A GLOBAL UNDERSTANDING OF THE FACTORS FACILITATING PLANT INVASIONS.

A Dissertation Presented

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ABSTRACT

Globalization has resulted in the anthropogenic movement of plant species, many of which have established and become invasive in their secondary ranges. A fundamental goal in invasion ecology is to understand the factors that contribute to successful establishment and spread of invasive species on a global scale. Given the likelihood of a future with increased international connections leading to introductions of plant species, understanding why some species are successful invaders and which ecosystems are susceptible to invasion continues to be crucial to development of effective preventative policy and management strategies. Although there is a large body of literature on determinants of invasion success, substantial gaps remain in how the effects of evolutionary history, global connectivity, and habitat suitability of native and introduced regions affect the propensity for a species to become invasive and the propensity for a region to be invaded. This dissertation research addresses these uncertainties with three independent but complementary studies using global databases: 1) evaluating the relative likelihood of successful plant invasions by comparing phylogenetic diversity, habitat suitability, and anthropogenic connectivity between native and non-native regions; 2) incorporating the effect of spatial scale on outcomes of those processes; and 3) determining contributing factors of regional invasibility and predicting potential future invasions. A global approach to invasion science is powerful in building a general understanding of factors that influence establishment and spread. Cumulatively, results showed that characteristics of invasive species' native ranges were more important than characteristics of the invaded range when modeling invasiveness, namely phylogenetic diversity. In addition, this work highlighted the effects scale on factors of invasion success. Finally, we developed a novel method to quantify invasibility of regions and predict which regions have high potential for future invasions. Conclusions from this work suggest that development of effective preventative policy and management strategies should include diversity of invasive species' native range. Furthermore, prevention of invasive species requires careful consideration of the future potential of invasibility. A global approach to invasion science is powerful in building a general understanding of factors that influence establishment and spread. The outcomes of this work have numerous implications for understanding global dynamics of how and why species invade.

DEDICATION

For my mother, Janice Fairhurst.

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INTRODUCTION

Globalization has resulted in the anthropogenic movement of plant species, many of which have established and become invasive in their secondary ranges (Pyšek et al. 2012; Van Kleunen et al. 2015). A fundamental goal in invasion ecology is to understand the factors that determine successful establishment and spread of invasive species on a global scale. Given the likelihood of a future with increased international connections leading to introductions of plant species, understanding which species are successful invaders and which ecosystems are susceptible to invasion continues to be crucial to development of effective preventative policy and management strategies (review in Hulme, 2006; Hulme et al., 2008; Rout et al. 2011).

Research suggests that successful plant invasion is a multi-step process with four interrelated spatio-temporal stages: introduction, establishment, spread, and impact (Theoharides and Dukes 2007; Richardson and Pyšek 2012; Grarock et al. 2013). This invasion process (figure I-1) is a helpful framework to examine and understand the ecological factors that act as successive filters of invasion success. The limiting factors determined at each stage will be used as variables in explaining invasion success throughout this dissertation.

First, a species is introduced intentionally or unintentionally to a new location. The introduction of invasive species is controlled by human movements and global trade networks (Elton 1958; Mack et al. 2000; Seebens et al. 2015; Turbelin et al. 2016; Chapman et al. 2017). Therefore, as the connectivity between regions increases, so

should the likelihood of species that are transferred between them (Lockwood et al. 2005). Second, the introduced species establishes a self-sustaining population in the new location. Environmental characteristics such as temperature, precipitation, and seasonality are known to affect the distribution of all species (e.g. environmental filtering), including invasive species (Nobel and Slayter 1977; van der Valk 1981; Bazzaz 1991). Therefore, it can be assumed that establishment success is dependent upon existence of suitable habitat in the new location (Guisan and Thuiller 2005; reviewed in Gallien et al. 2010; Barbet-Massin et al. 2018). Third, the established population increases its initial range, spreading to new locations. The spread stage is likely limited by the ability to compete with or tolerate native species in the new location (Mack 2003; Stachowicz and Tilman 2005; Vermeij 2005; Golivets and Wallin 2018). Adaptations or traits that give a species the competitive advantage necessary to spread in a new location may be dependent on the biodiversity of its native range (Fridley and Sax 2014). Species with diverse native ranges could have been subject to constant selection pressure from competitors, thereby increasing the likelihood of adaptations that aid in competition or tolerance in a wide range of communities (Darwin 1858; Fridley and Sax 2014). In contrast, biodiversity of the new location reflects the number open niches available for incoming species (MacArthur 1955, 1972). Greater biodiversity in a new location may mean higher competition and an increased resistance to invasion (Elton 1958; Davis et al. 2000; Sax and Brown 2000; Gerhold et al. 2011; Fridley and Sax 2014; Whitfeld et al. 2014; Iannone et al. 2016). Therefore, the spread of invasive species to new locations could be determined by both

the diversity of their native range and the diversity of the new location. Lastly, when a species has made a measurable detrimental impact on the ecosystem in the new location, it is deemed invasive. A comprehensive approach to increase understanding of how species invade should include important and unequal drivers of invasion success at each stage in the invasion process.

The management strategies developed for invasive species vary in efficiency and cost, depending on the stage of invasion (Simberloff et al. 2013; figure I-2). For example, when an introduced species has reached the impact stage, the management strategy is mitigation of that species and restoration of the ecosystem. Efficiency is low and cost is high at this stage. However, before introduction ("pre-introduction"), the management strategy is prevention. Efficiency is high and cost is low at this stage. Using this framework, the most cost-efficient strategy to manage invasive species is to prevent them from invading. The best way to prevent invasions is to predict them before introduction. This dissertation threads a common theme of prediction through each of the three studies.

This dissertation research aims to 1) measure the relative effects of known drivers on global invasion success; 2) incorporate the effect of spatial scale on outcomes of those processes; and 3) model the density of invasive species in global regions to estimate invasibility. We completed three independent but complimentary studies that investigate invasiveness of species and invasibility of regions over multiple scales using novel approaches.

Study 1 evaluates the relative likelihood of successful plant invasion in a given region using factors at each stage of the invasion process for 215 woody plant species. For each plant in the study, the factors at each stage include connectivity (introduction stage), habitat suitability (establishment stage), and biodiversity (spread stage) of native and non-native ranges. These factors are used as variables in explanatory models to determine if they facilitate plant species' invasiveness.

Study 2 analyzes invasion patterns over three spatial scales to understand how scale affects the observed outcomes of processes driving species invasiveness. We tested whether the effect of factors at each stage in the invasion process change over different spatial scales. For each plant in the study, the factors at each stage include connectivity (introduction stage), habitat suitability (establishment stage), and biodiversity (spread stage) of native and non-native ranges. These factors and interactions among them are used as variables in explanatory models to determine if they facilitate plant species' invasiveness over three spatial scales.

Study 3 models factors of exotic fraction (EF) to identify regions with high potential of invasion. We modelled EF as a function of factors found at each stage of the invasion process 1) regional connectivity; 2) eco-realm as determined by Ecoregions2017©Resolve (Dinerstein et al. 2017); and 3) native diversity. The results from this study can be used as a predictive tool to determine future invasibility of regions.

This dissertation research investigates factors facilitating global invasion success at each stage of the invasion process, illuminating the cross-scale relationships

between connectivity, habitat suitability, and biodiversity. The conclusion section broadly summarizes the scientific findings of this dissertation with emergent themes and potential future directions.

I.1 Figures

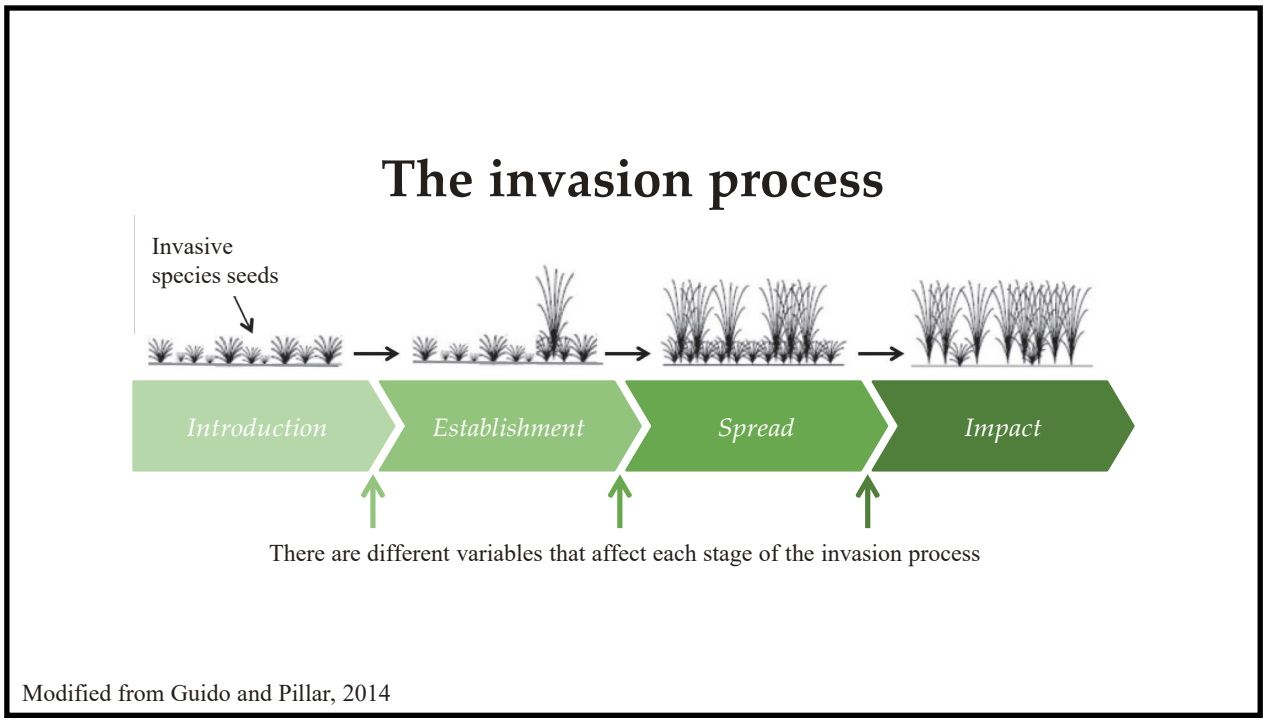

Figure I-1: The invasion process depicted in four stages as modified from Simberloff et al. 2013.

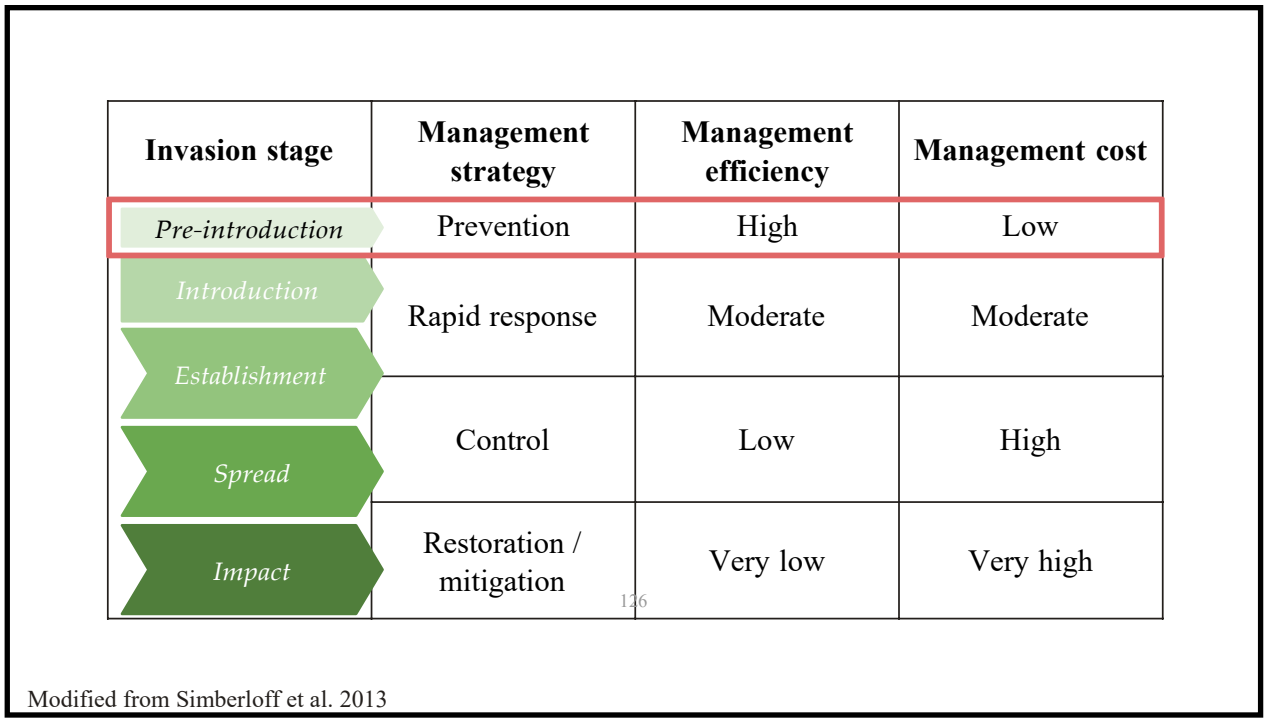

Figure I-2: The management strategies used for invasive species as depicted for each stage of invasion. The strategies range in efficiency and cost, depending on the stage of invasion.

CHAPTER 1: REGIONAL PHYLOGENETIC DIVERSITY DRIVES INVASION SUCCESS IN PLANTS ON A GLOBAL SCALE

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1.1. Abstract

Globalization has resulted in the anthropogenic movement of plant species, many of which have established and become invasive in their secondary ranges despite independent evolutionary histories. Comparing characteristics between and interactions among native and non-native regions of invasive species are the basis for hypotheses explaining invasion success yet we still lack evidence in explaining the factors facilitating successful plant invasion. This study uses multiple publicly available databases to evaluate the relative likelihood of successful plant invasion in a given region by comparing characteristics between native and non-native regions. We estimated the likelihood of invasion success as a function of 1) divergence of evolutionary history between regions; 2) suitability of habitat in the non-native region; and 3) connectedness of native and non-native regions. We found that divergence of evolutionary history between regions was the strongest factor contributing to invasion

success. For example, when the diversity of a species' native range was lower than that of the non-native range, invasion success was low. Surprisingly, we found this to be the case even when habitat suitability and connectivity were high. This study is the first to highlight the importance of the diversity of a species' native range on a global scale.

1.2. Introduction

Globalization has resulted in the anthropogenic movement of plant species, many of which have established and become invasive in their secondary ranges despite independent evolutionary histories (Pyšek et al. 2012; van Kleunen et al. 2015). A fundamental goal in invasion ecology is to understand the factors that determine successful establishment and spread of invasive species on a global scale. Given the likelihood of a future with increased international connections leading to introductions of plant species, understanding which species are successful invaders and which ecosystems are susceptible to invasion continues to be crucial to development of effective preventative policy and management strategies (reviewed in Hulme 2006; Hulme et al. 2008; Rout et al. 2011; SCBD, 2011).

Comparing characteristics between and interactions among native and non-native regions of invasive species are the basis for hypotheses explaining invasion success (Broennimann and Guisan 2008; Buckley and Catford 2016; Fridley and Sax 2014; Iannone et al. 2016; Whitfeld et al. 2014). Specifically, the combined effects of evolutionary history on species invasiveness, or the propensity for species to invade, and regional invasibility, or the propensity for a region to be invaded, have been repeatedly hypothesized as drivers of invasion success (MacArthur 1972; Rejmanek

1989; Tilman et al. 1999; Sax and Brown 2000; Mack 2003; Stachowicz and Tilman 2005; Vermeij 2005; Leigh et al. 2009; Gerhold et al. 2011; Fridley 2013; Fridley and Sax 2014; Whitfeld et al. 2014). It remains unclear whether the divergence in evolutionary history between native and non-native regions plays a prominent role in driving invasion success on a global scale.

The role of evolutionary history on the invasion process can be explained in two parts. First, the ability of a species to occupy niche space outside its native range is associated with the presence of traits that allow for an alternative pathway to invasion success (Mack 2003; Stachowicz and Tilman 2005; Vermeij 2005; Baltazar-Soares et al. 2017; Golivets and Wallin 2018). Adaptations of traits that increase fitness occur through the acquisition of beneficial mutations as a response to constant selection pressure (Fisher 1930). Therefore, species native to regions with higher net rate of trait diversification (i.e. deep evolutionary histories) are predicted to become invasive (Fridley and Sax 2014; MacArthur 1972) compared to those lacking deep evolutionary histories. Second, resistance to invasion of non-native species in regions with deep evolutionary histories can be similarly explained by a lack of functional trait space available, implying an increased overlap of niches due to higher competition for resources and the presence of superior adaptations in a diverse suite of resident species (MacArthur 1955, 1972; Elton 1958; Ashley et al. 2003; Davis et al. 2000; Sax and Brown 2000; Gerhold et al. 2011; Fridley and Sax 2014; Whitfeld et al. 2014; Iannone et al. 2016). These relationships can be represented in trait diversity of a regional pool. Although these concepts have been hypothesized and tested at local and regional scales

(Fridley and Sax 2014; Gerhold et al. 2011; Whitfeld et al. 2014), a global scale study quantifying the effect of divergent regional evolutionary history on invasion success remains untested. A rigorous test of the divergence between evolutionary history of native and non-native regions would address this gap in understanding invasiveness of species and invasibility of regions.

Although regional evolutionary history may be an important driver in determining the success of invasive species, it is not the only one. It is likely coupled with regional connectivity and abiotic factors. It is widely known that patterns of invasion are affected by human movements and global trade networks (Office of Technology Assessment 1993; Daehler and Carino 1999; U.S. Department of Agriculture 1999; Levine et al. 2000; Perings et al. 2000; Convention on Biological Diversity 2002; Levine and D'Antonio 2003; Seebens et al. 2015; van Kleunen et al. 2015; Turbelin et al. 2016; Chapman et al. 2017). For example, trade networks are a proxy for propagule pressure and, when included in species distribution models, increase predictive accuracy (Cardador et al. 2016). Therefore, as the connectivity between regions increases, so should the likelihood of the species transferred between them. Despite the clear link between regional connectivity and invasion success, there are gaps in our understanding of the relative effects of this driver combined with evolutionary history.

Environmental characteristics such as temperature, precipitation, and elevation are known to affect the distribution of all species, commonly termed environmental filtering (Nobel and Slayter 1977; van der Valk 1981; Bazzaz 1991). We argue that the

utilization of environmental characteristics in explaining species invasions requires estimates of habitat suitability because as the similarity between native and recipient regions increases, so might the potential for invasion (Peterson 2003; reviewed in Gallien et al. 2010; Barbet-Massin et al. 2018). While the influence of environmental factors on invasive plant distribution has been tested elsewhere (Guisan and Thuiller 2005; reviewed in Gallien et al. 2010; Barbet-Massin et al. 2018), to our knowledge this study is the first to couple habitat suitability with divergent regional evolutionary history and global connectivity to analyze the interactions and combined effects of these drivers on a global scale.

This study posits that the links among the divergence of regional evolutionary histories, habitat suitability, and regional connectivity are important drivers of invasion successes. We frame this study with two complimentary hypotheses. First, we hypothesize that species native to phylogenetically rich regions are more likely to establish and become invasive outside their native range. This could be explained in two ways: a) invasive species could occupy different niches or trait states than resident species, following the coexistence hypothesis (Prinzing et al. 2008; Webb et al. 2002); and b) established invasive species could outcompete residents in the non-native range due to superior competitive traits obtained through repeated interspecific interactions in the native range (Fridley and Sax 2014). Second, we hypothesize a negative relationship between phylogenetic diversity (PD) and regional invasibility. This is based on the finding that PD estimates trait diversity within a region (Davis et al. 2000; Elton 1958; Fridley and Sax 2014; Gerhold et al. 2011; Iannone et al. 2016; MacArthur

1955; MacArthur 1972; Sax and Brown 2000; Whitfeld et al. 2014), inferring a negative relationship between PD and niche space available for incoming species.

Here, we analyze invasion patterns of 214 woody invasive plant species in 368 global regions. We test whether their global invasive distributions were driven by the relative differences in PD, connectivity, and habitat suitability between native and non-native regions. We develop models that incorporate these variables and the interactions between them to explain plant invasiveness on a global scale.

1.3. Methods

1.3.1. Study species

Non-native woody species have become prominent invaders on lists such as '100 of the World's Worst Invaders' (Lowe et al. 2000) and '100 of the worst' invasive species in Europe (Nentwig et al. 2018). Woody plants, trees and shrubs, represent an ecologically defined group with historical records in many parts of the world, making them suitable taxa to study plant invasiveness (Pyšek et al. 2009; Pyšek and Richardson 2007; Richardson and Rejmánek 2004). In this study, we initially considered 751 invasive woody species from 90 families compiled previously (Rejmanek and Richardson 2013). Of these, we included data from 214 for which native and non-native distributional data were available. Invasive species are defined as those that were transported by humans and have successfully established and spread in the introduced region (Richardson et al. 2000).

1.3.2. Data collection

Three explanatory variables were evaluated in this study including ΔPD , habitat suitability, and connectivity. Explanations of data collection for those variables are found in the sections below.

1.3.2.1. Phylogenetic diversity (PD)

We used a five-step process to measure the effect of evolutionary history on invasiveness of species and invasibility of regions. First, we compiled 368 regional floras of all vascular plants. Next, we generated regional phylogenies by pruning a recently comprised megaphylogeny with regional floras (Qian and Jin 2019). Next, we used the pruned regional phylogenies to estimate PD for each region. Then, using native distributions (CABI ISC 2019; GISD 2015) we assigned each species in the dataset a PD value that corresponds to the mean PD value of regions overlapping their native range. Lastly, we calculated the difference in PD between invasive species' native and non-native ranges to assign a ΔPD value to each region for each species. ΔPD values are used as an explanatory variable in our model examining the probability of successful invasion as a function of PD of the native range.

1.3.2.1.1. Compiling regional floras

We determined the geographical units for this study following the Biodiversity Information Standards (formally Taxonomic Database Working Group; TDWG; Brummit et al. 2001). We used TDWG level 3 (n = 368 regions) corresponding to countries or large intra-national regions because these spatial units and digitized georeferenced maps are based largely on phylogeography or existing floristic knowledge and commonly used in ecological studies (Dawson et al. 2017; Fontaneto et

al. 2012; Pyšek et al. 2017; van Kleunen et al. 2015, 2018; Weigelt et al. 2019). We obtained regional occurrences of vascular plant distribution and taxonomic information from the Royal Botanic Gardens, Kew (POWO, 2018). The resulting 368 regional floras were used to build phylogenetic trees for PD estimations.

1.3.2.1.2. Generating regional phylogenies and estimating PD

We estimated regional evolutionary history using the proxy of PD because this approach measures the gradual changes in traits across phylogenetic nodes in a regional phylogeny (Faith 1992). Traits are defined as nucleotides of a gene, which could change to multiple character states via mutation. PD is estimated using the sum of all branch lengths in a phylogenetic tree, which indicate the difference between two genes. Relative branch lengths are measured by taking the quotient of nucleotide substitutions per sequence site and length of the sequence. This estimation infers the number of traits in a regional species pool, which conveys far more information than just measuring species richness, a metric that doesn't consider trait diversification over evolutionary time (Faith 1992). The number of traits in a region could be reflective of the competitive intensity, environmental consistency, and adaptations accumulated by the species in question, allowing regional evolutionary history to be represented by PD (Leigh et al. 2009; Vermeij 1996).

Using regional floras, we generated regional phylogenies by pruning the most recent and comprehensive published megaphylogeny of vascular plant species in the Newick format (Qian and Jin 2016). The species-level phylogeny was originally generated with maximum-likelihood estimates using sequence data of seven gene

regions (i.e. 18S rDNA, 26S rDNA, ITS, matK, rbcL, atpB and trnL-F) and time-scaled with 39 fossil calibrations (Zanne et al. 2014). Gene regions of the megaphylogeny include both slowly and quickly evolving gene regions. This phylogeny was recently improved to include all extant families of gymnosperms and angiosperms with standardized botanical nomenclature of species names per The Plant List (Qian and Jin 2016). Species present in the floras were matched to tips in the phylogeny using the "match.phylo.comm" function and the phylogeny was trimmed into regional phylogenies using the "prune.sample" function, both found in the picante package (Kembel et al. 2010). The resulting regional phylogenies include labeled nodes (families), labeled tips (species), and branch lengths that connect nodes.

To estimate phylogenetic diversity of each region, we used Faith's PD method (Faith 1992) in the picante package (Kembel et al., 2010) calculating the total branch length of each regional phylogeny (figure 1-1). Regional PD scores were used to calculate the divergence of evolutionary histories between native and non-native regions of invasive plants in the dataset.

1.3.2.1.3. Species distributions in native and non-native regions

To compare PD between native and non-native regions for species in our dataset, we used three publicly available databases: GBIF (2020), CABI ISC (2019) and GISD (2015).

We retrieved native occurrence data from CABI ISC and GISD. To extract data from CABI ISD, we performed a database query of invasive species found in our dataset using genus and species names. We downloaded .csv files directly from the

CABI ISC website and merged them, resulting in a data frame that includes species names, native regions where recorded, and the geographic coordinates for the centroid (central point) of each region. To extract information from GISD, we exported all Plantae records and subset those for the invasive species found in our dataset. The resulting data frame includes species names, native countries where recorded, and source. GISD reports country-wise checklists of species native occurrences rather than geographic coordinates, therefore we assigned a TDWG level 3 region to each record. To do this, we assigned centroid coordinates to countries using the "gCentroid" function in the package rworldmap (South, 2011). Then, using a spatial left join (the "st_join" function in the nngeo package) we assigned centroid points to the corresponding regional polygon in the TDWG level 3 shapefile. We compiled a data frame with regional centroids by creating a world map using the "getMap" function and determined centroids of regions using the gCentroid function, both in the rgeos package (Bivand and Rundel, 2017). After merging the datasets using the rbind function and removing duplicate and erroneous occurrences, the resulting data frame includes binary native occurrences in TDWG level 3 regions for species in our dataset.

We retrieved non-native occurrence data from GBIF, which is a collection of the most comprehensive inventories of plant occurrences to date. We subset the download to include binary non-native occurrences in TDWG level 3 regions for species in our dataset.

1.3.2.1.4. Assigning PD values and calculating ΔPD

Invasive species in the dataset were assigned a PD value that corresponds to the mean PD value of regions overlapping their native range. We compared native region PD to all non-native regions' PD by calculating the difference between them (ΔPD = native_PD – non_native_PD). Greater PD in the native region produces a positive ΔPD value, while greater PD in the non-native region produces a negative ΔPD value. As the absolute value of ΔPD increases, we assume that the divergence in evolutionary history of the regions is increased. If ΔPD is zero, we assume no relative difference in the evolutionary history between the two regions. The variable ΔPD was used in our model along with regional connectivity and habitat suitability values described below.

1.3.2.2. Habitat suitability

To estimate habitat suitability of non-native regions, we constructed species distribution models (SDMs) for invasive species in the dataset using geographic coordinates of known species occurrences and environmental characteristics at associated sites. SDMs are widely used to explain species distributions by statistically correlating observed species occurrences with environmental variables. We pooled environmental data from all ranges (native, casual, naturalized, and invasive) to inform SDMs because the naturalized climatic niches of invasive species i.e., "realized niche" may differ from that of the native region (Barbet-Massin et al. 2018; Broennimann and Guisan 2008; Early and Sax 2014; Gallien et al. 2012; Petitpierre et al. 2017). To account for sampling bias, which is a drawback frequently associated with occurrences of invasive species (Broennimann and Guisan 2008), we used only binary regional occurrences instead of abundances. SDMs were used to assign habitat suitability scores

to non-native regions for each species. Habitat suitability scores were used as a covariate in the model explaining the probability of invasion success in an introduced region.

1.3.2.2.1. Global distribution data

Geographic coordinates of known species occurrences were compiled to calibrate the SDMs using the CABI ISC (2019), GISD (2018), and GloNAf databases. We chose to use all global occurrences in all stages of invasion or nativity for species to account for the full distribution of suitable habitats in non-native regions (Broennimann and Guisan 2008; Gallien et al. 2010; Peterson and Soberón 2012). This method differs from the one used in estimating PD because, to assign habitat suitability scores for each region, it is best to account for regions inside and outside of the native climatic range (Broennimann and Guisan 2008; Broennimann et al. 2007; Early and Sax 2014). The CABI ISC and GloNAf databases use centroids of TDWG regions. The GISD database does not use the TDWG format, therefore we used the same method (see above) to assign TDWG level 3 regional centroids to each coordinate. As above, data was combined and duplicate and nonsensical data removed.

1.3.2.2.2. Environmental variables

The accuracy of SDMs relies strongly on the choice of environmental predictors used in the models (Petitpierre et al. 2017). Predictors for this study were chosen based on the results found in a global comparison of strategies (Petitpierre et al. 2017) and includes altitude range, average annual precipitation, precipitation seasonality, temperature annual range, minimum annual temperature, maximum annual

temperature, and temperature seasonality. Values of environmental predictors for all TDWG level 3 units were obtained from the Worldclim package (Fick and Hijmans, 2017).

1.3.2.2.3. Determining habitat suitability scores

Environmental predictors were used to fit models that estimate similarity to the sites of occurrence using the "bioclim" function in the dismo package (Hijmans et al. 2017). Bioclim is a "climate-envelope model" and has been widely used and is relevant for species distribution modeling (Booth 2014; Hijmans and Elith 2017). Specifically, the bioclim model calculates the suitability of a region by comparing the values of environmental variables at any region to a percentile distribution of the values at known occurrences. More suitable locations are found in the 50^{th} percentile and the tails (10^{th} percentile and 90^{th} percentile; equivalent to each other) are considered unsuitable regions. To extract a suitability value for each region, the upper tail is transformed to the lower tail and the minimum percentile score across all environmental variables is subtracted from 1 then multiplied by 2 so the results are between 0 and 1. A value of 1 represents the highest probability of occurrence and a value of 0 represents the lowest - an unsuitable region. Bioclim models were fit using multivariate models and previously mentioned environmental predictors for occurrence coordinates of each species. To create a map of suitability scores for each species, we provided the "predict" function in the dismo package with the environmental predictors (raster object) and model output (model object).

To statistically evaluate SDMs, we employed the correlation coefficient and the Area Under the Receiver Operator Curve (AUROC, usually abbreviated to AUC) (Phillips et al. 2006). AUC characterizes the performance of a presence only SDM by measuring the sensitivity of predictions (the fraction of all positive instances that are classified as suitable) and specificity of predictions (the fraction of randomly chosen background points that are classified as unsuitable). A receiver operating characteristic (ROC) curve is created by plotting SDM sensitivity on the y axis and 1-specificity on the x axis. For each predicted value of suitability, the ROC will hold one point. The AUC is determined by connecting those points with lines, and indicates the probability that a presence point and a random negative point are correctly ordered. A higher AUC score indicates that high predicted suitability scores will be areas of known occurrences (presence) and low predicted suitability scores will be areas of unknown occurrences, or known absence. We applied these methods to evaluate accuracy and explanatory power of SDMs.

1.3.2.3. Connectivity

1.3.2.3.1. Global trade networks

We used information on global trade networks as a proxy for propagule pressure, to consider the connectivity of regions in explaining species invasions. As shown in previous studies, invasion potential is strongly affected by regional connectivity through import volume of global trade networks (Chapman et al. 2017; Levine and D'Antonio 2003; Seebens 2013; Seebens et al. 2018, 2015). We used commodity-specific trade data to estimate a pairwise connectivity index for all regions

in this study, as agricultural and live plant imports through shipping networks have a stronger effect on plant invasion potential than total import volumes (Chapman et al. 2017). To do this, we obtained raw data from the USDA Foreign Agricultural Service's Global Agricultural Trade System (FAS GATS) on imports of live plant commodities ("live plants" in tonnes) to countries from all global trading partners and created a bilateral trade network that consists of data from 1994 to 2013. As a measure of network connection, we used average trade volumes (in tonnes) from reporting countries to partners over the 19-year period. Import data was downloaded directly from the FAS GATS (USDA-FAS 2020).

We assigned centroids to reporter and partner countries using the "gCentroid" function in the rworldmap package, then converted the coordinates to spatial points to overlay on to the TDWG regional shapefile. This allowed us to assign TDWG regions to countries for analysis. Some small island countries were found to be outside of the shapefile thus unable to be captured using traditional overlay techniques. Using the sf (Pebesma 2018) and nngeo packages, we created a tolerance buffer around the shapefile and then using the "nearest neighbor" approach in the "st_join" function, assigned points outside of the shapefile (coastal / small islands) to the nearest polygon (TDWG region).

1.3.3. Data analyses

All statistical analyses were performed in R (R Core Team 2020). Our analyses evaluated the influence of evolutionary history using the proxy PD, habitat suitability, and connectivity on probability of invasion success in global regions. The unit of all

analyses was detection of the species as an invader in the region, so a binary response variable coded invasive (1) or not found (0) in each region. To this, we fit generalized linear mixed effects models (GLMM) with logit link functions for binomial errors and fixed effects of delta PD, habitat suitability, and connectivity and random effects of species and origin region using the lme4 package (Bates, Mächler, Bolker, and Walker 2015). GLMM approach allowed us to test our hypotheses while accounting for spatial heterogeneity between regions and species using random effects (Hamil et al. 2016) and Type I error (Anderson et al. 2000; Spanos 2014; Woodall and Westfall 2010). Before model fitting, fixed effects were scaled and centered on zero to evaluate them on relative terms. All possible models and a null model were fitted along with two- and three-way interactions between fixed effects. Models were ranked according to corrected Akaike's information criterion (AICc) values (Akaike 1974; Nakagawa and Schielzeth 2013) using the MuMIn package (Barton and Barton 2015). Assumptions were visually evaluated using plots created from simulated residuals from the DHARMa package (Hartig 2017).

1.4. Results

We retrieved native and non-native occurrence data from 214 woody invasive species totaling 78,271 observations. Of the candidate models, the global model received the most support with a weight of one (table 1-1).

Overall, the probability of invasive presence was positively affected by all covariates (figures 1-2 and 1-3). Habitat suitability had a positive effect (odds ratios estimate of the coefficient was 1.32 and 95% confidence interval 1.29 – 1.35; figure 1-

2A). Delta PD had an odds ratio estimate of the coefficient was 1.29 and 95% confidence interval 1.25 – 1.33 (figure 1-2B). Connectivity had an odds ratio estimate of the coefficient was 1.12 and 95% confidence interval 1.09 – 1.15 (Figure 1-2C). All covariates had 95% confidence intervals that did not overlap 1.0, indicating with 95% confidence that the values of those coefficients were positive. We calculated the marginal and conditional R^2 values to estimate variation explained by the fixed effects and both fixed and random effects in the model (marginal $R^2 = 0.033$; conditional $R^2 = 0.275$; table 1-2).

We estimated two-way interactions between explanatory variables (table 1-2; figures 1-4, 1-5, 1-6). Delta PD had a positive effect on the probability of being invasive regardless of habitat suitability (figure 1-4) and connectivity (figure 1-5). However, we found that delta PD had the strongest effect with a probability of invasion 75% when habitat suitability was greatest (two-way interaction odds ratios estimate of the coefficient was 1.16 with a 95% confidence interval of 1.12 – 1.20; table 1-2; figure 1-3). The two-way interaction between delta PD and connectivity was positive (odds ratios estimate of the coefficient was 1.04 with a 95% confidence interval of 1.01 – 1.07; Table 2; figure 1-5). The two-way interaction between habitat suitability and connectivity was slightly negative (odds ratios estimate of the coefficient was 0.92 and had a 95% confidence interval of 0.90 – 0.94; table 1-2; figure 1-6).

We estimated three-way interactions between explanatory variables (table 1-2; figures 1-7, 1-8, 1-9). The overall three-way interaction between all covariates was

positive (odds ratios estimate of the coefficient was 1.15 with a 95% confidence interval of 1.11 – 1.20; table 1-2).

1.5. Discussion

Understanding the factors determining successful establishment of invasive plant species is still a major challenge in invasion biology. To our knowledge, our study is the first to integrate the relationship between invasiveness of species and invasibility of regions by using phylogenetic diversity, habitat suitability, and connectivity between native and non-native regions on a global scale. Our analysis shows that the occurrences of invasive plant species in this study were strongly determined by all three covariates, however the determinacy was unequal.

Consistent with our first hypothesis, species native to phylogenetically diverse regions were more likely to establish and become invasive compared with species native to phylogenetically poor regions. High phylogenetic diversity can be characterized by high net trait diversification and exceedingly competitive environments (MacArthur 1972; Fridley and Sax 2014). Therefore, species native to regions with higher PD could be pre-adapted to have novel (novel weapons; Callaway et al. 2004), tolerant (Golivets and Wallin 2018), or superior competitive traits obtained through repeated interspecific interactions in their native range (MacArthur 1972; Fridley and Sax 2014). We found that when PD in the native range was lower than PD in a non-native region, probability of invasion was lowest. This was the case even when habitat suitability and connectivity were high, thereby reducing the roles of those variables. In contrast to previous studies highlighting the importance of habitat

suitability (Richardson and Thuiller 2007; Turbelin et al. 2017) and connectivity (van Kleunen et al. 2015; Seebens et al. 2018) to invasion success, our findings show that these factors are less important when delta PD is low.

Second, and consistent with our second hypothesis, regions were more likely to be invaded when their PD was lower than that of the native region of the introduced plant. Regions with PD greater than that of the introduced plant were less likely to be invaded. This suggests that phylogenetically diverse regions have a stronger ability of competitive exclusion (Stachowicz and Tilman 2005) or could have less niche space available for incoming species. This finding is also consistent with the biotic resistance hypothesis, which assumes that a greater number of niches are filled in species rich ecosystems (Tilman 1997; Stachowicz and Tilman 2005) and that superior competitors may exist (Crawley et al. 1999). Although our findings follow the biotic resistance hypothesis in theory, we suggest that the biotic resistance hypothesis should be updated with PD instead of species richness, as PD is more thorough in describing diversity in a region.

Similar climatic environments exist in many parts of the world and species are more likely to invade ecosystems similar to their established range. Therefore, it follows logic that our results show habitat suitability as a strong driver of invasiveness (Figures 1, 6, and 7). Propagule pressure is consistently shown to have a positive relationship with invasibility (Blackburn and Duncan 2001; Simberloff 2009; Lockwood et al. 2005). As the number of individuals introduced increases, so does the

probability of invasion success. This is consistent with our results, using connectivity as a proxy for propagule pressure (Seebens et al. 2015; Chapman et al. 2017; Figure 1).

Although results strongly support the hypotheses that invasiveness is affected by divergent evolutionary history between native and non-native ranges, habitat suitability, and regional connectivity, this study does not explain the effects of anthropogenic disturbance in ecosystems or secondary invasions, both very important factors in determining invasion outcomes. The occurrence information used in this study is only as strong as the sampling strength. For regions where there is less field work and plant inventory, there will be inherently lower sampling therefore less samples. This is a limitation of all data mining studies using global species occurrences. We understand that other metrics of connectivity exist and are possible vectors for the exchange of species. This may be the reason why connectivity had the weakest effect. The results in this study provide a framework for understanding species invasiveness and regional invasibility but do not suggest that all species from phylogenetically rich regions will become invasive in phylogenetically poor regions.

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1.7. Figures

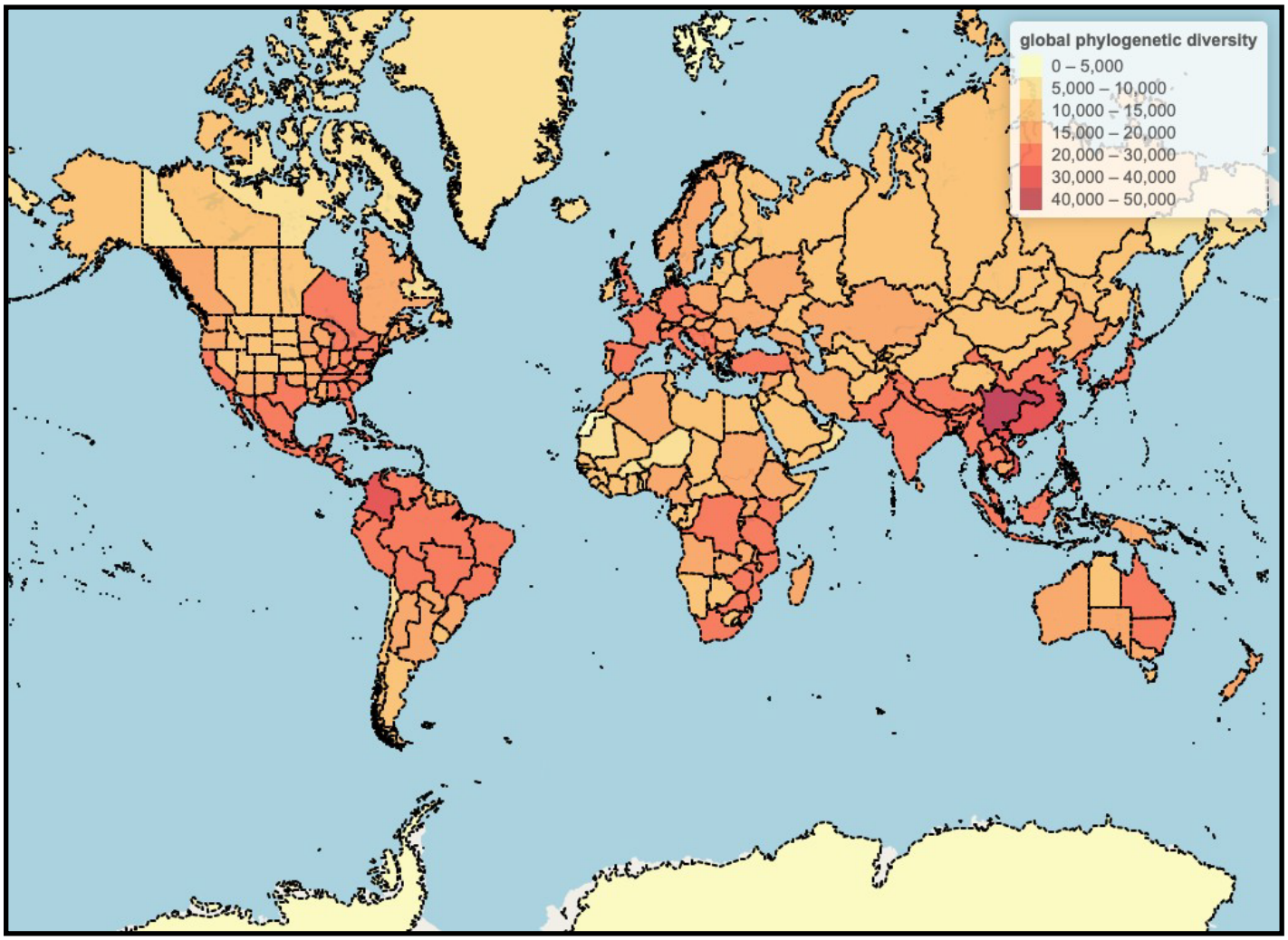

Figure 1-1. Choropleth map of global phylogenetic diversity values.

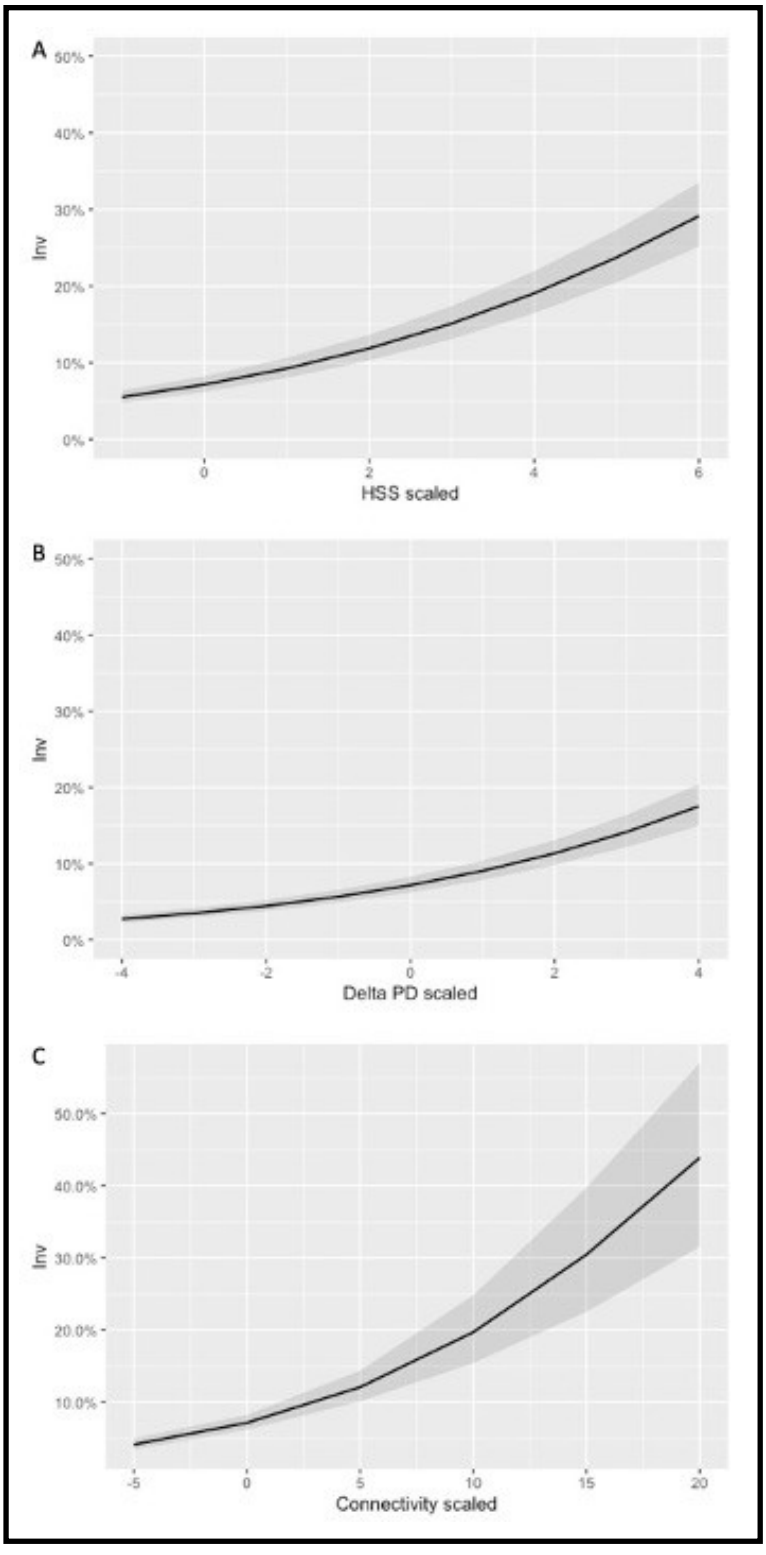
A
50%
40%
30%
20%
10%
0%
Inv
0
2
4
6
HSS scaled
B
50%
40%
30%
20%
10%
0%
Inv
-4
-2
0
2
4
Delta PD scaled
C
50.0%
40.0%
30.0%
20.0%
10.0%
Inv
-5
0
5
10
15
20
Connectivity scaled

Figure 1-2. Plots showing predicted probabilities of invasion success ("Inv") as a function of scaled individual variables (A. Habitat suitability; B. Delta PD; C. Connectivity) for 214 woody invasive plant species.

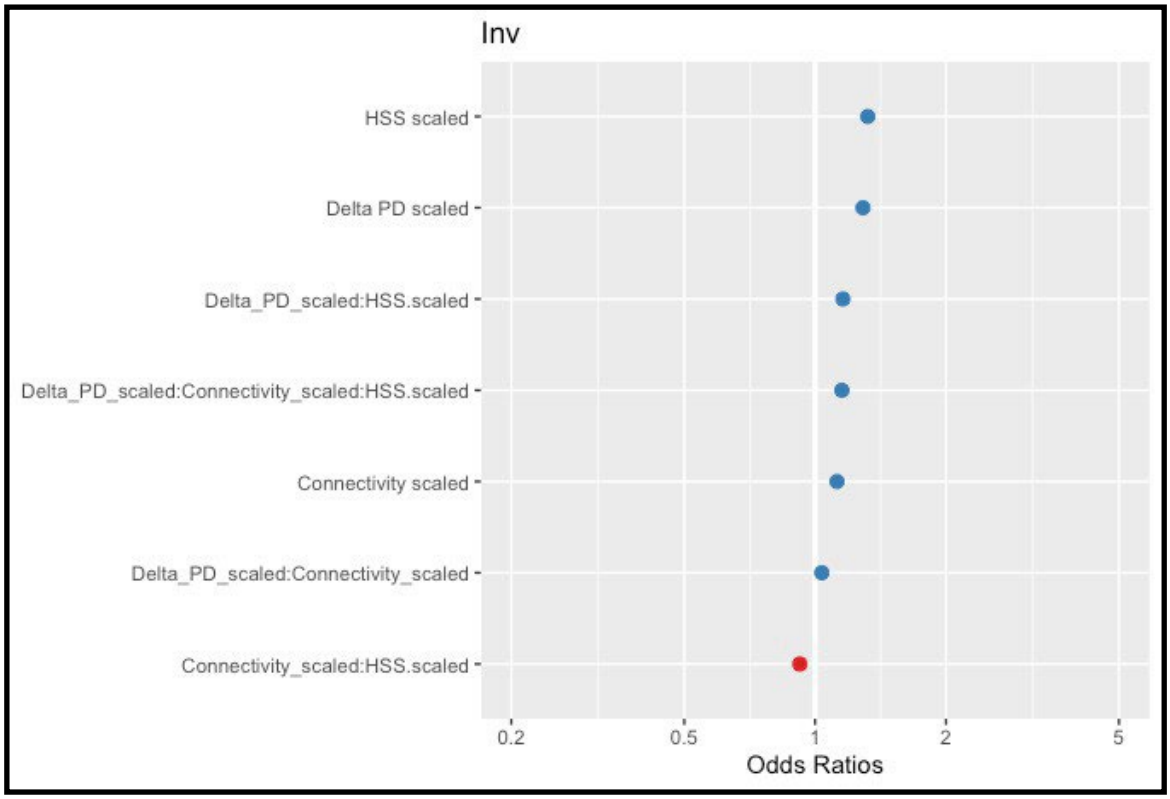

Figure 1-3. Odds ratios plot for effects of covariates on the probability of invasive presence. The vertical intercept indicates no effect (x-axis position 1) is drawn slightly thicker than the other grid lines. A positive effect will show dots on the right side of the line. A larger number indicates a relatively stronger effect.

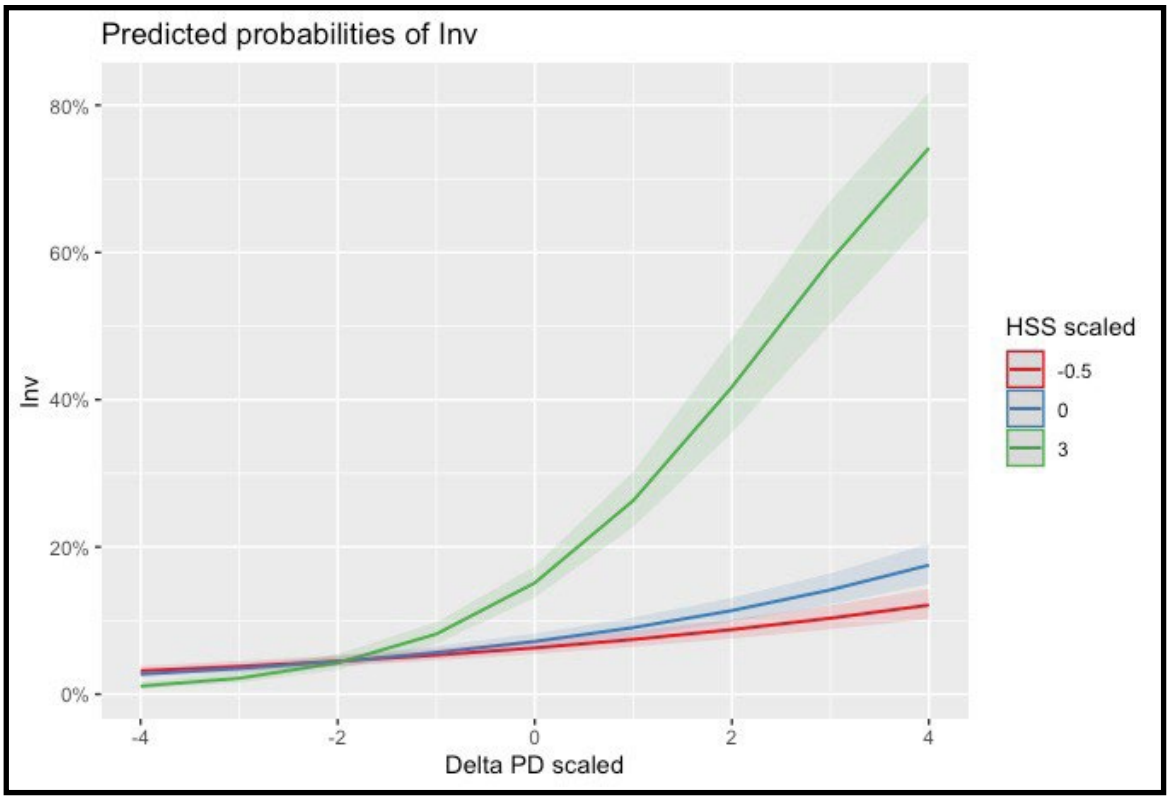

Figure 1-4. Two-way interaction plot showing the effect of habitat suitability on the role of delta PD in predicting the probability of invasion, Inv. The colored lines represent the value of delta PD when habitat suitability of regions is relatively low, medium, and high represented by red, blue, and green respectively.

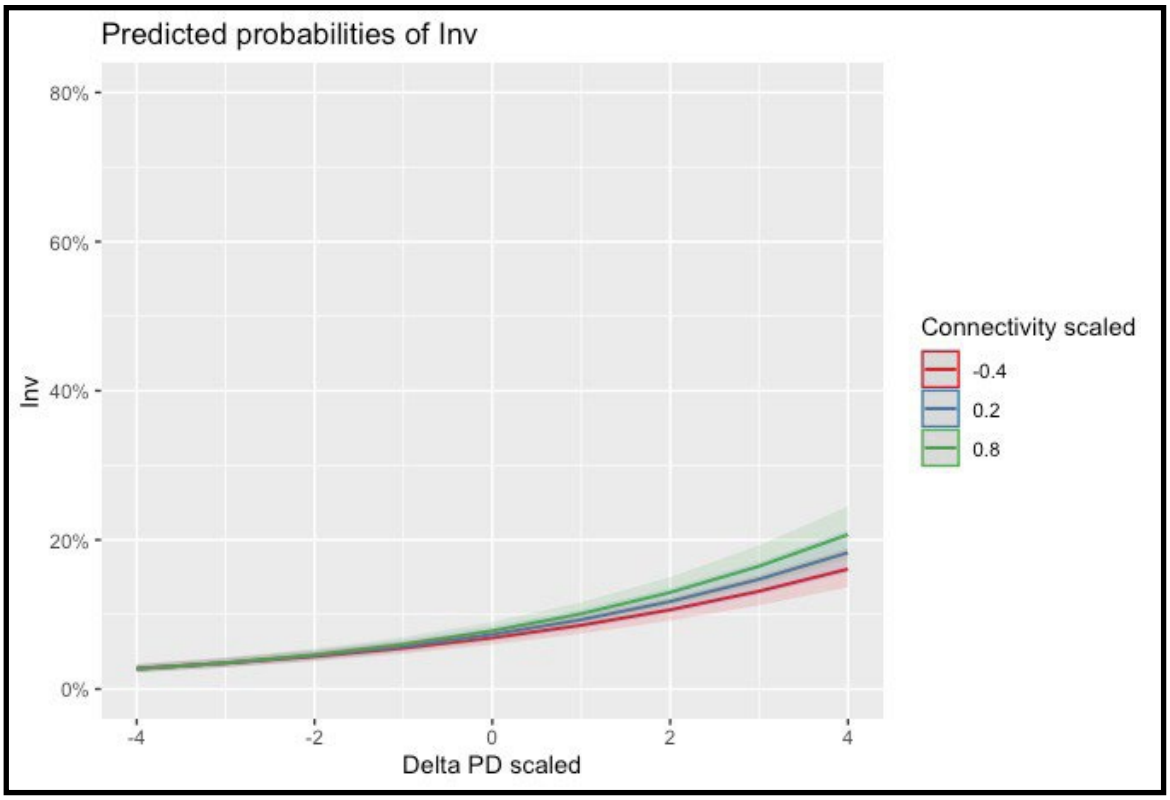

Figure 1-5. Two-way interaction plot showing the effect of connectivity between regions on the role of delta PD in predicting the probability of invasion, Inv. The colored lines represent the value of delta PD when connectivity between regions is relatively low, medium, and high represented by red, blue, and green respectively.

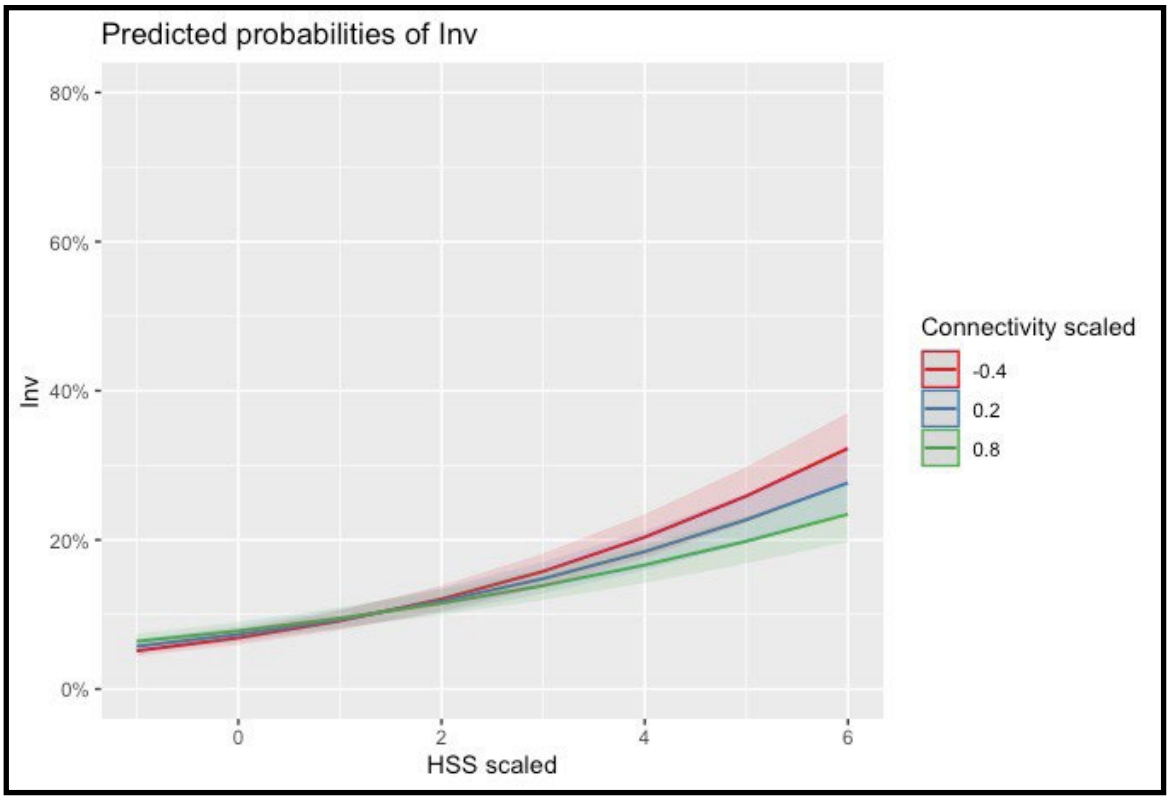

Figure 1-6. Two-way interaction plot showing the effect of connectivity between regions on the role of habitat suitability in predicting the probability of invasion, Inv. The colored lines represent the value of habitat suitability when connectivity is low, medium, and high as represented by red, blue, and green respectively.

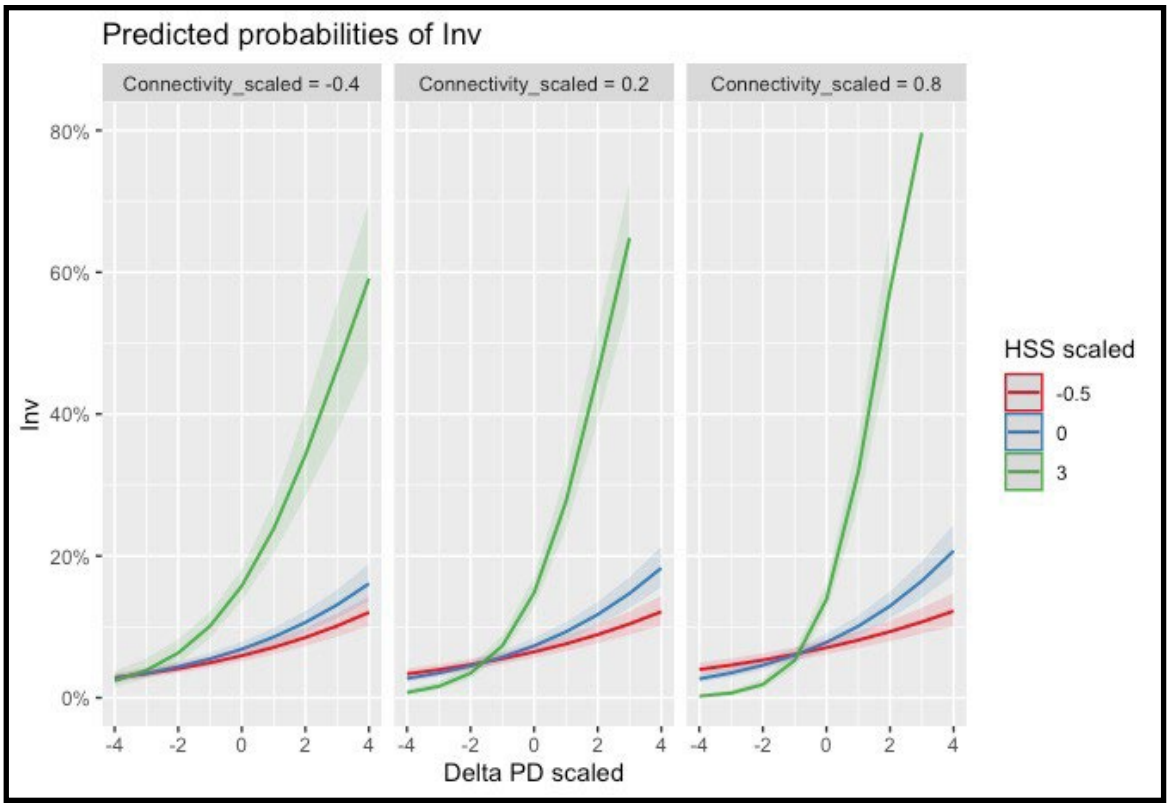

Figure 1-7. Three-way interaction plot showing the effect of delta PD on probability of invasion, Inv when habitat suitability is low, medium, and high as represented by red. blue, and green lines respectively. Plot is faceted by connectivity at three relative values of low, medium, and high in the first, second, and third facets respectively.

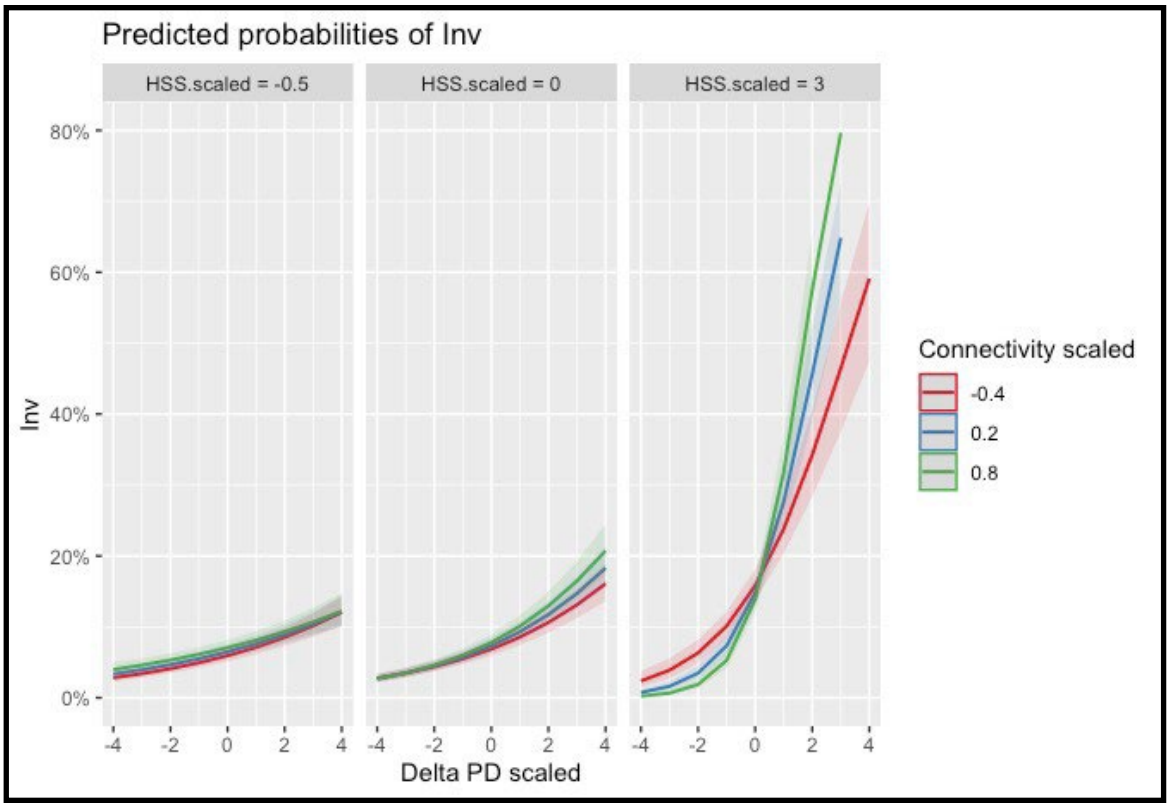

Figure 1-8. Three-way interaction plot showing the effect of delta PD on probability of invasion, Inv when connectivity is low, medium, and high as represented by red, blue, and green lines respectively. Plot is faceted by habitat suitability at three relative values of low, medium, and high in the first, second, and third facets respectively.

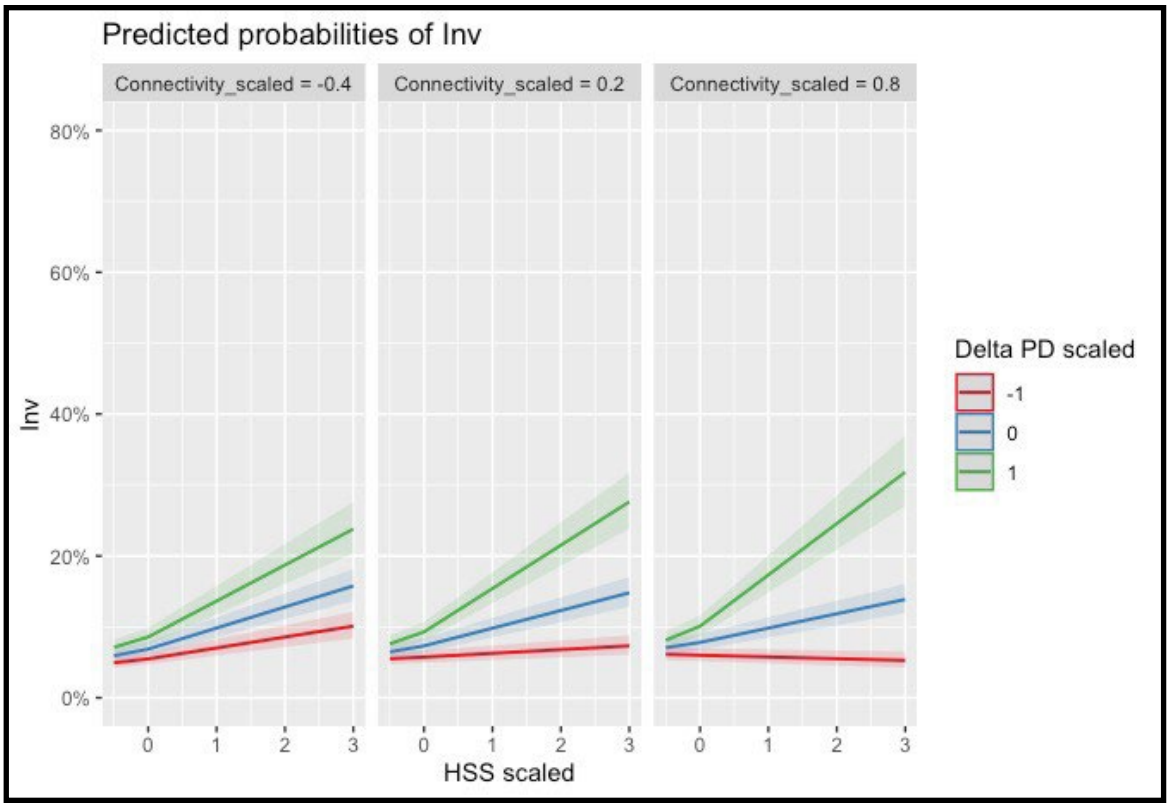

Figure 1-9. Three-way interaction plot showing the effect of habitat suitability on probability of invasion, Inv when delta PD is low, medium, and high as represented by red, blue, and green lines respectively. Plot is faceted by connectivity at three relative values of low, medium, and high in the first, second, and third facets respectively.

1.8. Tables

Table 1-1. Model selection table showing ten best candidate models.

Model	k	logLik	AICc	delta	weight
Delta_PD_scaled * Connectivity_scaled * HSS.scaled + (1 | fspecies) + (1 | fOrigin)	10	-22388.722	44797.4467	0	1
Delta_PD_scaled * Connectivity_scaled * HSS.scaled + (1 | fspecies)	9	-22411.271	44840.5441	43.0974255	4.38E-10
Delta_PD_scaled * HSS.scaled + Connectivity_scaled + (1 | fspecies)	6	-22475.623	44963.247	165.800307	9.93E-37
Delta_PD_scaled + Connectivity_scaled * HSS.scaled + (1 | fspecies)	6	-22477.982	44967.9652	170.518536	9.38E-38
Delta_PD_scaled * HSS.scaled + (1 | fspecies)	5	-22484.517	44979.0342	181.58749	3.70E-40
Delta_PD_scaled * Connectivity_scaled + HSS.scaled + (1 | fspecies)	6	-22519.739	45051.4794	254.03269	6.88E-56
Delta_PD_scaled + Connectivity_scaled + HSS.scaled + (1 | fspecies)	5	-22522.127	45054.2554	256.808686	1.72E-56
Delta_PD_scaled + HSS.scaled + (1 | fspecies)	4	-22528.472	45064.9446	267.497956	8.20E-59
Connectivity_scaled * HSS.scaled + (1 | fspecies)	5	-22591.169	45192.3388	394.892075	1.78E-86
Connectivity_scaled + HSS.scaled + (1 | fspecies)	4	-22631.659	45271.3177	473.871031	1.26E-103

Table 1-2. Summary statistics for global model predicting the probability of being invasive as a function of habitat suitability, delta PD, connectivity, and their interactions. Random effects are reported as species and origin region.

	Probability of Invasion	
Predictors	*Odds Ratios*	*CI (95%)*
(Intercept)	0.08	0.07 – 0.09
Delta PD scaled	1.29	1.25 – 1.33
Connectivity scaled	1.12	1.09 – 1.15
HSS scaled	1.32	1.29 – 1.35
Delta_PD_scaled:Connectivity_scaled	1.04	1.01 – 1.07
Delta_PD_scaled:HSS.scaled	1.16	1.12 – 1.20
Connectivity_scaled:HSS.scaled	0.92	0.90 – 0.94
Delta_PD_scaled:Connectivity_scaled:HSS.scaled	1.15	1.11 – 1.20
Random Effects		
σ^2	3.29	
$\tau_{00\ fspecies}$	1.08	
$\tau_{00\ fOrigin}$	0.02	
ICC	0.25	
$N_{\ fspecies}$	214	
$N_{\ fOrigin}$	133	
Observations	78271	
Marginal R^2 / Conditional R^2	0.033 / 0.275	

1.9. Supplemental information

1.9.1. Supplemental tables

Table S1-1. Full model selection table.

Model	k	logLik	AICc	delta	weight
Delta_PD_scaled * Connectivity_scaled * HSS.scaled + (1 | fspecies) + (1 | fOrigin)	10	-22388.722	44797.4467	0	1
Delta_PD_scaled * Connectivity_scaled * HSS.scaled + (1 | fspecies)	9	-22411.271	44840.5441	43.0974255	4.38E-10
Delta_PD_scaled * HSS.scaled + Connectivity_scaled + (1 | fspecies)	6	-22475.623	44963.247	165.800307	9.93E-37
Delta_PD_scaled + Connectivity_scaled * HSS.scaled + (1 | fspecies)	6	-22477.982	44967.9652	170.518536	9.38E-38
Delta_PD_scaled * HSS.scaled + (1 | fspecies)	5	-22484.517	44979.0342	181.58749	3.70E-40
Delta_PD_scaled * Connectivity_scaled + HSS.scaled + (1 | fspecies)	6	-22519.739	45051.4794	254.03269	6.88E-56
Delta_PD_scaled + Connectivity_scaled + HSS.scaled + (1 | fspecies)	5	-22522.127	45054.2554	256.808686	1.72E-56
Delta_PD_scaled + HSS.scaled + (1 | fspecies)	4	-22528.472	45064.9446	267.497956	8.20E-59
Connectivity_scaled * HSS.scaled + (1 | fspecies)	5	-22591.169	45192.3388	394.892075	1.78E-86
Connectivity_scaled + HSS.scaled + (1 | fspecies)	4	-22631.659	45271.3177	473.871031	1.26E-103
HSS.scaled + (1 | fspecies)	3	-22636.982	45279.9637	482.517036	1.67E-105
Delta_PD_scaled + Connectivity_scaled + (1 | fspecies)	4	-22774.04	45556.0799	758.633201	1.84E-165
Delta_PD_scaled * Connectivity_scaled + (1 | fspecies)	5	-22773.113	45556.2261	758.779441	1.71E-165
Delta_PD_scaled + (1 | fspecies)	3	-22792.794	45591.5891	794.142447	3.58E-173
Connectivity_scaled + (1 | fspecies)	3	-22867.157	45740.3151	942.868468	1.81E-205
1 + (1 | fspecies)	2	-22883.843	45771.6863	974.239636	2.80E-212

CHAPTER 2: THE EFFECT OF SPATIAL SCALE ON INVASION SUCCESS.

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2.1. Abstract

As movement of plants increases across the globe due to globalization, identifying ecological processes that determine species invasiveness and regional invasibility have become increasingly important. The scale at which non-native plant invasions are studied greatly affects the patterns observed, however, most studies of plant invasions focused on one spatial scale and although many have addressed the importance of scale, few have attempted to explain the variation among fine and coarse scale invasion processes. In this study, we used multiple publicly available databases to assess the global distribution patterns of woody invasive plants and the relative likelihood of their successful invasions over three spatial scales. We estimated the likelihood of invasion success as a function of 1) divergence of evolutionary history between regions; 2) suitability of habitat in the non-native region; and 3) connectedness of native and non-native regions over three spatial scales. We found that habitat suitability was the largest determinant of invasion success across scales, and that the

magnitude of this variable increased dramatically with scale. Surprisingly, connectivity between regions at all scales explained little to no variance in the probability of successful woody plant invasion. As suggested in previous studies but never tested rigorously on a global scale - scale matters.

2.2. Introduction

Ecological processes occur over complex spatiotemporal scales, and disentangling the interactions among pattern, process, and scale continue to be a major focus of ecology (Allen and Starr 1982; Wiens 1989; Levin 1992; Wu et al. 2000; Whittaker et al. 2001; Vekemans and Hardy 2004). identifying processes that determine species invasiveness have become increasingly important as movement of plants increases across the globe (Van Kleunen et al. 2015; Seebens et al. 2017) due to global trade, horticulture and other anthropogenic causes. Not surprisingly, the scale at which non-native plant invasions are studied greatly affects the patterns observed (Pauchard and Shea 2006; Guo et al. 2017). Most studies of plant invasions focused on one spatial scale and although many have addressed its importance, few have attempted to explain the continuity among fine and coarse scale invasion processes (Levine and Antonio 1999; Stohlgren et al. 1999; Sax and Gaines 2003; Pauchard and Shea 2006; Ward 2006; Guo et al. 2017; Deferrari et al. 2019).

Historically, it has been assumed that the distribution of plants is controlled by abiotic conditions (environmental filtering), biotic conditions (competitive interactions), and the confines of dispersal (Menge and Sutherland 2002). These processes affect distribution at different scales (table 2-1) and can be explained through a hierarchical framework of ecological systems as interrelated levels of organization (Simon 1962; Allen and Starr 1982). At the coarsest spatial scales (i.e. continental or regional), patterns observed are controlled by climate heterogeneity through environmental filtering (Wiens 1989; Keddy 1992; Levin 1992; McGill 2010). Coarse-

scale processes occur over hundreds of millions of years, such as tectonic plate movements and sea level changes. Disturbances such as fire and storms, which occur over one to one hundred years, generate change seen on finer scales (i.e. sub-regional or landscape) (Milne 1991). Finally, at the finest sub-regional or local scales, biotic processes such as competition are the main drivers of species distribution patterns (Menge and Sutherland 1976). Thus, the underlying processes that dictate observed patterns are temporally and spatially scale-dependent (Levin 1992), and the resulting outcomes from analyses on one scale might differ from those seen at other scales (Wiens 1989; Gould 1998; Pauchard and Shea 2006). To accurately understand and explain ecological processes, investigation into variation among scales is ultimately required (Levin 1992).

To date, three frequently considered processes have been associated with the successful establishment of non-native species outside their native region (Theoharides and Dukes 2007; Richardson and Pyšek 2012; Gallien and Carboni 2016; Tyler et al., (this dissertation). Species must 1) be introduced to a new location (global connectivity variable), 2) establish a self-sustaining population (habitat suitability variable), and 3) spread to new locations by outcompeting or tolerating resident species with adaptations previously attained (phylogenetic diversity variable). Each of these processes have been previously determined as important factors of invasion success, however it is unclear the strength of these drivers and interactions therein over various spatial scales.

2.2.1. Global connectivity

Non-native plant species exhibit human-mediated dispersal patterns that are unlike historic natural dispersal events (Mack et al. 2000; Van Kleunen et al. 2015; Pyšek et al. 2017). Fortuitous transoceanic dispersal and colonization events are historically rare due to biological and physical constraints (review in Fenner, 1985). However, in an increasingly connected globe, humans have transported plant species more frequently, contributing to novel introductions that occur at a much higher rate and intensity than natural dispersal (Holm et al. 1977; Pyšek and Hulme 2005). Consistent global trade patterns allow for repeated introductions of non-native plants, increasing propagule pressure and the potential for invasion success (Seebens et al. 2017). Although previous studies show that the connectivity between regions positively affects invasion success, it is less clear at which scale this driver is strongest. In addition, it is unknown how increased propagule pressure interacts with other known drivers and at which spatial scales these interactions are strongest.

2.2.2. Habitat suitability

Environmental characteristics such as temperature, precipitation, and elevation are known to affect the distribution of all species (environmental filtering) (Nobel and Slayter 1977; van der Valk 1981; Bazzaz 1991; Woodward and Diament 1991). Species distribution models (SDMs) are widely used to explain and predict invasion success by statistically correlating observed geographical occurrences with environmental variables, and development of powerful modeling tools have improved the explanatory and predictive power of these approaches (Guisan and Thuiller 2005; review in Gallien et al. 2010). Despite the frequent use of SDMs to determine invasion success, there are

substantial gaps in our understanding of the strength of this driver and interactions with other important factors over multiple spatial scales.

2.2.3. Phylogenetic diversity

The ability of one species to occupy niche space outside the native range is associated with the presence of favorable adaptations (pre-adaptations) that allow for a competitive advantage (Mack 2003; Fridley and Sax 2014) or tolerance (Golivets and Wallin 2018) in the introduced range. Current evidence suggests that species native to regions with high phylogenetic diversity (PD) may become better invaders (Fridley and Sax 2014) and those regions may better resist invasion (Gerhold et al. 2011; Whitfeld et al. 2014; Iannone et al. 2015). It is assumed that species living regions with high PD have undergone intense interspecific competition for extended periods of time, therefore have gained adaptations necessary to compete in a variety of environments, increasing invasiveness (Darwin 1859; MacArthur 1972; Fridley and Sax 2014). Using PD as a proxy for pre-adaptations to explain invasion success is fairly novel (Fridley and Sax 2014) and has never been combined with other drivers to explore the interactions among and between them over multiple spatial scales.

The overall goal of this study is to assess global patterns of invasive plant distributions at three spatial scales, focusing on factors that may affect invasiveness. Our specific objectives are 1) describe the variation in invasive plant distributions on each scale; and 2) to identify differences in magnitude of factors that account for variation in invasions on those scales. We tested global connectivity as a proxy for propagule pressure, habitat suitability, phylogenetic diversity of regions involved, and

interactions therein, as it has been argued that these are strong drivers of non-native species invasion, yet have never been combined and tested in a multi-scale analysis (Levine and Antonio 1999; Stohlgren et al. 1999; Sax and Gaines 2003; Allen and Shea 2006; Pauchard and Shea 2006; Ward 2006; Guo et al. 2017; Deferrari et al. 2019, Tyler and Wallin (in prep).

2.3. Methods

2.3.1. Overview

In this study, we initially considered 751 invasive woody species from 90 families compiled previously (Rejmanek and Richardson, 2013). Of these, we included data from 213 for which native and non-native distributional data were available. Invasive plant species are defined as those that were transported by humans and have successfully established and spread in the introduced region (Richardson et al., 2000).

To delineate global regions on three spatial scales, we used three levels determined by the Taxonomic Database Working Group (TDWG). We used TDWG because levels are based largely on phylogeography or existing floristic knowledge and have been commonly used in ecological studies (Fontaneto et al. 2012; Van Kleunen et al. 2015; Dawson et al. 2017; Pyšek et al. 2017; van Kleunen et al. 2018; Weigelt et al. 2019). The first level is at the continental scale and consists of 9 units. TDWG has largely maintained the use of popular concepts of continents of the world. One note: Australasia is used on the continental scale as a combination of Australia and New Zealand. The second level is on the regional scale and consists of 52 units. These are largely phytogeographical or based on existing botanical traditions. In some cases,

political boundaries are used. The third level, botanical countries, consist of 368 units that are usually politically defined countries. In this study, the third level is labelled "sub-regional". Minor political inconveniences (tiny enclaves of one country in another) are ignored. Decisions made for when to maintain geographically disjunct parts of countries (i.e. islands), information on botanical traditions, phytogeographical significance, size of island, and/or distance between islands are followed. Very large countries have been subdivided based on botanical traditions, internal political borders, or aggregations of constituent states (table 2-2).

We conducted all data extraction and formatting in R version 3.4.3 (R Core Team 2020).

2.3.3. Data collection

2.3.3.1. Global connectivity

We used information on global trade networks as a proxy for propagule pressure to consider how scale affects the ability of regional connectivity in explaining invasion success. As shown in previous studies, invasion potential is strongly affected by regional connectivity through import volume of global trade networks (Levine and D'Antonio 2003; Hulme 2006; Seebens et al. 2013, 2015, 2018; Chapman et al. 2017).

We obtained raw data from the United States Department of Agriculture Foreign Agricultural Service Global Agricultural Trade System (FAS GATS) on imports to countries from all global trading partners. We created a bilateral trade network that consists of data from 1994 to 2015. As noted in the section titled "Global trade networks" of Study 1 in this dissertation, we measured network connection using

average trade volumes (in tonnes) from reporting countries to partners over the 21-year period. Import data was downloaded directly from the FAS GATS (GATS 2021). We repeated the methodology from that section over the three scales to assign pairwise connectivity scores between spatial units. The resulting connectivity values were used as an explanatory variable in subsequent models predicting the probability of successful invasion in the non-native range.

2.3.3.2. Habitat suitability

To accurately estimate the effect of spatial scale on the role of habitat suitability in determining invasion success, we constructed species distribution models (SDMs) for invasive species in the dataset over three scales. To build the SDMs, we used geographic coordinates of known species occurrences and environmental characteristics at associated sites. We pooled data from all ranges (native, casual, naturalized, and invasive) to inform SDMs because the naturalized climatic niches of invasive species may differ from that of the native region (Broennimann et al. 2007; Broennimann and Guisan 2008; Gallien et al. 2012; Early and Sax 2014; Bocsi et al. 2016; Barbet-Massin et al. 2018). To account for sampling bias, which is a drawback frequently associated with occurrences of invasive species (Broennimann et al. 2007), we used binary occurrences instead of abundances. SDMs were used to assign suitability scores to non-native regions for each species. Suitability scores were used as a covariate in the model explaining the probability of invasion success in a non-native region.

2.3.3.2.1. Global distribution data

We compiled geographic coordinates of known species occurrences to calibrate SDMs using the GBIF database. We used the methodology in the "global distribution data" section of Study 1 in this dissertation. As mentioned in that section, we assigned TDWG spatial unit centroids to each coordinate. However, in this study we repeated this method over each of the three scales.

2.3.3.2.2. Environmental variables

The accuracy of SDMs relies strongly on the choice of environmental predictors used in the models (Petitpierre et al. 2017). Predictors for this study were chosen based on the results found in a global comparison of strategies (Petitpierre et al. 2017) and include altitude range, average annual precipitation, precipitation seasonality, temperature annual range, minimum annual temperature, maximum annual temperature, and temperature seasonality. Values of environmental predictors for all TDWG units over three scales were obtained from the Worldclim package (Fick and Hijmans, 2017).

2.3.3.2.3. SDM fitting and habitat suitability scores

Environmental predictors were used to fit models that estimate similarity to the sites of occurrence using the "bioclim" function in the dismo package. We used the methodology described in the section titled "SDM fitting and habitat suitability scores" of Study 1 in this dissertation to explain how the model works, validate its usage, and evaluate accuracy. We repeated bioclim models for all species in the dataset over three scales and used habitat suitability scores as an explanatory variable in subsequent models.

2.3.3.3. Phylogenetic diversity (ΔPD)

We used a five-step process to measure the effect of evolutionary history on invasiveness of species over three scales. First, we compiled floras of all vascular plants for every spatial unit over three scales (POWO 2020). Second, using these floras we generated phylogenies by pruning a recently comprised megaphylogeny (Qian and Jin 2016). Third, we used the phylogenies to estimate PD for each spatial unit over three scales. Fourth, we obtained native distributions for invasive species in the dataset and assigned each species a PD value that corresponds to the mean PD value of spatial units overlapping their native range (GBIF 2020; CABI ISC 2020; GISD 2020). Fifth, we calculated the difference in PD between invasive species' native and non-native spatial units to assign a ΔPD value to each spatial unit for each species. ΔPD values for each scale were used as explanatory variables in subsequent models examining the probability of successful invasion as a function of PD of the native region. Details for each step are listed below.

2.3.3.3.1. Compiling floras

To measure and compare PD among scales, first we compiled floras for all spatial units over three scales. To do this, we obtained occurrences of vascular plant distributions from the Royal Botanic Gardens, KEW (POWO, 2020). Using the regional delineations for each scale, we made lists of species (floras) for regions at each scale. These floras were used to build phylogenetic trees (see below).

2.3.3.3.2. Generating phylogenies and estimating PD

We used the floras to generate phylogenies for each region by pruning the most recent and comprehensive published megaphylogeny of plant species (Qian and Jin 2016). Species present in each regional flora were matched to tips in the phylogeny, then the phylogeny was trimmed to regional phylogenies using the picante package (Kembel et al. 2010). To estimate PD for each region, we used Faith's PD method (Faith 1992) in the picante package (Kembel et al. 2010) calculating the total branch length of each regional phylogeny. We repeated this methodology at each scale. More detailed methods are found in the section titled "Generating regional phylogenies and estimating PD" in Chapter 1 of this dissertation.

2.3.3.3.3. Determining and assigning native and non-native regions

To compare PD between native and non-native regions for species in our dataset, we obtained occurrence data for invasive distributions and native distributions using three publicly available databases: GBIF, CABI ISC, and GISD. We extracted occurrences from these databases using the methods found in the section titled "Species distributions in native and non-native regions" in Chapter 1 of this dissertation. For native regions, we combined native occurrences from CABI ISC and GISD to create the native range for each species. We repeated this methodology at each scale, creating a native range for each species at each scale. For non-native regions, we assigned a 1 (present) or 0 (absent) to each region using occurrence data from GBIF. We repeated this methodology at each scale, creating non-native binary datasets at three scales.

2.3.3.3.4. Assigning PD and calculating ΔPD for each spatial unit

Invasive species in the dataset were assigned a native-range PD value, corresponding to the mean PD value of regions overlapping their native range (Fridley and Sax 2014). To compare PD of the native range to PD of all non-native regions, we calculated the difference between them $\Delta PD_{i,j}$ = native_PD_i - non_native_$PD_{i,j}$ for species (i) in a non-native region (j). Greater PD in the native range produces a positive ΔPD value, while greater PD in a non-native region produces a negative ΔPD value. As the absolute value of ΔPD increases, we assume that the divergence in evolutionary history of the regions increases. If ΔPD is zero, we assume no relative difference in the evolutionary history between the native range and non-native region. The variable ΔPD was used as a covariate in our model below.

2.3.4. Statistical analyses

We examined the relative effects of ΔPD, habitat suitability (HS), global connectivity (GC), and interactions therein on the observed invasiveness of plant species over three spatial scales. The unit of all analyses was detection of the species as an invader in the region, so a binary response variable coded invasive (1) or not found (0) in each region. To this response variable, we fit generalized linear mixed effects models (GLMM) with logit link functions for binomial errors using the lme4 package (Bates et al. 2015). Explanatory variables included ΔPD, habitat suitability, and connectivity. ΔPD and connectivity were scaled and centered on zero to evaluate them on relative terms. Species and region were included as random effects. GLMM approach allowed us to test our hypotheses while accounting for heterogeneity between species and regions using random effects (Dixon et al. 2016) and Type I error

(Anderson et al. 2000). All possible models for each scale and a null model for each scale were fitted along with two- and three-way interactions between fixed effects. Models were ranked according to corrected Akaike's information criterion (AICc) values (Akaike 1974; Nakagawa and Schielzeth 2013) using the MuMIn package (Barton 2013). Assumptions were evaluated with qq-plots and summary tables using the DHARMa package (Hartig 2019). We repeated these analyses over three spatial scales. We conducted statistical analyses in R version 3.4.3 (R Core Team 2020).

2.4. Results

We found that the magnitude in effect size of covariates explaining invasion success changed across scales (figure 2-1). Across all three scales, invasion success was significantly positively correlated with habitat suitability and ΔPD. Habitat suitability had the strongest relationship to plant invasion success at all scales and the magnitude of this correlation increased with scale. A slightly negative correlation was found between connectivity and invasion success on the continental and regional scales but was so close to 1 it could be assumed that a lack of association exists between connectivity and invasion success at these scales; at the sub-regional scale, the confidence interval crossed 1, implying no association between sub-regional connectivity and invasion success.

The continental scale totaled 1,639,421 observations of 213 species in seven continents. Of the candidate models for the continental scale, the global model received the most support with a weight of one. Connectivity had an odds ratio of 0.93 and 95% confidence interval of 0.93 – 0.94 (table 2-3). Habitat suitability had an odds ratio of 16

* 1015 and 95% confidence interval of 14 * 1015 – 19 * 1015 (table 2-3). ΔPD had an odds ratio of 1.73 with 95% confidence interval of 1.69 – 1.78 (table 2-3). We estimated a three-way interaction between explanatory variables. The odds ratio was 0.20 with a 95% confidence interval of 0.77 – 1.721 (table 2-3). Residual variance (within each group) was 3.29. The random effect of species in the model had between-group-variance of 26.83 and the random effect of introduced-continent between-group-variance was 1.88. The intraclass-correlation coefficient, or variance explained by the grouping structure of the data was 0.90. The conditional R2 for the continental model was 0.907.

The regional scale totaled 473,634 observations of 213 species in 34 regions. Of the candidate models for the regional scale, the global model received the most support with a weight of one. Connectivity had an odds ratio of 0.91 and 95% confidence interval of 0.89 – 0.94 (table 2-4). Habitat suitability had an odds ratio of 7 * 106 and 95% confidence interval of 6 * 106 – 8.7 * 106 (table 2; figure 5). ΔPD had an odds ratio of 2.81 with 95% confidence interval of 2.61 – 3.04 (table 2-4). We estimated a three-way interaction between explanatory variables. The odds ratio was 1.15 with a 95% confidence interval of 0.77 – 1.721 (table 2-4). Residual variance (within each group) was 3.29. The random effect of species in the model had between-group-variance of 3.72 and the random effect of introduced-region between-group-variance was 6.896. The intraclass-correlation coefficient, or variance explained by the grouping structure of the data was 0.76. The conditional R2 for the regional model was 0.805.

The sub-regional scale totaled 66,082 observations of 213 species in 120 regions. Of the candidate models for the sub-regional scale, the model including an interaction between covariates ΔPD and habitat suitability received the most support with a weight of 0.596. Connectivity had an odds ratio of 0.97 and 95% confidence interval of 0.94 – 1 (table 2-5). Habitat suitability had an odds ratio of 6.8 * 102 and 95% confidence interval of 4.9 * 102 – 9.4 * 102 (table 2-5). ΔPD had an odds ratio of 1.49 with 95% confidence interval of 1.15 – 1.93 (table 2-5). We estimated a two-way interaction between explanatory variables ΔPD and habitat suitability. The odds ratio was 0.41 with a 95% confidence interval of 0.26 – 0.64 (table 2-5). Residual variance (within each group) was 3.29. The random effect of species in the model had between-group-variance of 2.17 and the random effect of introduced-sub-region between-group-variance was 4.62. The intraclass-correlation coefficient, or variance explained by the grouping structure of the data was 0.67. The conditional R2 for the sub-regional model was 0.699.

2.5. Discussion

The goal of this study was to assess global patterns of invasive woody plant distributions over three spatial scales to determine if variation exists in factors affecting invasiveness between each scale. Our research shows patterns and associations vary among covariates and between spatial scales (figure 2-1). The proportion of variability explained by covariates and random effects in the model, as expressed by the conditional R2 value, increases dramatically as spatial scale increases. This finding could be due primarily to broad-scale anthropogenic influences that affect invasion

dynamics and occur within the context of global systems, implying that the distribution of invasion plants is occurring on a global scale. Furthermore, distribution patterns at larger scales may be less impacted by local stochastic processes (Dawkins 1982; Levin 1992).

Habitat suitability is an important determinant of invasion success. This variable was estimated by generating SDMs for species in this study. As previously reported, using the realized niche to inform SDMs has shown to be widely successful in predicting the suitability of potential introduction sites (Broennimann and Guisan 2008; Gallien et al. 2010; Peterson and Soberón 2012). Previous studies show limited niche expansion in the invaded range of invasive plant species, linking distributions to environmental conditions and habitat suitability (Liu et al. 2020). However, a striking finding is the increase in magnitude of this variable with scale. The abiotic features used in the SDMs may have characteristic spatial scales themselves (Delcourt et al. 1983; Urban et al. 1987). Elevation, for instance, is a coarse-scale characteristic of topography. Temperature and precipitation may show little variation across scales and may be showing here that they affect the distribution of plant species on coarser scales. Accordingly, the distribution of woody plant species in this study is largely determined by environmental filtering rather than biological interactions or propagule pressure.

The association of ΔPD on the probability of invasion success was positive but varied widely across scales. This variable had the strongest association with invasion success at the regional scale, indicating the importance of larger scale studies when using diversity metrics as predictors of invasiveness.

We found that connectivity between continents, regions, and sub-regions via global trade networks explained little to no variance in the probability of successful woody plant invasion. Previous studies found the opposite relationship between connectivity and invasion success (Seebens et al. 2015) however most studies used taxa other than terrestrial plants, such as mollusks or insects (Levine and D'Antonio 2003; Lodge 2006; Ruiz et al. 2006; Tatem et al. 2006; Meyerson and Mooney 2007; Hulme 2009; Seebens et al. 2013; Chapman et al. 2017); other studies did not find a significant relationship between invasive plant success and connectivity via trade (Pÿsek et al. 2010). The lack of variability explained by global trade could be a result of the colonial history of much of the data analyzed here. As the introductions from Europe to former colonies occurred long before the trade data collected in this study, perhaps these invasions were not related to current connectivity (Seebens et al. 2018). Future work on the role of global connectivity in plant invasions should include "time since invasion" or "first records" (Seebens et al. 2017, 2018, 2021).

We assessed the global distribution patterns of woody invasive plants and found variation in effects of factors of invasiveness at each scale. As suggested in previous studies but never tested rigorously on a global scale, scale matters.

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2.7. Figures

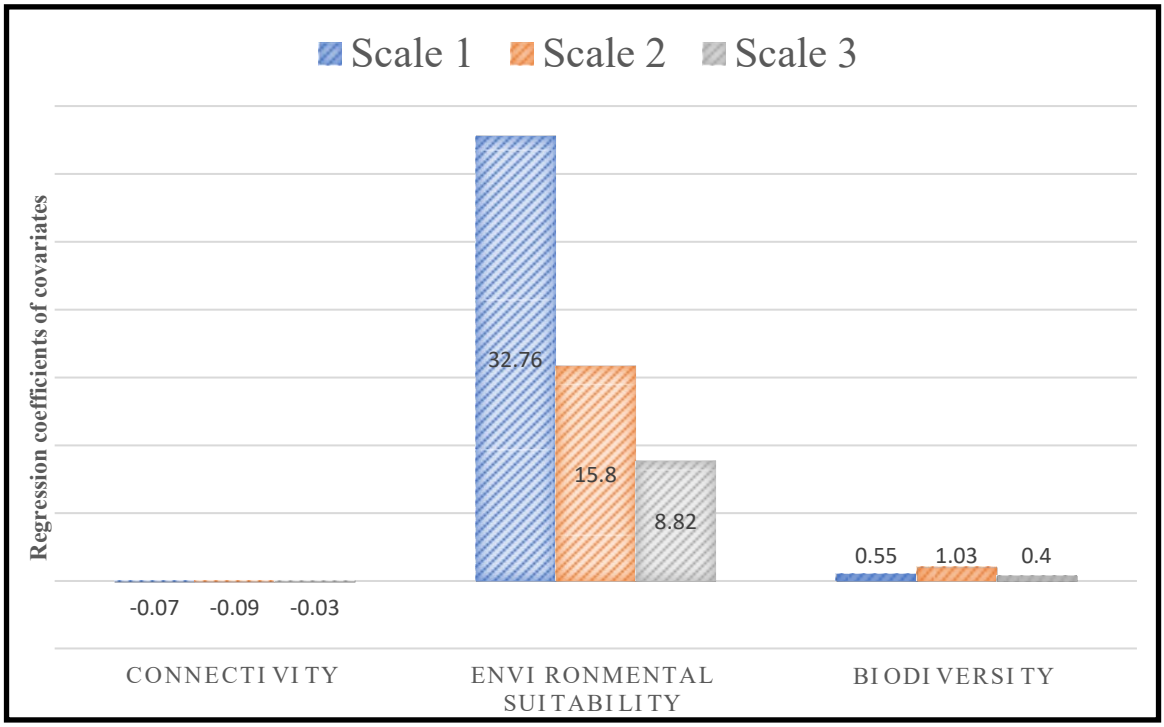

Figure 2-1. Bar chart showing the effect of spatial scale on covariates of invasiveness. Spatial scales are represented by colors. Variables on the x-axis are labeled below. Each bar is the regression coefficient of that variable at one spatial scale.

2.8. Tables

Table 2-1: Processes influencing biodiversity differ across various spatiotemporal scales (modified from Willis and Whittaker 2002).

Spatial scale	**Scale of species richness**	**Environmental variables predominantly responsible**	**Temporal scale at which processes occur**
Local scale	Species richness within communities, within habitat patches	Fine-scale biotic and abiotic interactions, e.g., habitat structure, disturbance by fires, storms	Processes occurring on time scales of -1-100 years
Landscape scale	Species richness between communities	Soils, altitude	Processes occurring on time scales of -100-1000 years
Regional scale	Species richness of large geographical areas within continents	Radiation budget and water availability, area, latitude	Processes occurring over the last 10,000 years; i.e., since end of last glacial
Continental scale	Differences in species lineages and richness across continents	Aridification events, glacial/interglacial cycles of the Quarternary, mountain building episodes	Processes occurring over the last 1-10 million years
Global scale	Differences reflected in the biogeographical realms; between continents	Continental plate movments, sea level changes	Processes occurring over the last 10-100 million years

Table 2-2: Three scales used in this study.

Scale	No. of units	Avg. area of units (km^2)
Continental	9	16,809,058
Regional	52	2,860,281
Botanical country	368	506,019

Table 2-3. Summary statistics for continental scale model predicting the probability of being invasive as a function of habitat suitability, delta PD, connectivity, and their interactions. Random effects are reported as species and origin region.

	invasive		
Predictors	*Odds Ratios*	*CI*	*p*
(Intercept)	0.22	0.18 – 0.26	**<0.001**
delta_PD_s	1.73	1.69 – 1.78	**<0.001**
mean_HSS	168308431031184.34	145477015708558.91 – 194723048298772.09	**<0.001**
connectivity_s	0.93	0.93 – 0.94	**<0.001**
delta_PD_s * mean_HSS	15.40	13.41 – 17.68	**<0.001**
delta_PD_s * connectivity_s	1.03	1.03 – 1.04	**<0.001**
mean_HSS * connectivity_s	24.28	20.91 – 28.20	**<0.001**
(delta_PD_s * mean_HSS) * connectivity_s	0.20	0.18 – 0.22	**<0.001**
Random Effects			
σ^2	3.29		
$\tau_{00\ species}$	26.83		
$\tau_{00\ intro\_continent}$	1.88		
ICC	0.90		
$N_{\ species}$	213		
$N_{\ intro\_continent}$	7		
Observations	1639421		
Marginal R^2 / Conditional R^2	0.096 / 0.907		

Table 2-4. Summary statistics for regional scale model predicting the probability of being invasive as a function of habitat suitability, delta PD, connectivity, and their interactions. Random effects are reported as species and origin region.

		invasive	
Predictors	*Odds Ratios*	*CI*	*p*
(Intercept)	0.01	0.00 – 0.02	**<0.001**
delta_PD_s	2.81	2.61 – 3.04	**<0.001**
mean_HSS	7303723.32	6099856.68 – 8745184.87	**<0.001**
connectivity_s	0.91	0.89 – 0.94	**<0.001**
delta_PD_s * mean_HSS	576.34	459.40 – 723.06	**<0.001**
delta_PD_s * connectivity_s	1.05	1.03 – 1.08	**<0.001**
mean_HSS * connectivity_s	1.28	1.02 – 1.62	**0.034**
(delta_PD_s * mean_HSS) * connectivity_s	1.15	0.77 – 1.72	0.507
Random Effects			
σ^2	3.29		
$\tau_{00\ species}$	3.72		
$\tau_{00\ intro\_region}$	6.90		
ICC	0.76		
$N_{\ species}$	213		
$N_{\ intro\_region}$	34		
Observations	473634		
Marginal R^2 / Conditional R^2	0.176 / 0.805		

Table 2-5. Summary statistics for sub-regional scale model predicting the probability of being invasive as a function of habitat suitability, delta PD, connectivity, and their interactions. Random effects are reported as species and origin region.

		invasive	
Predictors	*Odds Ratios*	*CI*	*p*
(Intercept)	0.01	0.00 – 0.01	**<0.001**
delta_PD_s	1.49	1.15 – 1.93	**0.002**
mean_HSS	6797.26	4929.49 – 9372.72	**<0.001**
connectivity_s	0.97	0.94 – 1.00	0.097
delta_PD_s * mean_HSS	0.41	0.26 – 0.64	**<0.001**
Random Effects			
σ^2	3.29		
$\tau_{00\ species}$	2.17		
$\tau_{00\ intro\_area}$	4.62		
ICC	0.67		
$N_{\ species}$	213		
$N_{\ intro\_area}$	120		
Observations	83137		
Marginal R^2 / Conditional R^2	0.078 / 0.699		

CHAPTER 3: MODELING EXOTIC FRACTION TO PREDICT REGIONS WITH HIGH POTENTIAL OF PLANT INVASION.

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3.1. Abstract

Invasive plant species contribute to alteration of ecosystem functioning, reduction of native diversity, and have negative effects on numerous ecosystem services. Increases in anthropogenic regional connectivity is effectively intensifying establishment of self-sustaining populations of invasive plants around the globe. However, some ecosystems are disproportionately susceptible to incoming species. In this study, we used a recently compiled global data set of invasive plant distributions to calculate exotic fraction and estimate regional invasibility on a global scale. We found islands in Australasia to have the highest potential for future plant invasions. An appropriate invasibility metric, as the one developed here, has been largely lacking from invasive species studies despite its potential to guide effective, pre-emptive strategies for invasion prevention. We suggest that this tool is used as an efficient

method to determine regions of greatest priority and opportunity for successful mitigation of threats from invasion.

3.2. Introduction

Invasive plant species contribute to alteration of ecosystem functioning, reduction of native diversity (Heywood 1989; Mack et al., 2000; Figueroa et al. 2011; Gaertner et al. 2011; Cardinale et al. 2012; Gamfeldt et al. 2013, Pyšek et al. 2020) and have negative effects on numerous ecosystem services (Castro-Díez et al. 2019). Increases in anthropogenic regional connectivity is effectively intensifying establishment of self-sustaining populations of invasive plants around the globe (Vilà and Pujadas 2001; Levine and D'Antonio 2003; Meyerson and Mooney 2007; Pyšek et al. 2010; Seebens et al. 2013, 2015, 2018; Chapman et al. 2017; Turbelin et al. 2017) with no saturation (Seebens et al. 2017). However, some ecosystems are disproportionately susceptible to incoming species (Lonsdale 1999; Mack et al. 2000). This range of potential susceptibility is described as invasibility, or the propensity for an ecosystem to be invaded by non-native organisms (Lonsdale 1999; Alpert et al. 2000; Fridley 2011). It is imperative to determine contributing factors of regional invasibility and predict potential future invasions. Yet, we lack a global picture of invasion potential.

The concept of invasibility has been a major focus in the field of invasion ecology however, inconsistencies in practice and conflicting results (Lonsdale 1999; Richardson and Pyšek 2006; Chytry et al. 2008; Jeschke et al. 2012; Catford et al. 2012) have resulted in misuse of the terminology (Guo et al. 2015). Invasibility is a characteristic of an ecosystem that reflects predicted potential for invasion (Richardson and Pyšek 2006; Guo et al. 2015). Thus, invasibility is a pre-invasion characteristic.

Variation in invasibility may result from intrinsic biotic and abiotic properties such as native diversity, temperature, precipitation, and seasonality, and extrinsic properties such as propagule pressure of incoming species (Crawley 1987; Tilman 1997; Lonsdale 1999).

In contrast, exotic fraction (EF), or the proportion of an ecosystem that is already invaded, is a post-invasion metric. Exotic fraction estimates the degree by which invasive species have established in an ecosystem by calculating the proportion of exotic plant species to native and exotic plant species in an ecosystem. This metric can be used retrospectively to identify contributing factors facilitating invasion success. Variation in EF may be attributed to native diversity (biotic resistance hypothesis; Grime 1973; Tilman 1997), environmental characteristics (Guisan and Thuiller 2005; reviewed in Gallien et al. 2010; Barbet-Massin et al. 2018), and global connectivity (Seebens et al. 2015; Turbelin et al. 2016; Chapman et al. 2017).

Predicting and preventing plant invasions is a fundamental goal in ecology, yet comprehensive prediction tools are still lacking. A closer look at differences in EF between regions could identify those with high potential for future invasions. Specifically, a region with lower-than-expected EF could have high invasibility and inform preventative measures.

In this study, we estimated EF and regional invasibility on a global scale to address the question "which areas of the globe have high potential for future plant invasions?". Using a recently compiled global data set of invasive plant distributions (n=13,939 taxa) across geographic regions (n=368 regions), we 1) identified

contributing factors of EF by creating explanatory models with three variables and 2) using the predicted values of regional EF from models, identified potentially high-risk regions. While invasibility has been estimated elsewhere, this study is the first to use EF to identify regions with high potential while controlling for contributing factors of invasion success.

3.3. Methods

3.3.1 Exotic fraction (EF)

We calculated EF as a proportion of invasive species to all native and invasive species in a region. We used the recently published The Global Naturalized Alien Flora (GloNAF 2018) database version 1.2, which is a collection of the most comprehensive and accurate inventories of invasive plant occurrences to date (van Kleunen et al. 2018). The authors have compiled data from 210 sources and standardized taxa names using The Plant List version 1.1 (TPL 2013). We downloaded the full dataset (n = 13,939).

We determined the geographical units for this study following the Biodiversity Information Standards (formally Taxonomic Database Working Group; TDWG; Brummitt et al. 2001). We used the spatial polygons from TDWG level 3 (n = 368 regions) corresponding to countries or large intra-national regions because these spatial units and digitized georeferenced map are based largely on phylogeography or existing floristic knowledge and commonly used in ecological studies (Fontaneto et al. 2012; van Kleunen et al. 2015; Dawson et al. 2017; Pyšek et al. 2017; van Kleunen et al.

2018; Weigelt et al. 2019). Invasive plant species in the GloNAF database are pre-assigned to TDWG level 3 regions.

To calculate EF, we compiled regional floras of all vascular plants using lists obtained for TDWG level 3 regions from the Royal Botanic Gardens, Kew (POWO 2020) (n=368). We added invasive plant species from the GloNAF data set, then took the proportion of invasive species to all native and invasive species in the region (EF = invasive / native + invasive).

3.3.2. Objective 1: identify contributing factors associated with relatively high EF

To test the relationship between contributing factors of invasion success and regional exotic fraction, we modelled regional variation in EF using three key variables: global connectivity, eco-realm, and native diversity.

3.3.2.1. Global connectivity

We used data on global trade networks to inform regional connectedness, or global connectivity. As shown in previous studies, invasion potential is strongly affected by regional connectivity through import volume of global trade networks (Levine and D'Antonio 2003; Seebens et al. 2013, 2015, 2018; Turbelin et al. 2017; Chapman et al. 2017). We used commodity-specific trade data to estimate a connectivity index for all regions in this study, as agricultural and live plant imports through shipping networks have a stronger effect on plant invasion potential than total import volumes (Chapman et al. 2017). To do this, we obtained raw data from the USDA Foreign Agricultural Service's Global Agricultural Trade System (FAS GATS)

on imports of live plant commodities ("live plants" in tonnes) to countries from all global trading partners from 1994 to 2013 (USDA-FAS 2020). As a measure of network connection, we used total global trade volumes (in tonnes).

We used country codes for reporter and partner to overlay on to the TDWG regional shapefile. We used the "extract" function in the raster package to assign a total global trade volume to each region in the study (Hijmans and Etten 2012). The FAS GATS data set did not have complete global coverage, therefore 223 regions were used for analyses.

3.3.2.2. Ecoregions and eco-realms

We used the global terrestrial Ecoregions2017©Resolve (Dinerstein et al. 2017) to assign habitat designations to the 223 regions used in this study (figure 1). We converted the Ecoregions2017 shapefile to a raster using the "raster" function in rdgal package (Bivand et al. 2010). We assigned ecoregions and eco-realms to 223 regional polygons using the "extract" function in the raster package (Hijmans and Etten 2012).

3.3.2.3. Native diversity

We used the biodiversity metric phylogenetic diversity (PD; Faith 1992), as it reflective of open niche space in an ecosystem and a known contributing factor of invasion success (Tyler et al. (Chapter 1 of this dissertation); Yessoufou et al. 2018; Fridley and Sax 2014; Gerhold et al. 2011). This approach measures gradual changes in traits across a regional phylogeny (Faith 1992). The number of traits in a region could be reflective of the competitive intensity and therefore invasion resistance or susceptibility (Vermeij 1996; Leigh et al. 2009; Fridley and Sax 2014).

To estimate PD (figure 2), first we used the compiled regional floras of all vascular plants obtained from the Royal Botanic Gardens, Kew (POWO 2020) (n=368). Next, we created 223 regional phylogenies by pruning a recently comprised megaphylogeny (Qian and Jin 2016) using the plant species listed in regional floras. Species present in the floras were matched to tips in the phylogeny using the "match.phylo.comm" function and the phylogeny was trimmed into regional phylogenies using the "prune.sample" function, both found in the picante package (Kembel et al., 2010). The resulting regional phylogenies include labeled nodes (families), labeled tips (species), and branch lengths that connect nodes. We estimated PD using Faith's PD method (1992) with the "pd" function in the picante package, which calculates the total branch length of each regional phylogeny (Kembel et al. 2010).

3.3.2.4. Statistical analyses

To test the strength of contributing factors on EF, we performed linear regressions. We constructed models containing three independent variables global connectivity, eco-realm (categorical), and native diversity (PD). We added an interaction term to account for an interaction between the covariates global connectivity and PD. The global model:

EF ~ global connectivity * PD + eco-realm

Assumptions were evaluated using qq-plots, plotting residuals, and summary tables. We compared the performance of models using AIC values (Akaike 1974; Nakagawa and Schielzeth 2013; table S1). We conducted statistical analyses in R

version 3.4.3 (R Core Team 2021) using the lme4 package (Bates et al. 2018) to construct models.

3.3.3. Objective 2: identify regions with high potential for future invasion

We estimated regional invasibility by comparing predicted values and observed values of EF. We used the best performing explanatory model above to predict EF given covariates in Objective 1. We identified regions with high potential for future invasions by taking the difference between their observed values of EF and predicted values from our explanatory model. Regions with high potential for future invasions would have lower than expected EF compared to predicted EF values. This deviation from model prediction informs the regional invasibility metric. We created the invasibility metric by multiplying this value by (-1) for ease of the reader. As the value increases, so does regional invasibility.

3.4. Results

In this study, we modelled EF to estimate regional invasibility on a global scale, addressing two objectives; 1) identify contributing factors associated with relatively high EF; 2) identify regions with high potential for future invasion. Overall, we found that global connectivity was a stronger predictor of EF than native diversity and we found much variation in eco-realms (table 3-1). The regions with greatest invasibility were both found in Australasia and the regions with least invasibility were found in the Palearctic (table 3-2).

Of the candidate models, the global model received the most support with a weight of 0.938 ($R^2 = 0.441$; table 3-3). Overall, EF was positively affected by global

connectivity and native diversity. Mean connectivity had a positive effect (estimate of the coefficient was 0.12 and 95% confidence interval 0.03 – 0.20; figures 3, 4a, 4b). Native diversity had a positive effect (estimate of the coefficient was 0.03 and 95% confidence interval 0.01 – 0.05; figures 3-5, 3-6a, 3-6b). The relationship between EF and eco-realm varied widely, with Oceania and Australasia having the highest values of EF (figure 3-7). We estimated a two-way interaction between connectivity and native diversity (estimate of the coefficient was 0.10 and 95% confidence interval 0.04 – 0.16; table 1, figure 3-8). Connectivity had a positive effect on EF except when PD was lowest.

According to the model, the regions with the highest potential for invasion are both located in the eco-realm Australasia, New Caledonia and New Guinea. These island regions have relatively low values of connectivity (1 and 2,883 respectively) and relatively high values of diversity (PD values of 15,084 and 19,561 respectively), with lower-than expected EF (model residuals as observed-predicted values of -0.1613 and -0.1524 respectively). Conversely, Japan and Sweden, both in the Palearctic realm, have the lowest invasibility.

3.5. Discussion

The model developed here supports previous research emphasizing international connectivity as a major contributing factor of regional EF (Vilà and Pujadas 2001; Levine and D'Antonio 2003; Meyerson and Mooney 2007; Pyšek et al. 2010; Seebens et al. 2013, 2015, 2017, 2018; Chapman et al. 2017; Turbelin et al. 2017). This novel

method will be valuable in the development of regulations and policies that work toward invasion prevention.

We found considerable variation in regional invasibility, with some trends in high and low values (table 3-3). New Caledonia is a French archipelago and like other French territories, is signatory to the highest number of global and regional international treaties mentioning invasive species (n = 30) in the world (Turbelin et al., 2017). Furthermore, New Caledonia has extensive legislation and regulations dedicated to prevention and management of invasive species, showing a genuine effort to mitigate introduction of invasive species at point of entry (Turbelin et al., 2017). These efforts may be reactionary, stemming from the high EF found in the archipelago. Alternatively, a value of EF lower than expected might show that efforts are working to prevent further invasions in New Caledonia. Pre-emptive policies, if effective are probably best, however legislation and regulations that specifically target the prevention and management of new incoming invasive species are hopeful for future threats. As New Caledonia has high potential for future invasions, careful attention should be paid to the effectiveness of current policies on EF.

The island of New Guinea was colonized by the Dutch but is currently two separate entities: the independent state of Papua New Guinea and the Indonesian provinces of Western New Guinea. Conversely, New Guinea does not have legislation or regulations dedicated to prevention or management of invasive species. The island is signatory to 12 international treaties mentioning invasive species, ranking in the 30th percentile globally (Turbelin et al., 2017). New Guinea is considered to have high

potential for future invasion, according to our model. With little to no efforts in the prevention and management of invasive species, this could be an area of great concern and potential opportunity.

Our analyses revealed high invasibility for these island regions, with discernable similarities and differences between them. They are vastly different in terms of the legislative efforts in preventing establishment of invasive species. This might be reflective of the fact that New Caledonia is still a European territory, affording access to French resources. However, both regions are influenced by colonialism, past and present, which is well documented as contributing to global invasion patterns (Elton, 1958; Mooney and Cleland, 2001; Courchamp et al., 2003; Lockwood et al., 2005). Both regions are islands, therefore more susceptible to invasions and sensitive to introduced species (Elton, 1958; Brockie et al. 1988; Tershy et al. 2002; Sax and Gaines 2008; Clavero et al. 2009; Bellard et al. 2016; Bellard et al. 2017). Therefore, more efforts should focus on preventing and managing invasive species on these Australasian islands.

There are limitations to our approaches that are discussed here. First, this study does not take interregional or secondary invasions into account, which are important contributing factors in regional invasibility. The binary occurrences used does not reflect invasive species abundance, which may overestimate or underestimate the EF of a region. Sampling bias is frequently considered a limitation of global invasion studies, so the information in this study is only as strong as the sampling strength. Although

these are current limitations, future work to incorporate secondary invasions and invasive species abundance could benefit the field of invasion ecology.

An appropriate invasibility metric, as the one developed here, has been largely lacking from invasive species studies despite its potential to guide effective, pre-emptive strategies for invasion prevention. We suggest that this tool is used as an efficient method to determine regions of greatest priority and opportunity for successful mitigation of threats from invasion.

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3.7. Figures

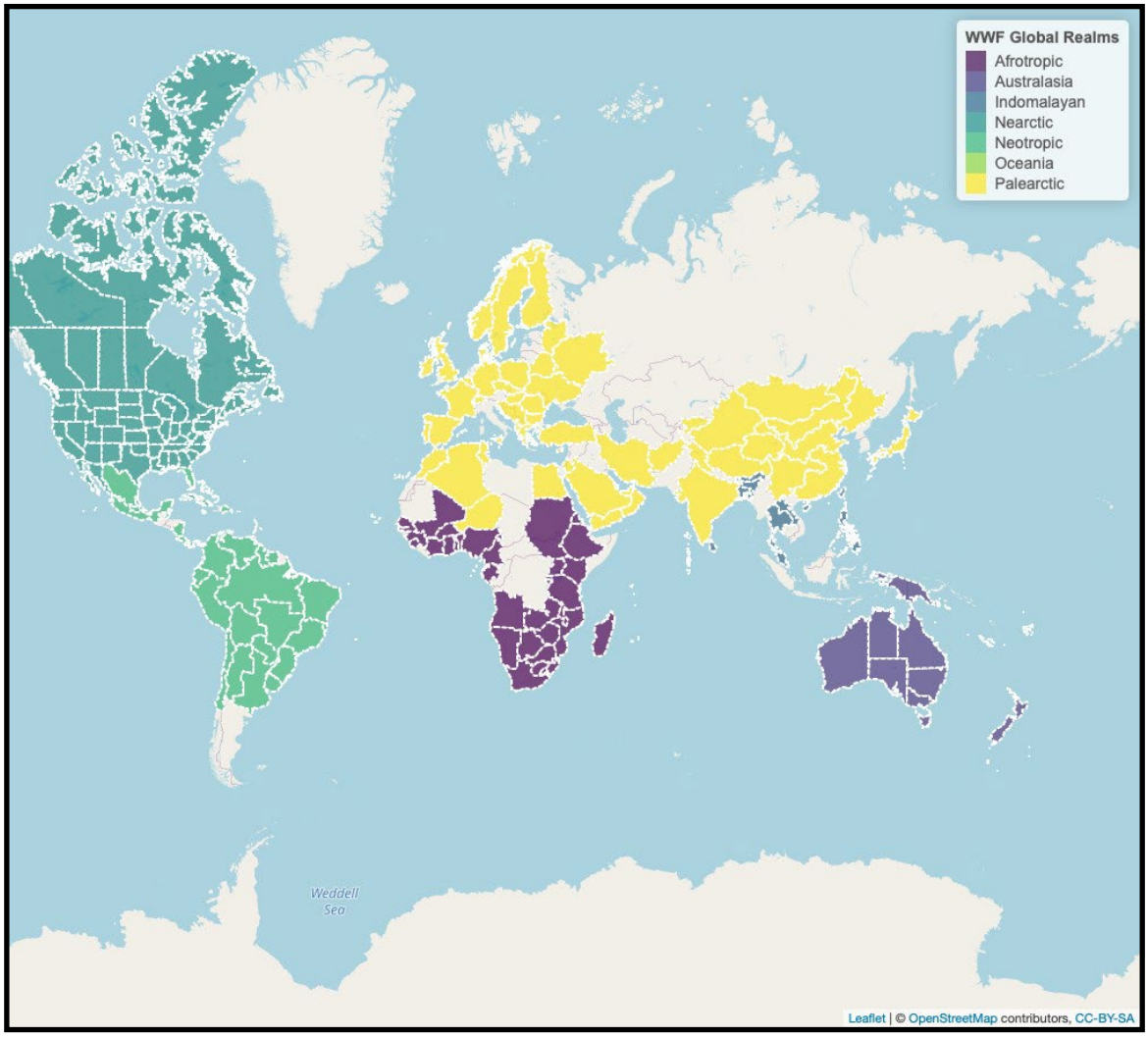

Figure 3-1. Map of global Ecoregions2017©Resolve used in this study (Dinerstein et al. 2017). Polygons are delineated as TDWG level 3 regions. Regions in white were lacking data, so not included in the study.

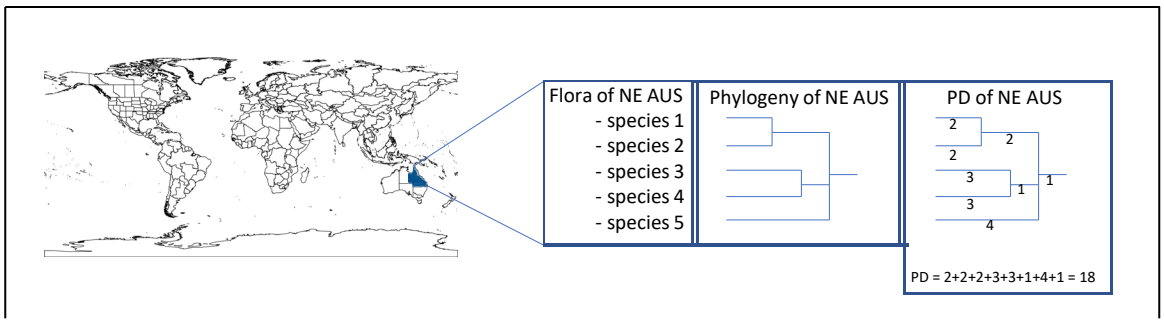

Figure 3-2. Conceptual diagram of PD estimation workflow. Example using the Northeast Australia region (NE AUS). First, compile flora, a list of species in the region. Second, prune megaphylogeny to create regional phylogeny. Third, calculate PD using Faith's method (1992).

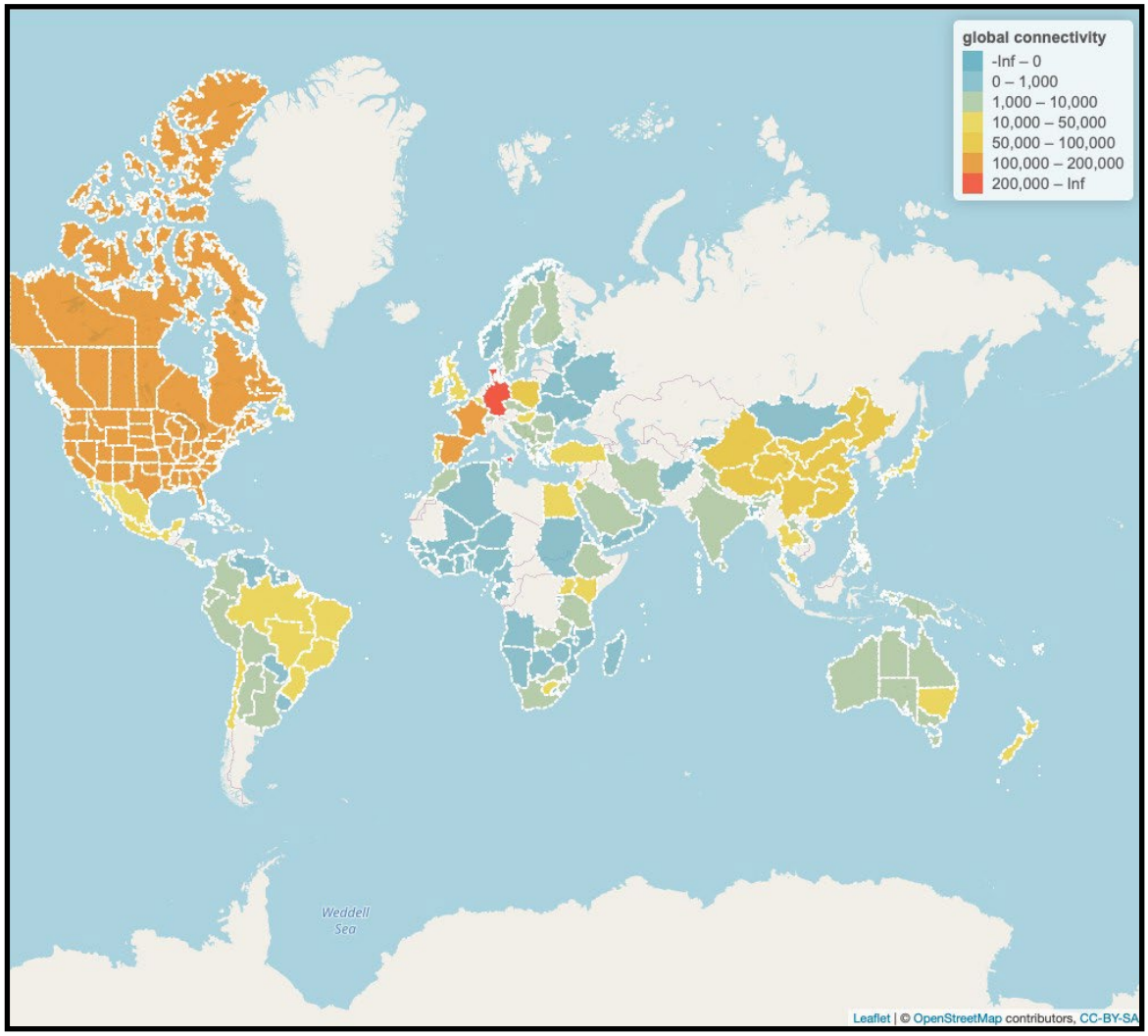

Figure 3-3. Map of global connectivity. Polygons are delineated as TDWG level 3 regions. As a measure of global connectivity, we used total global trade volumes (in tonnes) of agricultural and live plant commodities. Regions with highest global connectivity are those shown in red. Regions with lowest global connectivity are those shown in blue. Regions in white were lacking data, so not included in the study.

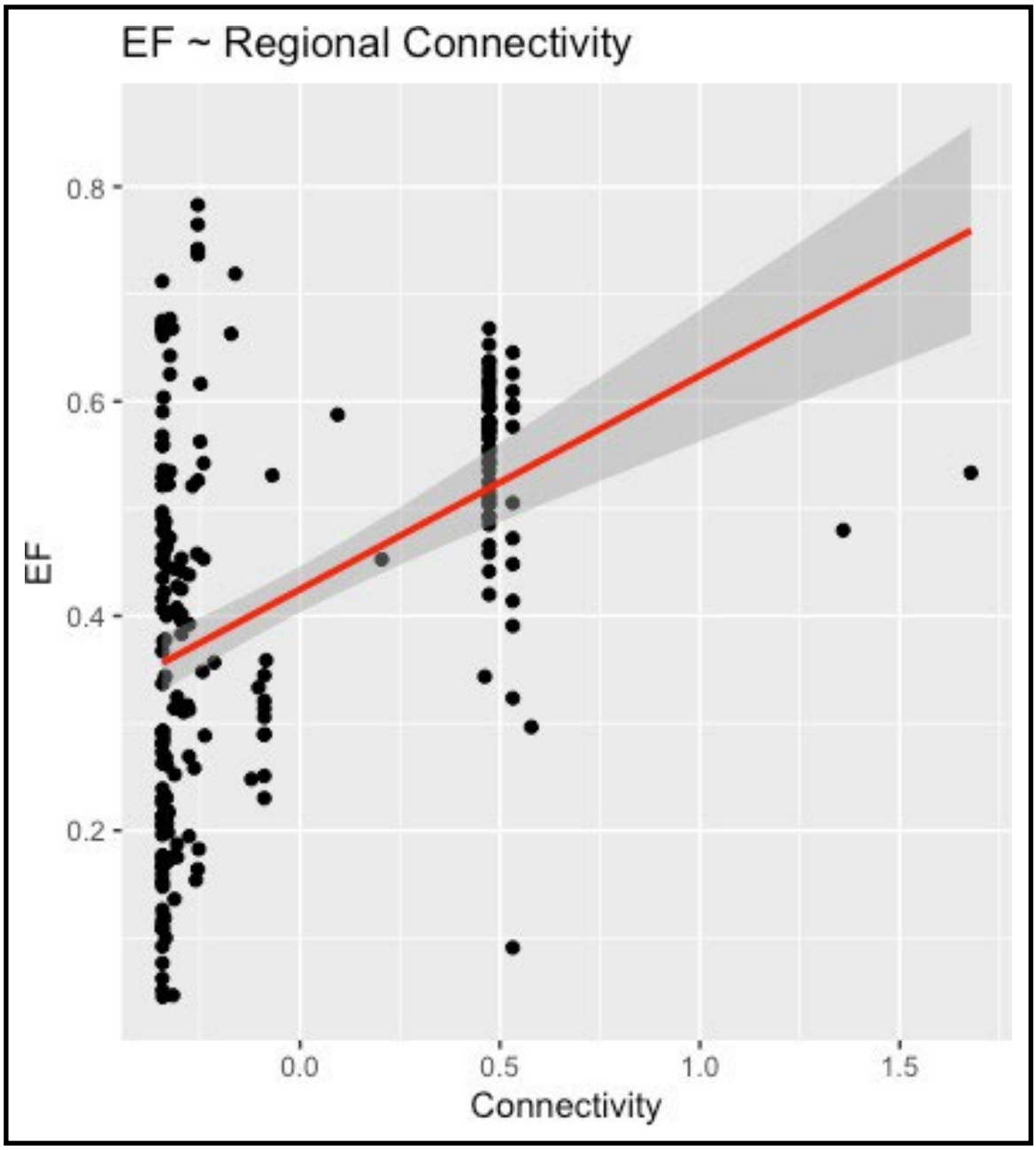

Figure 3-4a. Observed values of EF as a factor of global connectivity for 223 regions. 95% confidence interval shown in the smoother.

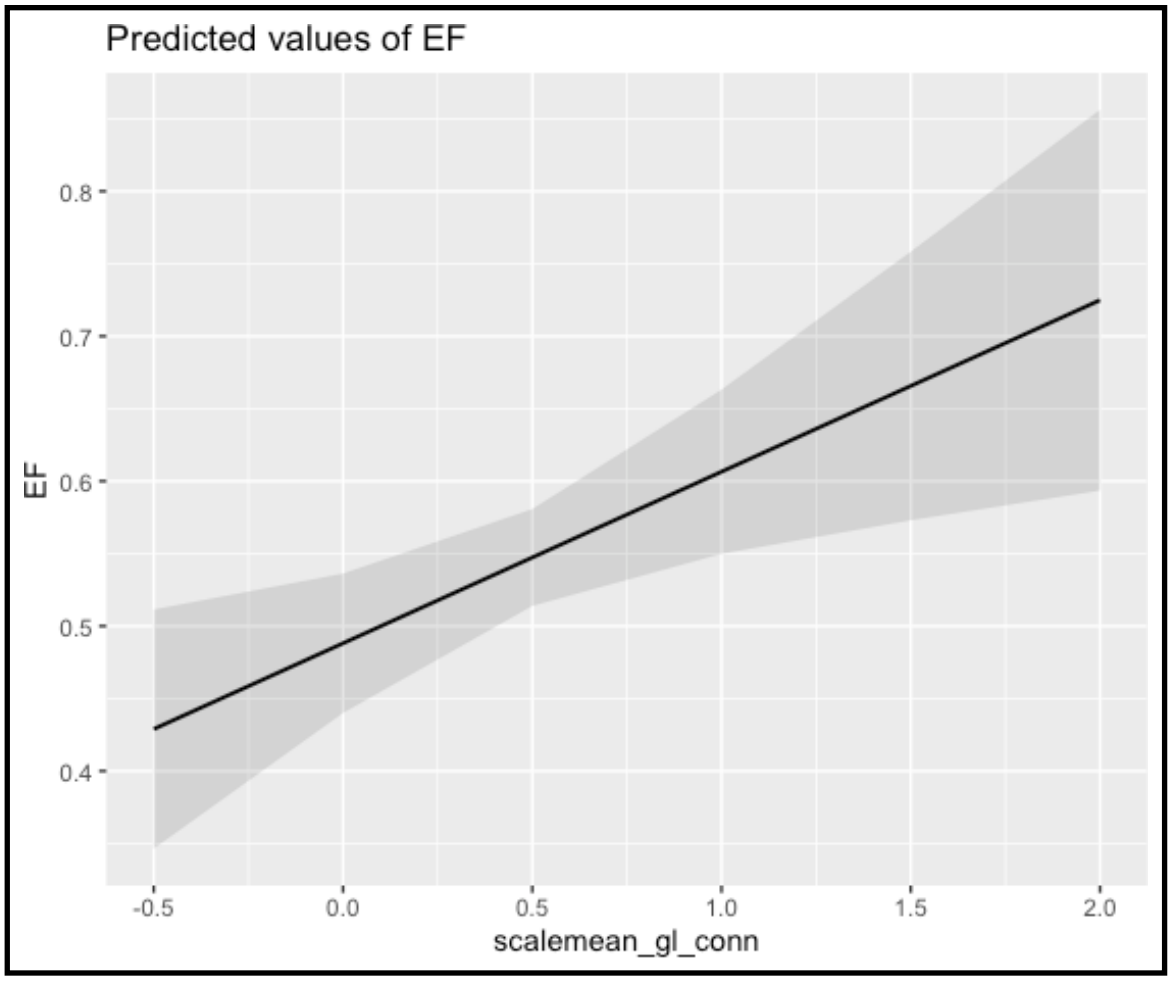

Figure 3-4b. Predicted values of EF as a factor of global connectivity for 223 regions. Estimate of the coefficient was 0.12 and the 95% confidence interval 0.03 – 0.20, as shown in the smoother.

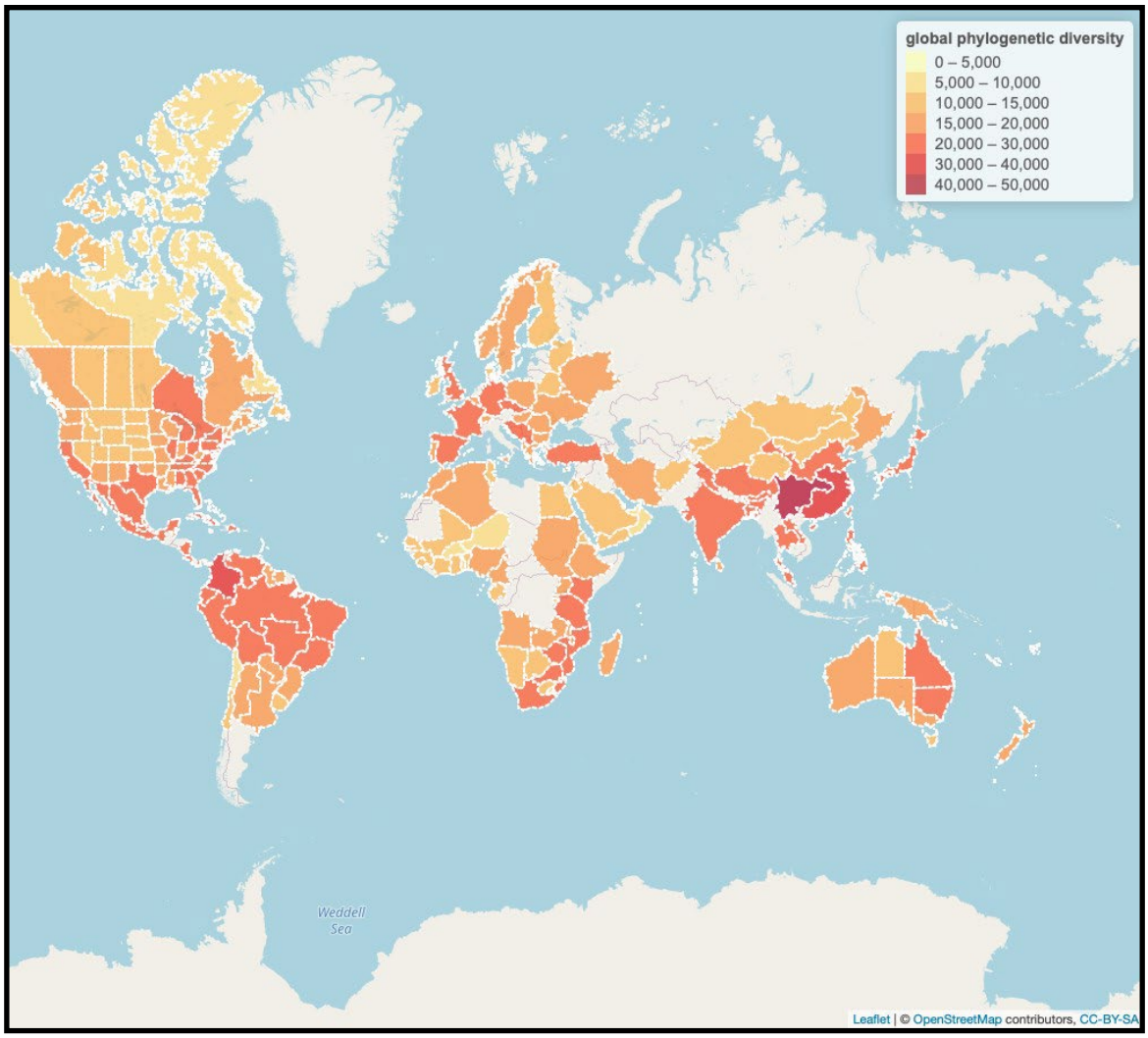

Figure 3-5. Map of global plant diversity. Polygons are delineated as TDWG level 3 regions. As a measure of global plant diversity, we used phylogenetic diversity, as it accounts for the number of species in a region and their genetic differences. Regions with highest global PD are those shown in red. Regions with lowest global PD are those shown in blue. Regions in white were lacking data, so not included in the study.

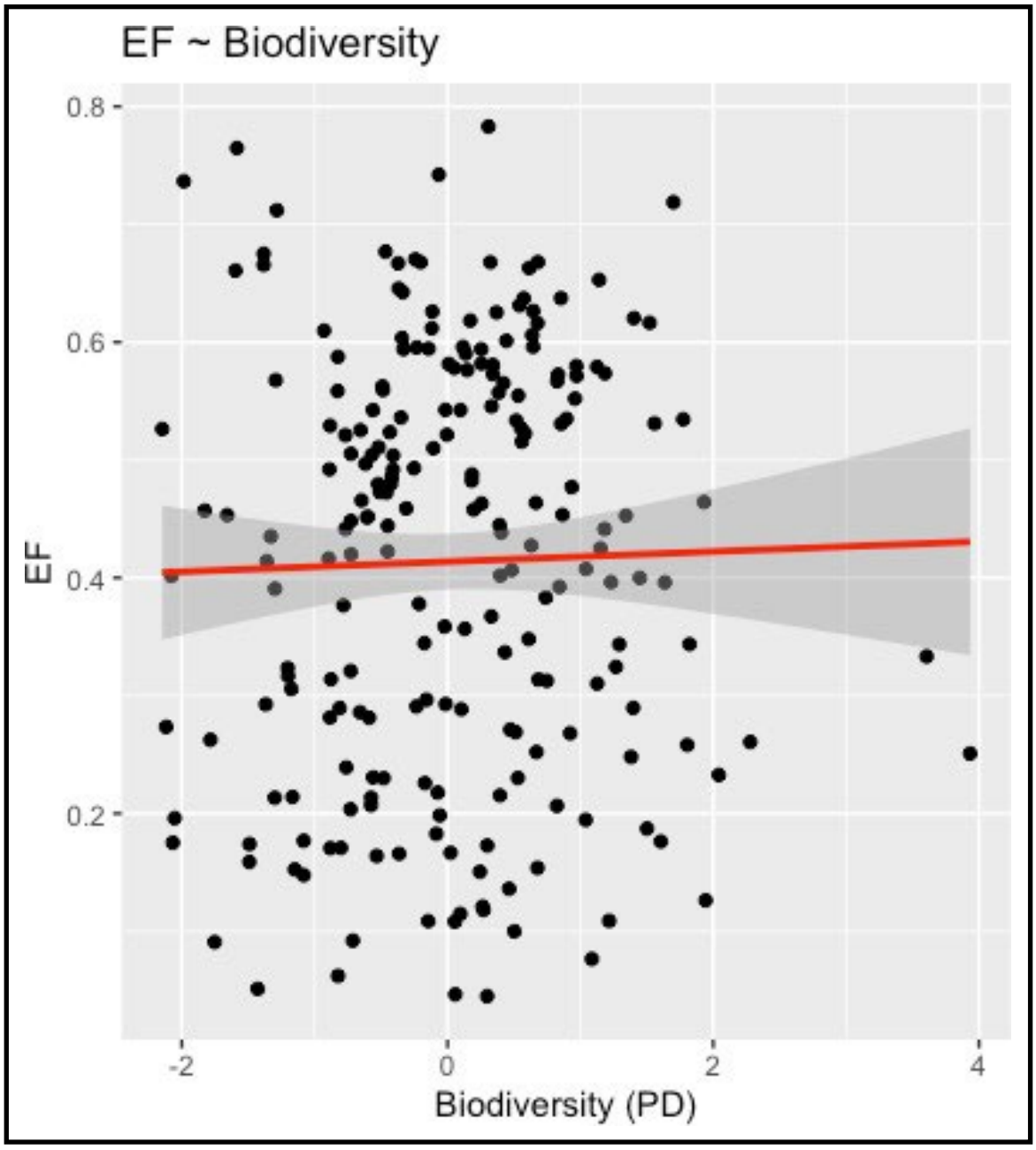

Figure 3-6a. Observed values of EF as a factor of global plant diversity for 223 regions. 95% confidence interval shown in the smoother.

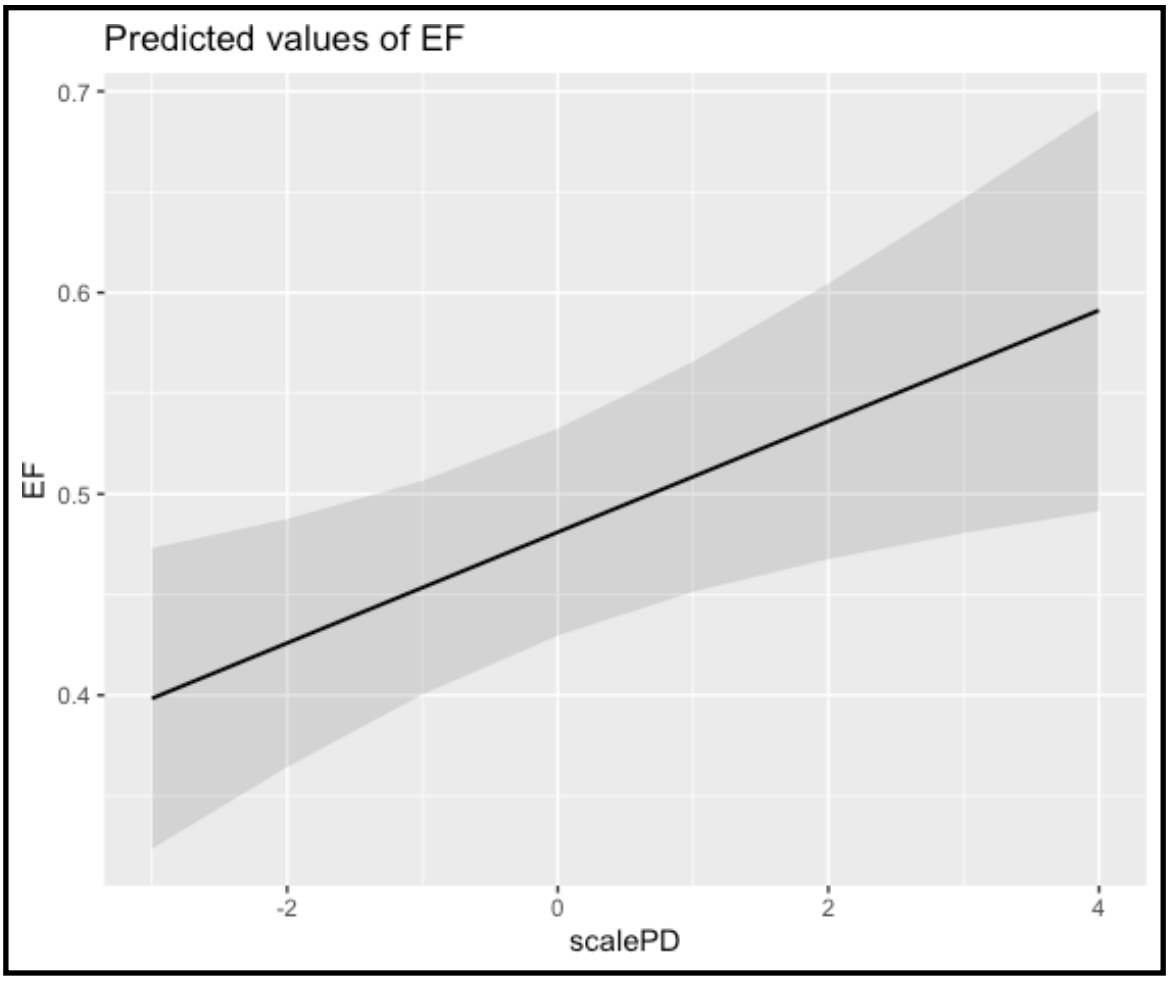

Figure 3-6b. Predicted values of EF as a factor of global plant diversity for 223 regions. Estimate of the coefficient was 0.03 and 95% confidence interval 0.01 – 0.05, as shown in the smoother.

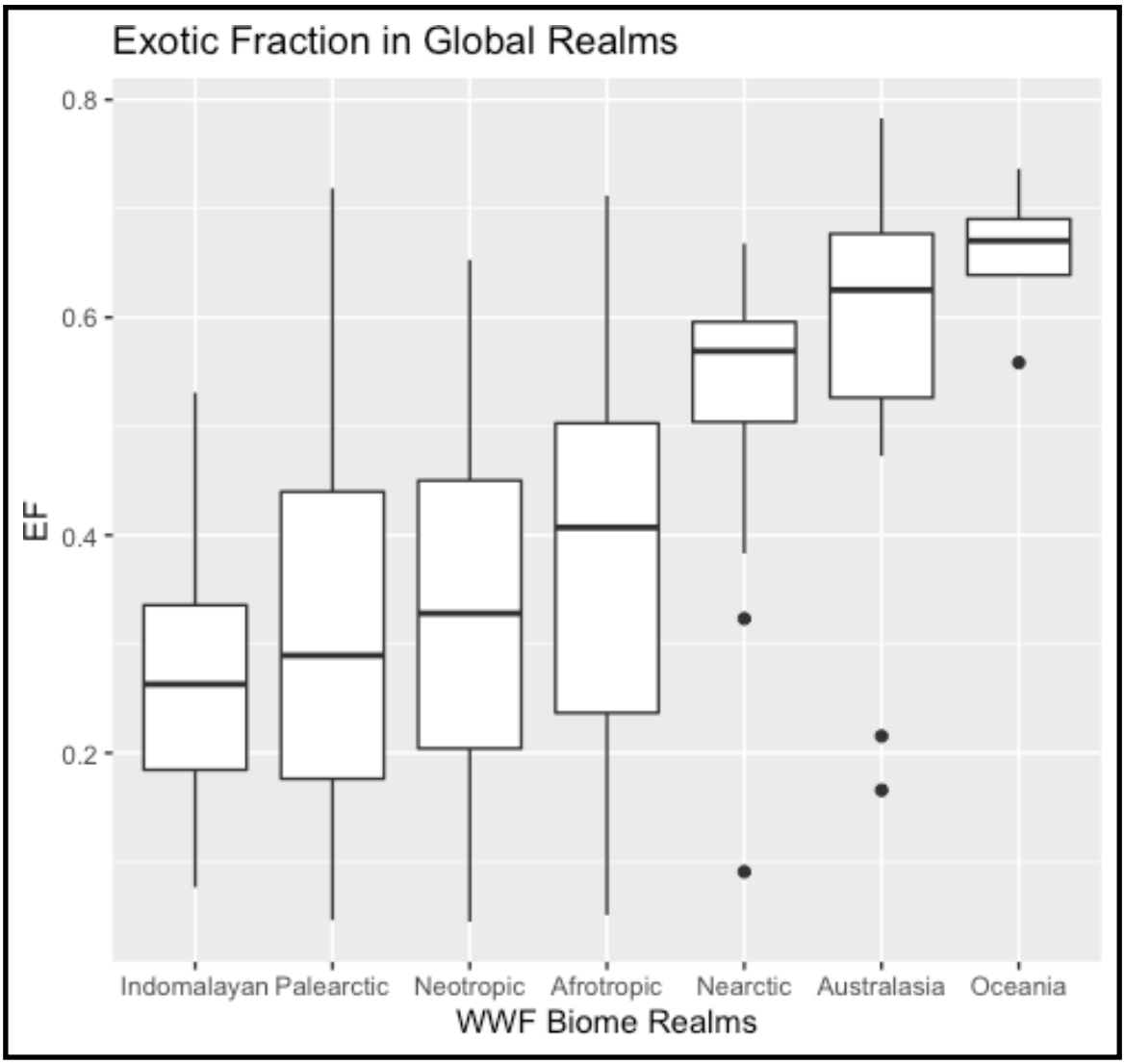

Figure 3-7. Boxplot of exotic fraction in global eco-regions. Error bars show 95% confidence intervals. Outliers are shown as points.

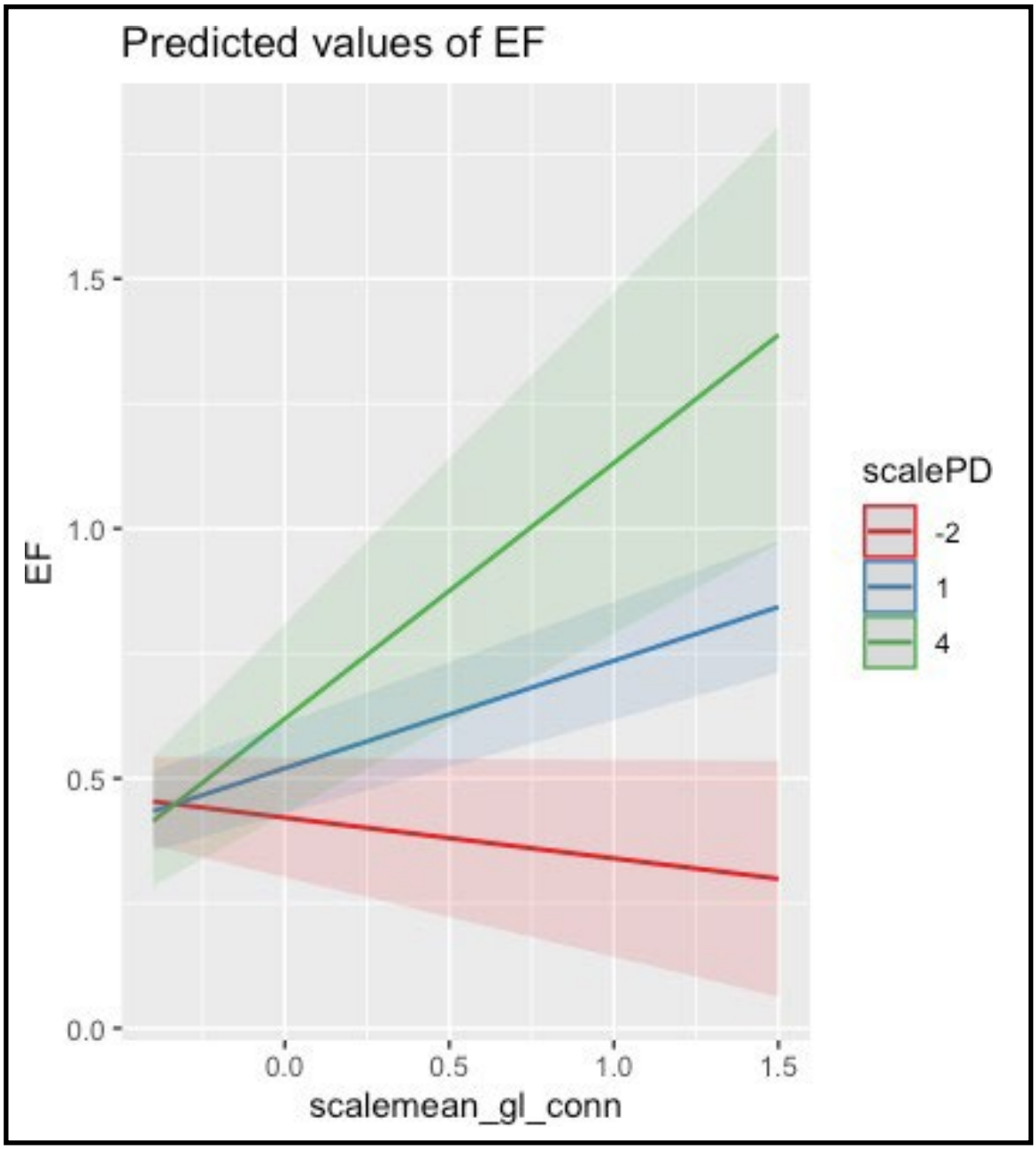

Figure 3-8. Two-way interaction plot showing the effect of global plant diversity (scalePD) on the role of global connectivity (scalemean_gl_conn) in predicting regional EF. The colored lines represent the value of global connectivity when global plant diversity is low, medium, and high as represented by red, blue, and green respectively.

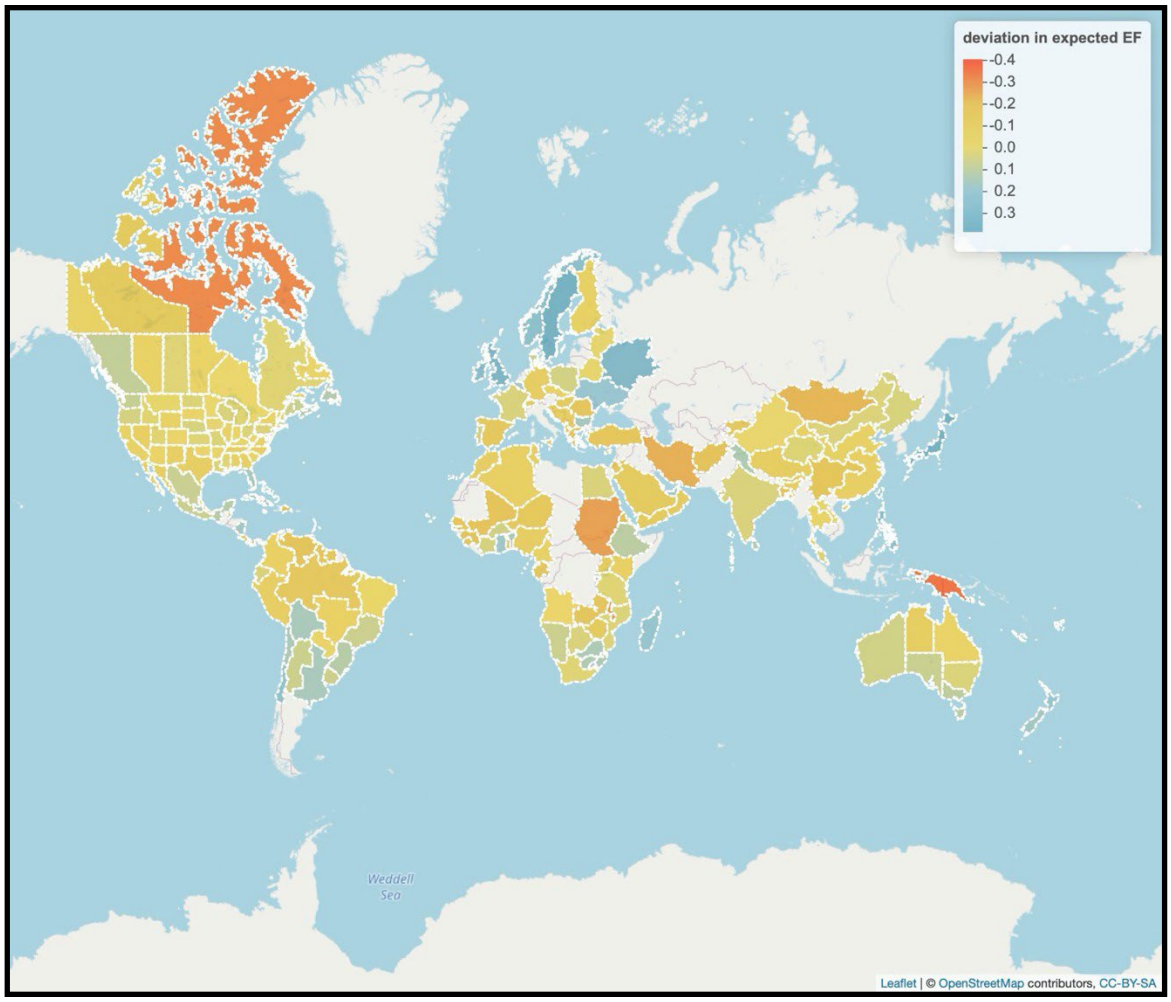

Figure 3-9. Map of deviation in expected EF. Polygons are delineated as TDWG level 3 regions. Regions with lower than predicted EF are shown as red. These regions are considered to have high invasibility. Regions with higher-than-expected EF are shown in blue. Regions in white were lacking data, so not included in the study.

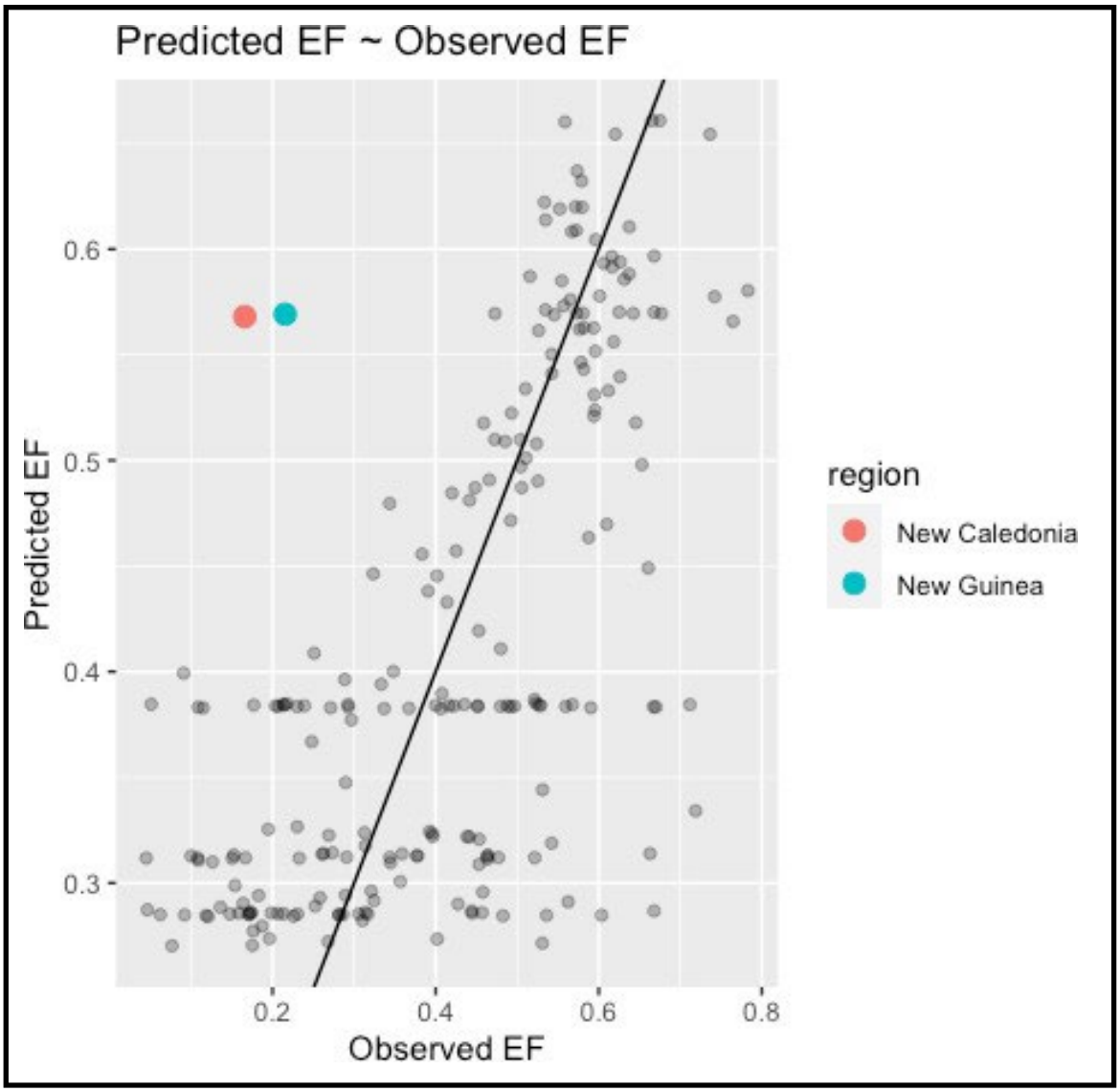

Figure 3-10. Predicted values of EF compared to observed values of EF. The 223 regions used in this study are plotted as points. Highlighted in color are the two regions with the greatest deviation in EF.

3.8. Tables

Table 3-1. Summary statistics for the global model predicting EF as a function of global connectivity (scalemean_gl_conn, global plant diversity (scalePD), eco-realm (REALMs), and the interaction between connectivity and plant diversity.

	EF		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	0.42	0.37 – 0.47	**<0.001**
scalePD	0.03	0.01 – 0.05	**0.002**
scalemean_gl_conn	0.12	0.03 – 0.20	**0.005**
REALM [Australasia]	0.18	0.10 – 0.27	**<0.001**
REALM [Indomalayan]	-0.11	-0.20 – -0.02	**0.016**
REALM [Nearctic]	0.06	-0.02 – 0.15	0.125
REALM [Neotropic]	-0.07	-0.14 – -0.01	**0.033**
REALM [Oceania]	0.28	0.13 – 0.42	**<0.001**
REALM [Palearctic]	-0.10	-0.16 – -0.04	**0.001**
scalePD * scalemean_gl_conn	0.10	0.04 – 0.16	**0.002**
Observations	223		
R^2 / R^2 adjusted	0.441 / 0.418		

Table 3-2. The top five and bottom five regions with the greatest and least values of invasibility, according to the model. Also shown are biome, realm, PD, connectivity, EF, and predicted EF. The covariates realm, PD, and connectivity were used to model EF and find values of predicted EF for global regions. To calculate invasibility, we took the difference between the predicted EF and EF values. Based on data from GloNAF (2018). See table S1 for complete information on all regions in this study.

rank	region	biome	realm	PD	connectivity	EF	predictedEF	invasibility
1	New Caledonia	Tropical and Subtropical Dry Broadleaf Forests	Australasia	15084	1	0.166	0.568	0.402
2	New Guinea	Tropical and Subtropical Moist Broadleaf Forests	Australasia	19561	2883	0.215	0.569	0.354
3	Gambia, The	Tropical and Subtropical Grasslands, Savannas and Shrublands	Afrotropic	8800	0	0.051	0.385	0.333
4	Nunavut	Tundra	Nearctic	6890	196054	0.091	0.399	0.308
5	Malawi	Tropical and Subtropical Grasslands, Savannas and Shrublands	Afrotropic	16377	21	0.109	0.383	0.274
219	Central European Russia	Temperate Broadleaf and Mixed Forests	Palearctic	15208	615	0.604	0.285	-0.319
220	Seychelles	Tropical and Subtropical Moist Broadleaf Forests	Afrotropic	9651	0	0.712	0.384	-0.328
221	Great Britain	Temperate Conifer Forests	Palearctic	20855	38480	0.663	0.314	-0.349
222	Sweden	Temperate Broadleaf and Mixed Forests	Palearctic	16037	5710	0.668	0.287	-0.381
223	Japan	Temperate Broadleaf and Mixed Forests	Palearctic	27268	40774	0.719	0.334	-0.385

3.9. Supplemental Information

1.9.1. Supplemental tables

Table S3-1. Model selection table showing all candidate models.

weight	0.93843443	0.03163071	0.02069039	0.00855759	0.00065609	3.08E-05
delta	0	6.78016921	7.62908766	9.3947881	14.5313271	20.6494196
AICc	-242.13219	-235.35202	-234.5031	-232.7374	-227.60086	-221.48277
logLik	132.691687	134.996398	127.770419	125.791236	123.222966	144.249157
df	11	16	10	9	9	29
REALM:scalemean_gl	NA	NA	NA	NA	NA	+
scalemean_gl_conn:scalePD	0.09891865	NA	NA	NA	NA	-1.529744
REALM:scalePD	NA	NA	NA	NA	NA	+
REALM:scalemean_gl	NA	+	NA	NA	NA	+
scalePD	0.03298546	0.02084824	0.01973598	NA	0.02372729	-0.4950066
scalemean_gl_conn	0.11628598	-0.2117939	0.12574619	0.13668685	NA	-0.0681276
REALM	+	+	+	+	+	+
(Intercept)	0.42305689	0.32078035	0.43340546	0.43044672	0.39264849	0.37561168

4.04E-14	61.5507626	-180.58143	95.4289623	5	NA	0.1046856	NA	NA	0.01460328	0.19699177	NA	0.42173502
5.23E-15	65.641022	-176.49117	91.3003783	3	NA	NA	NA	NA	NA	0.19929082	NA	0.42479161
1.86E-15	67.7057598	-174.42643	91.304958	4	NA	NA	NA	NA	-0.0010408	0.1994693	NA	0.42482336
8.66E-25	110.68552	-131.44667	67.7506076	2	NA	NA	NA	NA	NA	NA	NA	0.41382589
3.30E-25	112.614767	-129.51742	67.813506	3	NA	NA	NA	NA	0.00427638	NA	NA	0.41373587

Table S3-2. Full data set showing invasibility for all regions in this study, according to the model. Also shown are biome, realm, PD, connectivity, EF, and predicted EF. The covariates realm, PD, and connectivity were used to model EF and find values of predicted EF for global regions. To calculate invasibility, we took the difference between the predicted EF and EF values. Based on data from GloNAF (2018).

rank	region	biome	realm	PD	connectivity	EF	predictedEF	invasibility
1	New Caledonia	Tropical and Subtropical Dry Broadleaf Forests	Australasia	15084	1	0.166	0.568	0.402
2	New Guinea	Tropical and Subtropical Moist Broadleaf Forests	Australasia	19561	2883	0.215	0.569	0.354
3	Gambia, The	Tropical and Subtropical Grasslands, Savannas and Shrublands	Afrotropic	8800	0	0.051	0.385	0.333
4	Nunavut	Tundra	Nearctic	6890	196054	0.091	0.399	0.308
5	Malawi	Tropical and Subtropical Grasslands, Savannas and Shrublands	Afrotropic	16377	21	0.109	0.383	0.274
6	Sudan	Deserts and Xeric Shrublands	Afrotropic	17801	4	0.115	0.383	0.268
7	Jamaica	Mangroves	Neotropic	18993	270	0.045	0.312	0.267
8	Iran	Deserts and Xeric Shrublands	Palearctic	17577	5953	0.046	0.287	0.241
9	Mongolia	Deserts and Xeric Shrublands	Palearctic	12369	7	0.062	0.285	0.223

10	Dominican Republic	Mangroves	Neotropic	20201	1926	0.1	0.313	0.213
11	Eritrea	Deserts and Xeric Shrublands	Afrotropic	10846	0	0.177	0.384	0.207
12	Belize	Tropical and Subtropical Grasslands, Savannas and Shrublands	Neotropic	17552	15	0.108	0.312	0.204
13	Panama	Tropical and Subtropical Moist Broadleaf Forests	Neotropic	24411	88	0.109	0.311	0.202
14	Bangladesh	Tropical and Subtropical Moist Broadleaf Forests	Indomalayan	23644	20	0.077	0.27	0.194
15	Afghanistan	Deserts and Xeric Shrublands	Palearctic	13027	0	0.092	0.285	0.193
16	Venezuela	Mangroves	Neotropic	28701	92	0.126	0.31	0.184
17	Sierra Leone	Tropical and Subtropical Grasslands, Savannas and Shrublands	Afrotropic	12927	0	0.204	0.384	0.18
18	Guinea	Tropical and Subtropical Grasslands, Savannas and Shrublands	Afrotropic	13836	1	0.207	0.384	0.176
19	Togo	Tropical and Subtropical Moist Broadleaf Forests	Afrotropic	9559	5	0.213	0.384	0.171
20	Mali	Flooded Grasslands and Savannas	Afrotropic	10347	148	0.214	0.384	0.17
21	Zambia	Tropical and Subtropical Grasslands, Savannas and Shrublands	Afrotropic	16799	3462	0.218	0.385	0.167
22	Romania	Temperate Broadleaf and Mixed Forests	Palearctic	18831	1245	0.118	0.285	0.166
23	Albania	Temperate Broadleaf and Mixed Forests	Palearctic	18788	436	0.121	0.284	0.163
24	Guyana	Mangroves	Neotropic	18671	4	0.151	0.312	0.161
25	Bahamas	Mangroves	Neotropic	10446	6	0.153	0.313	0.161
26	China South-Central	Temperate Broadleaf and Mixed Forests	Palearctic	40444	57054	0.251	0.409	0.158
27	Gabon	Tropical and Subtropical Moist Broadleaf Forests	Afrotropic	14393	0	0.23	0.384	0.154
28	Greece	Mediterranean Forests, Woodlands and Scrub	Palearctic	19968	6780	0.136	0.289	0.152
29	Surinam	Mangroves	Neotropic	17370	25	0.167	0.312	0.145
30	Turkey	Mediterranean Forests, Woodlands and Scrub	Palearctic	21228	18791	0.154	0.299	0.145
31	Senegal	Tropical and Subtropical Grasslands, Savannas and Shrublands	Afrotropic	12735	76	0.239	0.384	0.145
32	Kirgizistan	Temperate Grasslands, Savannas and Shrublands	Palearctic	10845	238	0.148	0.285	0.138
33	Spain	Temperate Broadleaf and Mixed Forests	Palearctic	24860	180367	0.344	0.48	0.136
34	Brazil North	Mangroves	Neotropic	23369	14927	0.195	0.325	0.131
35	Niger	Deserts and Xeric Shrublands	Palearctic	8431	8	0.159	0.286	0.127
36	Palestine	Mediterranean Forests, Woodlands and Scrub	Palearctic	14085	19847	0.164	0.29	0.126
37	Northwest Territories	Tundra	Nearctic	10135	196054	0.323	0.446	0.123

38	Costa Rica	Tropical and Subtropical Dry Broadleaf Forests	Neotropic	25385	49894	0.248	0.367	0.119
39	Saudi Arabia	Deserts and Xeric Shrublands	Palearctic	12032	2477	0.171	0.285	0.115
40	Yemen	Deserts and Xeric Shrublands	Palearctic	12499	362	0.171	0.285	0.114
41	Switzerland	Temperate Conifer Forests	Palearctic	18998	3614	0.173	0.286	0.113
42	Zimbabwe	Deserts and Xeric Shrublands	Afrotropic	20017	600	0.271	0.383	0.112
43	Oman	Temperate Grasslands, Savannas and Shrublands	Palearctic	8436	107	0.174	0.286	0.112
44	Hungary	Temperate Broadleaf and Mixed Forests	Palearctic	16734	20408	0.183	0.294	0.111
45	Uganda	Tropical and Subtropical Moist Broadleaf Forests	Afrotropic	17844	23727	0.289	0.396	0.108
46	Fiji	Tropical and Subtropical Dry Broadleaf Forests	Oceania	12349	8	0.559	0.66	0.102
47	East Himalaya	Tropical and Subtropical Moist Broadleaf Forests	Indomalayan	26707	6187	0.176	0.277	0.101
48	Northern Territory	Tropical and Subtropical Grasslands, Savannas and Shrublands	Australasia	14224	4277	0.473	0.569	0.097
49	Tibet	Montane Grasslands and Shrublands	Palearctic	20357	57054	0.23	0.327	0.096
50	Laccadive Is.	Tropical and Subtropical Moist Broadleaf Forests	Indomalayan	5034	8249	0.175	0.27	0.095
51	Assam	Tropical and Subtropical Moist Broadleaf Forests	Indomalayan	26093	8249	0.187	0.28	0.092
52	Cape Verde	Tropical and Subtropical Dry Broadleaf Forests	Afrotropic	9161	24	0.293	0.384	0.092
53	Nigeria	Tropical and Subtropical Moist Broadleaf Forests	Afrotropic	17149	431	0.293	0.383	0.09
54	Germany	Temperate Conifer Forests	Palearctic	20283	452327	0.533	0.622	0.089
55	Morocco	Mediterranean Forests, Woodlands and Scrub	Palearctic	16888	3238	0.198	0.286	0.087
56	Sicilia	Mediterranean Forests, Woodlands and Scrub	Palearctic	16299	206379	0.297	0.377	0.081
57	Peru	Tropical and Subtropical Moist Broadleaf Forests	Neotropic	29280	1419	0.233	0.312	0.079
58	Yugoslavia	Mediterranean Forests, Woodlands and Scrub	Palearctic	22091	2575	0.206	0.286	0.079
59	Texas	Temperate Conifer Forests	Nearctic	22512	182840	0.535	0.614	0.079
60	Maldives	Tropical and Subtropical Moist Broadleaf Forests	Indomalayan	5114	0	0.196	0.274	0.078
61	Mexico Northwest	Deserts and Xeric Shrublands	Nearctic	21595	10717	0.383	0.456	0.072
62	Tunisia	Temperate Conifer Forests	Palearctic	13838	2519	0.213	0.285	0.072
63	Tennessee	Temperate Broadleaf and Mixed Forests	Nearctic	20532	182840	0.516	0.587	0.071
64	Georgia	Temperate Broadleaf and Mixed Forests	Nearctic	22896	182840	0.552	0.619	0.067
65	Nevada	Deserts and Xeric Shrublands	Nearctic	12947	182840	0.42	0.485	0.065
66	North Carolina	Temperate Broadleaf and Mixed Forests	Nearctic	24223	182840	0.574	0.637	0.063
67	China Southeast	Temperate Broadleaf and Mixed Forests	Palearctic	38509	53846	0.333	0.394	0.061

68	New Mexico	Temperate Conifer Forests	Nearctic	15399	182840	0.459	0.518	0.059
69	Algeria	Deserts and Xeric Shrublands	Palearctic	16229	30	0.226	0.284	0.059
70	China North-Central	Deserts and Xeric Shrublands	Palearctic	25481	57054	0.29	0.348	0.058
71	Finland	Temperate Broadleaf and Mixed Forests	Palearctic	13924	2304	0.231	0.285	0.055
72	Brazil West-Central	Tropical and Subtropical Moist Broadleaf Forests	Neotropic	20262	14927	0.269	0.323	0.053
73	Alabama	Temperate Broadleaf and Mixed Forests	Nearctic	23873	182840	0.579	0.632	0.053
74	Colombia	Mangroves	Neotropic	30679	2732	0.261	0.314	0.053
75	Kenya	Flooded Grasslands and Savannas	Afrotropic	20837	22509	0.348	0.4	0.052
76	Netherlands Antilles	Mangroves	Neotropic	6701	4	0.263	0.314	0.051
77	California	Temperate Grasslands, Savannas and Shrublands	Nearctic	22969	182840	0.571	0.62	0.049
78	Yukon	Tundra	Nearctic	9570	196054	0.391	0.438	0.047
79	Cameroon	Tropical and Subtropical Moist Broadleaf Forests	Afrotropic	19782	38	0.337	0.383	0.046
80	Mexican Pacific Is.	Mediterranean Forests, Woodlands and Scrub	Nearctic	4966	10717	0.402	0.445	0.044
81	Illinois	Temperate Grasslands, Savannas and Shrublands	Nearctic	22104	182840	0.567	0.608	0.041
82	Aruba	Mangroves	Neotropic	4733	0	0.274	0.314	0.041
83	Virginia	Temperate Broadleaf and Mixed Forests	Nearctic	22952	182840	0.58	0.62	0.04
84	Wyoming	Temperate Conifer Forests	Nearctic	12699	182840	0.442	0.481	0.04
85	Alberta	Temperate Conifer Forests	Nearctic	12941	196054	0.448	0.487	0.039
86	Manitoba	Temperate Grasslands, Savannas and Shrublands	Nearctic	14515	196054	0.472	0.51	0.038
87	Czechoslovakia	Temperate Conifer Forests	Palearctic	21185	6935	0.252	0.289	0.037
88	Queensland	Tropical and Subtropical Grasslands, Savannas and Shrublands	Australasia	27701	4277	0.535	0.571	0.037
89	South Carolina	Temperate Broadleaf and Mixed Forests	Nearctic	22144	182840	0.573	0.609	0.036
90	Antipodean Is.	Tundra	Australasia	4559	19891	0.526	0.561	0.035
91	Thailand	Tropical and Subtropical Moist Broadleaf Forests	Indomalayan	27880	17884	0.258	0.293	0.035
92	New York	Temperate Broadleaf and Mixed Forests	Nearctic	25509	182840	0.62	0.654	0.034
93	Mexico Gulf	Deserts and Xeric Shrublands	Nearctic	24025	10717	0.425	0.457	0.032
94	Kentucky	Temperate Broadleaf and Mixed Forests	Nearctic	20378	182840	0.555	0.585	0.03
95	Arizona	Temperate Conifer Forests	Nearctic	15746	182840	0.493	0.522	0.029
96	South Dakota	Temperate Grasslands, Savannas and Shrublands	Nearctic	13412	182840	0.466	0.491	0.025
97	Oklahoma	Temperate Grasslands, Savannas and Shrublands	Nearctic	16603	182840	0.51	0.534	0.024

98	Colorado	Deserts and Xeric Shrublands	Nearctic	14754	182840	0.485	0.509	0.024
99	Arkansas	Temperate Broadleaf and Mixed Forests	Nearctic	19189	182840	0.546	0.569	0.023
100	Paraguay	Tropical and Subtropical Moist Broadleaf Forests	Neotropic	15855	40	0.291	0.312	0.021
101	Labrador	Boreal Forests/Taiga	Nearctic	9205	196054	0.414	0.433	0.019
102	West Virginia	Temperate Broadleaf and Mixed Forests	Nearctic	19503	182840	0.557	0.573	0.016
103	Angola	Montane Grasslands and Shrublands	Afrotropic	19177	0	0.367	0.383	0.015
104	Brazil Northeast	Mangroves	Neotropic	21642	14927	0.313	0.324	0.011
105	Indiana	Temperate Grasslands, Savannas and Shrublands	Nearctic	19716	182840	0.565	0.576	0.011
106	Ontario	Boreal Forests/Taiga	Nearctic	21032	196054	0.596	0.604	0.008
107	Minnesota	Temperate Grasslands, Savannas and Shrublands	Nearctic	17807	182840	0.542	0.55	0.008
108	Montana	Temperate Grasslands, Savannas and Shrublands	Nearctic	14818	182840	0.504	0.51	0.006
109	Xinjiang	Deserts and Xeric Shrublands	Palearctic	12439	57054	0.289	0.294	0.005
110	Laos	Tropical and Subtropical Dry Broadleaf Forests	Indomalayan	22680	2028	0.268	0.272	0.004
111	Hainan	Tropical and Subtropical Moist Broadleaf Forests	Indomalayan	21270	57054	0.314	0.318	0.004
112	Cyprus	Mediterranean Forests, Woodlands and Scrub	Palearctic	12009	104	0.281	0.285	0.004
113	Belarus	Temperate Broadleaf and Mixed Forests	Palearctic	13752	43	0.281	0.285	0.004
114	Northwest European Russia	Temperate Broadleaf and Mixed Forests	Palearctic	13342	615	0.286	0.285	-0.001
115	Iowa	Temperate Grasslands, Savannas and Shrublands	Nearctic	17136	182840	0.543	0.541	-0.001
116	Vermont	Temperate Broadleaf and Mixed Forests	Nearctic	19246	182840	0.573	0.57	-0.003
117	Samoa	Tropical and Subtropical Moist Broadleaf Forests	Oceania	9064	1	0.666	0.661	-0.005
118	Utah	Deserts and Xeric Shrublands	Nearctic	13869	182840	0.504	0.497	-0.007
119	Idaho	Temperate Conifer Forests	Nearctic	14173	182840	0.511	0.501	-0.01
120	Mississippi	Temperate Broadleaf and Mixed Forests	Nearctic	19242	182840	0.581	0.57	-0.011
121	Michigan	Temperate Broadleaf and Mixed Forests	Nearctic	20990	182840	0.606	0.593	-0.013
122	Tonga	Tropical and Subtropical Moist Broadleaf Forests	Oceania	9065	0	0.675	0.661	-0.014
123	QuV©bec	Tundra	Nearctic	18111	196054	0.576	0.562	-0.014
124	Kansas	Temperate Grasslands, Savannas and Shrublands	Nearctic	14675	182840	0.524	0.508	-0.016
125	Cape Provinces	Mediterranean Forests, Woodlands and Scrub	Afrotropic	25773	2265	0.4	0.384	-0.016
126	Tanzania	Tropical and Subtropical Moist Broadleaf Forests	Afrotropic	23383	7952	0.408	0.39	-0.018
127	Saskatchewan	Temperate Grasslands, Savannas and Shrublands	Nearctic	12945	196054	0.505	0.487	-0.018

128	Missouri	Temperate Grasslands, Savannas and Shrublands	Nearctic	18740	182840	0.582	0.563	-0.019
129	Ohio	Temperate Broadleaf and Mixed Forests	Nearctic	21232	182840	0.616	0.596	-0.02
130	Qinghai	Deserts and Xeric Shrublands	Palearctic	10294	57054	0.306	0.285	-0.02
131	North Dakota	Temperate Grasslands, Savannas and Shrublands	Nearctic	11989	182840	0.492	0.472	-0.02
132	Louisiana	Temperate Broadleaf and Mixed Forests	Nearctic	19847	182840	0.601	0.578	-0.023
133	Mozambique	Tropical and Subtropical Grasslands, Savannas and Shrublands	Afrotropic	20079	36	0.407	0.382	-0.024
134	Inner Mongolia	Deserts and Xeric Shrublands	Palearctic	12928	57054	0.321	0.296	-0.025
135	New South Wales	Montane Grasslands and Shrublands	Australasia	26207	21379	0.617	0.591	-0.025
136	Pennsylvania	Temperate Broadleaf and Mixed Forests	Nearctic	22271	182840	0.637	0.611	-0.027
137	Baleares	Mediterranean Forests, Woodlands and Scrub	Palearctic	12057	6643	0.314	0.286	-0.028
138	Malaya	Mangroves	Indomalayan	23880	11819	0.31	0.282	-0.028
139	Wisconsin	Temperate Grasslands, Savannas and Shrublands	Nearctic	18731	182840	0.594	0.563	-0.031
140	Egypt	Deserts and Xeric Shrublands	Palearctic	10150	14010	0.317	0.285	-0.031
141	Ecuador	Montane Grasslands and Shrublands	Neotropic	27983	1617	0.344	0.312	-0.032
142	New Hampshire	Temperate Broadleaf and Mixed Forests	Nearctic	17529	182840	0.578	0.546	-0.032
143	Botswana	Tropical and Subtropical Grasslands, Savannas and Shrublands	Afrotropic	11953	3	0.416	0.384	-0.032
144	New Jersey	Temperate Broadleaf and Mixed Forests	Nearctic	21034	182840	0.626	0.594	-0.033
145	India	Deserts and Xeric Shrublands	Palearctic	24711	8249	0.324	0.292	-0.033
146	France	Temperate Conifer Forests	Palearctic	25156	122720	0.453	0.419	-0.033
147	Manchuria	Flooded Grasslands and Savannas	Palearctic	16204	57054	0.345	0.31	-0.035
148	Nebraska	Temperate Grasslands, Savannas and Shrublands	Nearctic	13368	182840	0.525	0.49	-0.035
149	Oregon	Temperate Conifer Forests	Nearctic	17285	182840	0.582	0.543	-0.038
150	Ivory Coast	Tropical and Subtropical Moist Broadleaf Forests	Afrotropic	14571	824	0.422	0.384	-0.039
151	Delaware	Temperate Grasslands, Savannas and Shrublands	Nearctic	17915	182840	0.596	0.552	-0.044
152	Poland	Temperate Broadleaf and Mixed Forests	Palearctic	17105	58050	0.359	0.314	-0.045
153	Connecticut	Temperate Broadleaf and Mixed Forests	Nearctic	20430	182840	0.631	0.586	-0.046
154	Maryland	Temperate Broadleaf and Mixed Forests	Nearctic	20617	182840	0.637	0.588	-0.049
155	Burkina	Tropical and Subtropical Grasslands, Savannas and Shrublands	Afrotropic	9385	6	0.435	0.384	-0.051
156	Western Australia	Deserts and Xeric Shrublands	Australasia	19409	4277	0.625	0.57	-0.055

157	Portugal	Temperate Broadleaf and Mixed Forests	Palearctic	17998	28952	0.357	0.301	-0.056
158	Maine	Temperate Broadleaf and Mixed Forests	Nearctic	18242	182840	0.618	0.556	-0.062
159	Rhode I.	Temperate Broadleaf and Mixed Forests	Nearctic	16390	182840	0.595	0.531	-0.064
160	Uruguay	Tropical and Subtropical Moist Broadleaf Forests	Neotropic	12606	486	0.377	0.313	-0.064
161	Argentina Northwest	Montane Grasslands and Shrublands	Neotropic	15965	1585	0.378	0.313	-0.065
162	Burundi	Tropical and Subtropical Moist Broadleaf Forests	Afrotropic	13652	43	0.451	0.384	-0.068
163	Brazil Southeast	Tropical and Subtropical Moist Broadleaf Forests	Neotropic	22203	14927	0.392	0.324	-0.068
164	Namibia	Tropical and Subtropical Grasslands, Savannas and Shrublands	Afrotropic	13696	267	0.452	0.384	-0.068
165	Denmark	Temperate Broadleaf and Mixed Forests	Palearctic	14717	380872	0.48	0.411	-0.069
166	Massachusetts	Temperate Conifer Forests	Nearctic	21249	182840	0.668	0.597	-0.071
167	District of Columbia	Temperate Broadleaf and Mixed Forests	Nearctic	15857	182840	0.595	0.524	-0.072
168	Mexico Southwest	Tropical and Subtropical Dry Broadleaf Forests	Neotropic	26885	10717	0.396	0.323	-0.073
169	South Australia	Deserts and Xeric Shrublands	Australasia	15247	4277	0.642	0.57	-0.073
170	New Brunswick	Temperate Broadleaf and Mixed Forests	Nearctic	15277	196054	0.594	0.521	-0.073
171	Mexico Northeast	Tropical and Subtropical Dry Broadleaf Forests	Neotropic	24495	10717	0.396	0.322	-0.074
172	Washington	Temperate Conifer Forests	Nearctic	16535	182840	0.612	0.533	-0.079
173	Kermadec Is.	Tropical and Subtropical Moist Broadleaf Forests	Oceania	5518	19891	0.737	0.654	-0.082
174	British Columbia	Tundra	Nearctic	16560	196054	0.626	0.54	-0.086
175	Swaziland	Montane Grasslands and Shrublands	Afrotropic	14148	12	0.48	0.384	-0.096
176	Victoria	Montane Grasslands and Shrublands	Australasia	19135	4277	0.668	0.57	-0.098
177	Ethiopia	Deserts and Xeric Shrublands	Afrotropic	18317	1674	0.488	0.384	-0.104
178	Tasmania	Temperate Broadleaf and Mixed Forests	Australasia	14476	4277	0.677	0.569	-0.107
179	Gulf of Guinea Is.	Tropical and Subtropical Moist Broadleaf Forests	Afrotropic	14806	0	0.492	0.383	-0.108
180	Rwanda	Tropical and Subtropical Moist Broadleaf Forests	Afrotropic	13584	18	0.497	0.384	-0.113
181	Brazil South	Tropical and Subtropical Moist Broadleaf Forests	Neotropic	19617	14927	0.438	0.322	-0.116
182	Mexico Southeast	Tropical and Subtropical Grasslands, Savannas and Shrublands	Neotropic	24205	10717	0.441	0.322	-0.12
183	Newfoundland	Boreal Forests/Taiga	Nearctic	12364	98071	0.588	0.463	-0.124
184	Nova Scotia	Temperate Broadleaf and Mixed Forests	Nearctic	15062	196054	0.646	0.518	-0.128
185	Sri Lanka	Deserts and Xeric Shrublands	Indomalayan	19575	3600	0.402	0.274	-0.128

186	Mexico Central	Tropical and Subtropical Dry Broadleaf Forests	Neotropic	22342	10717	0.453	0.321	-0.133
187	Free State	Tropical and Subtropical Grasslands, Savannas and Shrublands	Afrotropic	12694	16807	0.521	0.387	-0.134
188	West Himalaya	Montane Grasslands and Shrublands	Palearctic	20951	8249	0.427	0.29	-0.137
189	KwaZulu-Natal	Tropical and Subtropical Grasslands, Savannas and Shrublands	Afrotropic	20674	3462	0.523	0.385	-0.138
190	Prince Edward I.	Temperate Broadleaf and Mixed Forests	Nearctic	11750	196054	0.61	0.47	-0.14
191	Northern Provinces	Tropical and Subtropical Grasslands, Savannas and Shrublands	Afrotropic	20504	2265	0.527	0.384	-0.142
192	Chile North	Deserts and Xeric Shrublands	Neotropic	7445	23079	0.453	0.309	-0.144
193	Benin	Tropical and Subtropical Moist Broadleaf Forests	Afrotropic	12018	0	0.529	0.384	-0.145
194	Argentina Northeast	Tropical and Subtropical Moist Broadleaf Forests	Neotropic	18743	1585	0.463	0.313	-0.15
195	Bolivia	Tropical and Subtropical Grasslands, Savannas and Shrublands	Neotropic	28627	2461	0.464	0.313	-0.151
196	Cuba	Mangroves	Neotropic	21156	133	0.464	0.311	-0.152
197	Florida	Mangroves	Neotropic	23964	182840	0.653	0.498	-0.155
198	Canary Is.	Mediterranean Forests, Woodlands and Scrub	Palearctic	14578	6643	0.444	0.287	-0.157
199	Bulgaria	Mediterranean Forests, Woodlands and Scrub	Palearctic	19540	2866	0.445	0.286	-0.159
200	Belgium	Temperate Broadleaf and Mixed Forests	Palearctic	18392	19404	0.458	0.296	-0.162
201	New Zealand South	Temperate Grasslands, Savannas and Shrublands	Australasia	16845	19891	0.742	0.577	-0.165
202	Nicaragua	Tropical and Subtropical Moist Broadleaf Forests	Neotropic	22753	1209	0.477	0.312	-0.165
203	Gulf States	Temperate Grasslands, Savannas and Shrublands	Palearctic	6446	619	0.457	0.286	-0.171
204	Ghana	Mangroves	Afrotropic	14363	184	0.559	0.384	-0.176
205	Lesotho	Tropical and Subtropical Grasslands, Savannas and Shrublands	Afrotropic	9600	15	0.568	0.384	-0.183
206	Taiwan	Tropical and Subtropical Moist Broadleaf Forests	Indomalayan	26431	61505	0.531	0.344	-0.187
207	Ukraine	Temperate Conifer Forests	Palearctic	18312	851	0.483	0.284	-0.198
208	Chatham Is.	Temperate Broadleaf and Mixed Forests	Australasia	7877	19891	0.765	0.566	-0.199
209	New Zealand North	Temperate Broadleaf and Mixed Forests	Australasia	19048	19891	0.783	0.58	-0.203
210	Madagascar	Tropical and Subtropical Dry Broadleaf Forests	Afrotropic	18034	166	0.59	0.383	-0.207
211	Windward Is.	Mangroves	Neotropic	17206	13	0.521	0.312	-0.21
212	Bermuda	Tropical and Subtropical Coniferous Forests	Nearctic	7816	296	0.661	0.449	-0.212
213	Chile Central	Mediterranean Forests, Woodlands and Scrub	Neotropic	13917	23079	0.542	0.319	-0.224

214	Norway	Tundra	Palearctic	15168	544	0.536	0.285	-0.251
215	Philippines	Tropical and Subtropical Moist Broadleaf Forests	Indomalayan	22277	1155	0.531	0.272	-0.259
216	Ireland	Temperate Broadleaf and Mixed Forests	Palearctic	14341	21166	0.563	0.291	-0.271
217	Rv©union	Tropical and Subtropical Moist Broadleaf Forests	Afrotropic	15040	30	0.667	0.383	-0.284
218	Mauritius	Tropical and Subtropical Moist Broadleaf Forests	Afrotropic	15806	9	0.67	0.383	-0.287
219	Central European Russia	Temperate Broadleaf and Mixed Forests	Palearctic	15208	615	0.604	0.285	-0.319
220	Seychelles	Tropical and Subtropical Moist Broadleaf Forests	Afrotropic	9651	0	0.712	0.384	-0.328
221	Great Britain	Temperate Conifer Forests	Palearctic	20855	38480	0.663	0.314	-0.349
222	Sweden	Temperate Broadleaf and Mixed Forests	Palearctic	16037	5710	0.668	0.287	-0.381
223	Japan	Temperate Broadleaf and Mixed Forests	Palearctic	27268	40774	0.719	0.334	-0.385

CONCLUSIONS

Identifying and ultimately preventing future plant invasions constitutes an ongoing challenge for ecologists and land managers over the last half-century, despite the general understanding that it is the most cost-efficient strategy to manage invasive species (CBD 2002; Simberloff et al. 2013). Previous research has made considerable progress in this field, however there is still much uncertainty in which plants will become invaders and which regions will be invaded (Elith 2017; Capinha et al. 2018; Rocchini et al. 2019). A universal approach to predicting plant invasions is difficult, given the various pathways of introduction (Hulme et al. 2008) and spread (Seebens et al. 2018; Seebens et al. 2021).

The goal of this dissertation research was to use the multi-step invasion process as a framework to evaluate factors facilitating invasiveness of species and invasibility of regions. We sought to measure and evaluate the relative effects of limiting factors on plant species' global invasion success and incorporate the effect of spatial scale on those limiting factors. We also aimed to develop a novel method to quantify invasibility and highlight regions with potential for future invasions. The objectives of this work were investigated through three independent but complimentary chapters. Key findings of each chapter are included below.

Chapter 1: *Regional phylogenetic diversity drives invasion success in plants on a global scale* found evidence that the phylogenetic diversity of the native range is an important determinant of invasion success for woody plant species. Specifically, species with lower diversity in the native range than in the introduced range had a low

probability of invasion success. To our knowledge, this is the first study to reveal the importance of low phylogenetic diversity in the native range when evaluating the invasiveness of plant species. We also found that species with higher diversity in the native range than in the introduced range had a higher probability of invasion success. This research suggests that subsequent studies predicting the invasiveness of species should include native-range phylogenetic diversity as a limiting or facilitating factor. Species had a high probability of invasion success in regions found to be environmentally suitable but less so when diversity of the native range was low. This finding is consistent with previous work highlighting the importance of environmental filtering on the distribution of invasive plant species (Richardson and Thuiller 2007; Turbelin et al. 2017), suggesting its inclusion in subsequent studies predicting the invasiveness of plant species. Regional connectivity was not influential in this study, perhaps highlighting an important caveat of missing first records and temporal trends of invasive plant species. The connectivity variable represented current trade dynamics and may not match invasion dynamics of species chosen in this study. Specifically, some species in this dataset may have been introduced long before the trade calculations of this study. For instance, many species were introduced during European colonization of the 1800s, with further accelerations after WWII (Seebens et al. 2017; Seebens et al. 2021). Recently developed was the first Alien Species First Record Database (Seebens et al. 2017), allowing analyses of long-term trends in invasive species establishment and spread. Future studies using current connectivity values should consider first records.

Chapter 2: *The effect of spatial scale on invasion success* analyzed the invasion patterns from Chapter 1 over three spatial scales to understand how scale affects the observed outcomes of processes driving species invasiveness. Again, native-range phylogenetic diversity positively correlated with invasion success of plant species, but the importance of this variable was greatest at the regional scale (the second scale in this study). Results emphasized the importance of environmental suitability in invasion success, and the correlation of this variable increased and strengthened with scale. Chapter 2 also found a lack of support for the influence of connectivity at any scale. Similar caveats exist here as did in Chapter 1, with first records and therefore temporal trends missing from this study.

Chapter 3: *Modeling exotic fraction to predict regions with high potential of plant invasion* found that total regional connectivity was influential in explaining the exotic fraction of global regions. This study also revealed that regions with fewer-than-expected invasive species have a high potential for future invasions. We developed a novel way to quantify invasibility of regions, revealing New Caledonia and New Guinea, both Australasia, as regions with highest potential for future invasions. The results from this study can be used as a predictive tool to determine future invasibility of regions.

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