Lankester and Peterson 1996; Maskey et al. 2015), while colder winters likely have fewer freeze-thaw cycles that improve overwinter larval survival. Here, we were unable to account for parasitized intermediate hosts due to the unavailability of epidemiological data for snail. Future research could employ our risk maps to track parasite infestations in intermediate hosts. Areas predicted with parasite transmission risk may also be used to assess chemical-based snail control interventions to interrupt the lifecycle of parasites, which

have proved to be effective for snail-borne parasites control (Lo et al. 2018; Wang et al. 2018). While we employed standard methods for parasite identification (e.g., Forrester and Lankester 1997), complementing identification with diagnostic methods based on molecular techniques would reduce risks of misidentification of species.

The longitudinal and latitudinal transect was developed for sampling aimed at capturing landscape variability; however, we recognize the potential sampling bias implicit in this strategy (Kadmon et al. 2004). Increasing the sampling effort in terms of geographic area covered may provide more information to the models. Thus, our niche estimation is dependent on the sampled area (\hat{E}_o in Peterson et al. 2011). That is, based on the model calibration experiments, we found that changes in the model calibration area M result in changes in the environmental data employed and, in turn, result in changes in the parameters selected and final predictions in agreement with previous contributions (Barve et al. 2011). Correlative ecological niche modeling is a field with constant improvements in the theory and methods employed. A critical step in the development of models is the experimental design, which may include the sampling protocols, data cleaning, algorithm selection, and post-modeling analysis. A re-analysis of current ecological niche modeling protocols has shown that different ecological niche model algorithms reconstruct different features of the species' niche and that thresholding models may help in reducing the effects of sampling bias (Escobar et al. 2018). We note that there are not defined protocols for M delimitation, instead, calibration areas M should be based on the data available, the knowledge of the species, and the sampled areas (Johnson et al. 2019). Here, we estimated the calibration area M based on the data available and subsets of this area for a more informed interpretation of results that resemble the sampled area and capture uncertainty and variability among model estimations.

Changing the scale of the study to develop a finer-scale estimation of risk would require a sampling effort covering several years in the same locations to account for seasonal changes in the probability of presence of parasites by site. While we were focused on a coarse-scale estimation of parasites potential distribution to identify sites for intervention and research, fine-scale studies (population level) may provide information on the abundance of parasites and intermediate hosts that may be highly informative to identify the time and population for intervention. These fine-scale studies, however, usually are developed for small study areas and require considerable sampling effort and resources (MacKenzie et al. 2002). However, fine-scale focalized studies may allow development of highly informative temporal and spatial models (e.g., occupancy models).

Considering the coarse scale of our models, more data are needed in areas of high risk to understand fine-scale dynamics of transmission in Minnesota, including data on intermediate host density, parasite abundance and probability of detection, larval stages by site and season, the effect of landscape fragmentation on parasite prevalence, and WTD landscape use and displacement (Jacques et al. 2015; VanderWaal et al. 2015). White-tailed deer have an estimated home range of ~ 2 km² which can shift geographically in response to land use change (VerCauteren and Hygnstrom 1998), potentially affecting geographic areas utilized by infected deer. The seasonal displacement of deer also makes it challenging to identify variations in the geographic distribution of infectious stages of both parasites, restricting our results to distributional patterns during winter. Moose home ranges are large, between 14 and 26 km² (Cederlund and Sand 1994), and seasonal displacement also can have an effect on their exposure to these parasites. With the limited data, however, our risk maps summarize and propose a plausible pattern of potential parasite exposure and also may inform evidence-based efforts for moose conservation. Informed conservation efforts may allow adaptive management in the current moose range and in identifying areas for potential reintroduction and translocation of moose. While our maps are aimed at informing moose conservationists, managers of other sympatric species susceptible to these parasites may also find our study informative. For example, ongoing efforts to reintroduce elk (*Cervus canadensis*) in northern Minnesota (Albert 2017; Myers 2017) may use our modeling results to identify risk areas for reintroductions, considering that recent elk reintroductions have failed due to the translocation of individuals to *P. tenuis*-infected areas (Chitwood et al. 2018). Additionally, our risk maps may serve as a first step for explorations of *F. magna* and *P. tenuis*' population dynamics to elucidate endemic areas and recently colonized areas for parasites within WTD populations. Our workflow can also be applied to other wildlife and zoonotic disease systems of conservation or public health concern.

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Compliance with ethical standards

Approval for data collection was obtained from the Minnesota Department of Natural Resources, as well as animal care and use approvals from University of Minnesota, Duluth, and the Minnesota Zoo. Animal capture and handling protocols met American Society of Mammalogists recommended guidelines and were approved by the University of Minnesota Animal Care and Use committee (Protocol Number 1309-30915A for deer).

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