



A Bayesian geostatistical approach to modeling global distributions of *Lygodium microphyllum* under projected climate warming



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ABSTRACT

Species distribution modeling aimed at forecasting the spread of invasive species under projected global warming offers land managers an important tool for assessing future ecological risk and for prioritizing management actions. The current study applies Bayesian inference and newly available geostatistical tools to forecast global range expansion for the ecosystem altering invasive climbing fern *Lygodium microphyllum*. The presented modeling framework emphasizes the need to account for spatial processes at both the individual and aggregate levels, the necessity of modeling non-linear responses to environmental gradients, and the explanatory power of biotic covariates. Results indicate that *L. microphyllum* will undergo global range expansion in concert with anthropogenic global warming and that the species is likely temperature and dispersal limited. Predictions are undertaken for current and future climate conditions assuming both limited and unlimited dispersal scenarios.

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1. Introduction

Invasive plants pose a major threat to the biological integrity of the world's native natural communities (Pysek et al., 2012; Wilcove et al., 1998; Allen and Bradley, 2016). Non-indigenous plants adversely affect the suitability of habitat for native wildlife, disrupt successional trajectories, alter disturbance patterns, and compete with native plants for access to light and other resources (Gordon, 1998; Ehrenfeld, 2010; Pysek et al., 2012; Olden et al., 2004; McKinney and Lockwood, 1999). Exacerbating the effects of invasive plants, rising temperatures resulting from anthropogenic climate change may increase the risk, extent, and intensity of invasion by non-indigenous species (Rogers and McCarty, 2000; Bradley et al., 2010; Ayllón et al., 2013; Hulme, 2016). Because prevention is the less costly and more effective alternative to post-invasion treatment, intervention at the onset of, or prior to, infestation by invasive plants is the most viable and economically sound approach to safeguarding native function and diversity (Leung et al., 2002; Hulme, 2016; Hobbs et al., 2006). For these reasons, species distribution modeling (SDM) aimed at predicting the range of non-indigenous species under projected climate warming offers land managers an important tool for assessing invasion risk and for prioritizing management actions (Buckley, 2008).

SDM is increasingly used to anticipate the expansion of species in both environmental and geographic space, however, extrapolating the presence of invasive organisms to other locations, conditions, or times poses several challenges (Elith and Leathwick, 2009; Elith et al., 2010; Václavík and Meentemeyer, 2012; Elith, 2015). Among these modeling challenges is the need to consider the extent to which invasive species have obtained equilibrium within their introduced range (Guisan and Thuiller, 2005; Soberón and Nakamura, 2009; Václavík and Meentemeyer, 2012), their potential to exhibit non-linear climatic tolerances (Huntley et al., 1995; Austin et al., 2006; Austin, 2007), and the degree to which they interact with other organisms (Jablonski, 2008; Wiens, 2011; Leach et al., 2016).

Although climatic factors and evolutionary histories largely drive biogeographic patterns at regional or continental scales (Pearson et al., 2003), the realized distribution of an invasive species over its introduced range may not fully reflect that organism's true environmental tolerances, as time since introduction, dispersal limitation, biotic interactions, and other influences may constrain ecological opportunity (Guisan and Thuiller, 2005; Soberón and Nakamura, 2009; Václavík and Meentemeyer, 2012). It is critical that SDM efforts contemplate that given sufficient opportunity invasive species may spread to areas that are suitable for colonization but not yet accessible. Even when a species is at or near equilibrium, an a priori assumption of a mean response to underlying environmental gradients could potentially bias results in instances where the species actually experiences a skewed or non-

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linear response (Austin et al., 1990; Rydgren et al., 2003; Austin, 2007). Likewise, accounting for the role of biotic variables in shaping species distributions may be as important to understanding and modeling an organism's geographic distribution as is accounting for climatic or edaphic considerations (Pellissier et al., 2010; Leach et al., 2016). By incorporating information pertaining to the locations of allied or competing cohorts, models may explain more of the variance observed in the focal species distribution than can be accounted for by abiotic factors alone.

Beyond the equilibrium assumption, non-linear responses to environmental gradients, and biotic factors, understanding the reciprocity of pattern and process over environmental and geographic space requires the explicit examination of spatial structure and scale (Wiens, 1989). Because feedbacks between pattern and process influence the functioning of both organisms and communities, the spatial arrangement of a species encodes information about the ecology that shapes it (Hurtt and Pacala, 1995; Brown et al., 2011; Velázquez et al., 2015). A major goal of SDM is to reveal this ecology through analysis of geography. When a given geographic distribution cannot be fully articulated as functions of abiotic and biotic variables, then remaining uncertainty must be quantified. Indeed, performing SDM without consideration of latent spatial structure (spatial variability due to unconsidered covariates and spatial correlation errors) may result in coefficient estimates or predictions with significant error (Hoeting, 2009; Dormann, 2007; Renner et al., 2015). Accounting for latent spatial structure can be complex because numerous factors contribute to the spatial arrangement of documented occurrences; including not only species-specific ecological and evolutionary processes such as dispersal or competition, but also biased data collection (Kadmon et al., 2003; Dormann, 2007). As one example, sampling or observer bias influences the distribution of occurrence data and is often introduced when species records are dis-proportionally sampled from particular habitat types (Dennis and Thomas, 2000) or from areas that are more readily accessible by humans (Kadmon et al., 2004; Renner et al., 2015). It is therefore necessary that models account for the “unknown” influences that arise from spatial dependency, unmeasured variables, and biased data collection as well as the “known” physical and ecological parameters that shape species distributions.

Capable of accommodating both fixed and random effects, Bayesian hierarchical models offer a flexible approach to SDM. Their tiered configuration allows for incorporation of “known” environmental and ecological variables as well as the “unknown” effects associated with latent processes like spatial correlation. Within the hierarchical model framework, latent structural processes can be assimilated into models via random effect terms that serve to quantify the uncertainty remaining after accounting for the effects of fixed covariates (Elith and Leathwick, 2009; Elsnér et al., 2016). Until recently, fitting of Bayesian hierarchical models has been restricted to computationally demanding (read: potentially slow) Markov chain Monte Carlo (MCMC) simulation; however, integrated nested Laplace approximation (INLA) uses accurate approximations to the marginal posterior densities for the hyper parameters and latent variables providing a fast alternative to MCMC (Rue et al., 2009). Moreover, INLA when coupled with random effect terms as Gaussian random fields are shown to produce greater predictive accuracy than use of generalized additive models, logistic regression, and maximum entropy methods (Golding and Purse, 2016).

Although INLA provides a newly accessible alternative to MCMC, the specification of Gaussian random fields can still become quite computationally expensive, particularly over large study domains with dense matrices like those of interest to biogeographers and frequently encountered during SDM. To help overcome this issue, Lindgren et al. (2011) prescribe the use of approximate weak

solutions to stochastic partial differential equations (SPDE) as a means of linking Gaussian random fields in the Matérn class to discretely indexed Gaussian Markov random fields. Because properties of the Gaussian Markov random field enable estimation over sparse matrices, the SPDE approach permits the modeling of spatial random effects over a triangulated mesh; thereby, negating the need for dense grids and easing computational demand. The SPDE approach builds on the efficiency afforded through INLA by facilitating construction of complex point process models in a flexible and economical manner. From the perspective of spatial ecology, point process models allow for the extraction of ecologically relevant information pertaining to both pattern and process (Illian et al., 2013; Simpson et al., 2015; Fithian et al., 2015; Renner et al., 2015; Velázquez et al., 2016), which is critical for modeling species such as *Lygodium microphyllum*.

Indigenous to the pantropics of Africa, Asia, and Oceania (Pemberton and Ferriter, 1998), *L. microphyllum* (Old world climbing fern) is classified as a Noxious Weed by the United States Department of Agriculture (USDA et al., 2012) and a “Category One” invasive by the Florida Exotic Pest Plant Council, meaning that the plant impacts natural communities through the displacement of native species, the changing of community structure, and alteration of ecological function (Florida Exotic Pest Plant Council, 2015). Since first collected as isolated specimens in the mid-1960s (Beckner, 1968), *L. microphyllum* has spread throughout Florida's southern peninsula where it has enveloped canopy trees, enshrouded herbaceous marshes, entangled wildlife, and altered disturbance regimes by carrying fire into non-pyrogenic communities (Roberts, 1996; Wu et al., 2006; Volin et al., 2004). Because of its injurious effects to native biota, *L. microphyllum* has been reasonably well-studied in southern Florida. In addition to landscape-level models aimed at predicting growth rates and the probability of occupancy over the greater Florida Everglades (Volin et al., 2004; Wu et al., 2006; Fujisaki et al., 2010), greenhouse studies have investigated the fern's physiological response to changing hydrology (Gandiaga et al., 2009) and freezing temperature (Hutchinson and Langeland, 2014). The findings from these investigations highlight several important biophysical and ecological characteristics; *L. microphyllum* tolerates wetland habitats (Volin et al., 2010; Gandiaga et al., 2009), exhibits a tendency to cluster or aggregate within specific distance thresholds (Wu et al., 2006), is often located in proximity to other invasive species (Rodgers et al., 2014), and is likely limited by temperature (Hutchinson and Langeland, 2014).

The goal of the current study is to forecast the distribution of *L. microphyllum* under current and projected climate conditions through adoption of a Bayesian geostatistical perspective. Though our central ecological concern is the potential for the invasive to spread throughout the southeastern United States, we choose to model the species globally in order to include observations from both its native and introduced range. Key goals of the study include demonstrating the potential for random effects to estimate non-linear climatic tolerances, clustering distance thresholds, and spatial errors. In support of these goals, spatial models and non-linear terms are compared to their non-spatial and linear counterparts.

2. Materials and methods

2.1. Overview

The flowchart shown in Fig. 1 depicts the model development process adopted for this study beginning with species occurrence data and moving downward through geographic and environmental considerations, iterative model evaluation, and prediction. Incorporated data types and data sources are described in the

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