**Investigation of immigration-extinction dynamics as a controlling factor for peninsular effect for tree species in Florida**

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*Keywords*: Peninsular effect, species diversity, species richness, immigration-extinction hypothesis, Florida

**Abstract**

Patterns of tree species richness were examined in Florida (USA) in the context of peninsular effect for the first time using the USDA Forest Service’s Forest Inventory and Analysis (FIA) program. Species richness decreased significantly with distance from the mainland, with a significant and positive correlation to latitude (adjusted R2 = 0.97, P < 0.001), supporting Simpson’s (1964) peninsular effect. To determine whether peninsula geometry hypothesis explains the observed diversity trend, occurrence of individual tree species was calculated at 20 km × 20 km grid level and its pattern along peninsula was constructed using Huisman-Olff-Fresco (HOF) models (Oksanen & Minchin 2002). Simulated occurrence patterns showed that only 18 of the 113 tree species (~13%) experience significant occurrence attrition in the peninsula comparing to their counterparts in the mainland, while 48 of the 113 tree species (~42%) decreases in occurrence which aligns with its regional occurrence curve throughout its entire geographic range. The majority (~58%) exhibits no decline in occurrence along peninsular gradient. Therefore this analysis suggested that the observed diversity pattern of tree species in Florida could not be explained by the peninsula gradient. Rather, other stochastic factors, i.e. disturbances and species compositional variations, should be considered as the underlying causes for the diversity pattern.

**1. Introduction**

The study of spatial patterns of species richness (*sensu* “species diversity”) has been a continuing scientific inquiry since the nineteenth century (e.g. Wallace 1876) and remains as one of the most active area of research (Science 2005). Latitudinal diversity gradient is a primary biodiversity pattern recognized in a wide spectrum of taxa where the highest levels of species richness are seen in the tropics and declines toward the polar regions (Brown & Lomolino 1998; Gaston 1996; Rosenzweig 1995; Willig 2001). Various hypotheses have been proposed to explain this widely recognized pattern, but current empirical studies tend to be confined to only few selected taxa with unstandardized sampling campaign (Willig et al. 2003; Kreft and Jetz 2007). Woody plants in particular have received little attention although they are one of the most prominent organisms sustaining biodiversity and functions of ecosystems.

Studies, on the other hand, have shown notable exceptions as well as secondary (or more localized) biodiversity patterns (e.g. Simpson 1964; Robinson et al. 2000). Among these variations, peninsular effect is a pattern found in peninsulas where diversity declines from mainland to tip (Simpson 1964). The peninsular effect has attracted considerable attention over the past 50 years, but has not yet proved to be a cross-taxonomy general pattern, such as Jenkins et al. (2008) found that only 18 out of 37 studies (49%) supported the peninsula effect and concluded that the current state of peninsula research suffered from low illumination with limited quantitative data analysis. Battisti (2014) also stated that the peninsula effect is idiosyncratic, depending on context, taxonomic group, and analytic scales.

For studies with observed peninsular effect, explanations for diversity patterns also varied and three hypotheses (history, habitat, and geometry) have been proposed. Among these suggestions, geometry hypothesis by Simpson (1964) (later also known as immigration-extinction hypothesis) has shown explanatory power for some taxa in assemblages of various peninsulas, and such examples include birds in North America (MacArthur & Wilson 1967), heteromyid rodents in Baja California (Taylor & Regal 1978), scorpions in Florida (Due & Polis 1986) and forest vegetation in Maine (Milne & Forman 1986) as well as butterflies in Florida (Brown & Opler 1990). The geometry hypothesis emphasized the role of island-like nature of peninsulas on demographic processes - immigration and extinction. Simpson (1964) argued that immigration from population sources in mainland is restricted by peninsula geometry where geographic spread is along peninsula axis only, and thus the rate of immigration decreases with distance. As continuing colonization of peninsulas is inevitably hindered, and a high extinction rate is expected due to low population density. Consequently, an increasingly decline of immigration/extinction ratio along the peninsula from the mainland ultimately leads to a decline in species richness.

Many related studies have attributed low species richness in peninsular to the geometry hypothesis (Robertson 1955; Simpson 1964; MacArthur and Wilson 1967; Cook 1969; Kiester 1971), but this hypothesis has often been used as a verbal argument labeled as “*red herring*” (Busack and Hedges 1984) rather than being critically tested partly because collecting quantifiable data pertinent to immigration-extinction dynamics would be extremely onerous and unlikely to be attained especially for non-volant organisms.

Alternatively, population dynamics may provide insights as demographic processes, are closely related to population density distribution (Pimm et al. 1988; Gaston 2009; Sutton & Morgan 2009). Empirical studies from invasion ecology have shown high occurrence (in the form of phytosociological ‘importance values’) is significantly positively associated with successful immigration and establishment (Colautti et al. 2006). On the other hand, low occurrence has often been associated with high levels of extinction (Lavergne et al. 2006; Sutton & Morgan 2009). Therefore, current occurrence level of species may be regarded as a ramification of past immigration-extinction dynamics as well as an important predictor of such dynamics in the future. In this sense, one could expect an appreciable decrease in occurrence when a species range extends into a peninsula if the demographic process of this species is negatively impacted by peninsula geometry.

In this study, we examined occurrence patterns of tree species found in Florida across its entire geographic range in eastern North America. Specifically, we compared each species’ occurrence variations in the peninsula with its overall patterns in the mainland to look for occurrence decrease, which may attribute to peninsular geometry. Among the mixed records of whether peninsular effect is present, authors (Jenkins et al. 2008; Battisti 2014) have identified common issues relating to these studies which include 1) inconsistent definition of peninsular range or boarder; 2) incomplete data or inadequate sampling; 3) uncertainty in taxonomic identification; 4) verbal arguments with limited empirical evidence; 5) lack of studies on invertebrates and plants. We used a comprehensive annual inventory with standardized sampling scheme from forested areas to analyze field observations (e.g. occurence of the species). We also simulate occurrence patterns for each species across its entire geographic range to discern variations in a systematic manner. Bootstrapping technique (Efron 1979) is adapted in the models to compensate small number of sample size. More details of data preparation and analytic methods are provided in the later sections.

# 2. Materials and Analysis

In the United States, USDA Forest Service Forest Inventory and Analysis (FIA) program has been consistently providing nation-wide tree census information regarding the extent, condition, status and trends of the forest resources in the country (Smith 2002). FIA program adopted systematic five-year rolling annual inventory system with the unified plot design gaining significant credibility in timeliness of data acquisition and data comparability (Bechtold and Patterson 2005). FIA plot configuration consist of four 7.2 meter fixed-radius subplots to tally all trees with a diameter at breast height (d.b.h) of at least 12.7 cm and each subplot contains a microplot for seedlings and understory inventory.

In this study, we retrieved the most recent cycle of FIA annual inventory in 31 eastern states for a total of 77,523 inventory plots from FIADB version 6.0 (available at [http://apps.fs.fed.us/](http://apps.fs.fed.us/fiadb-downloads/datamart.html)). FIA plot locations were mapped by their provided geographic coordinates and data were further aggregated from plot level (1 hectare) to 20 × 20 km cells. FIA plot locations acquired on private lands were perturbed randomly when recorded (McRoberts et al. 2005), but this practice only had minimal or no effect on studies in broad scales (Bechtold and Patterson 2005; Gibson et al. 2014; Prisley et al. 2008). Because southern Florida tip does not meet the FIA standards for forest classification, the bay area in Monroe County was not sampled in the database. In addition, costal Louisiana and Mississippi contain a small area of the same latitude with Florida, and these regions were excluded to avoid their contribution to the latitudinal occurrence pattern, (i.e. areas in Louisiana and Mississippi south of the northernmost latitude in Florida 31.08o; see Figure 1). In total, 118,092 tally trees (113 distinct species) covering 7,320 cells (approx. 3.01 million km2) in the eastern U.S were used in the study.

We first evaluated latitudinal diversity patterns (γ-diversity level *sensu* Whittaker 1977; Magurran 2004) by extracting observed occurrence data at 20 × 20 km cells to the nearest 1o latitudinal band. In addition, a linear regression was modeled to evaluate the relationship between tree diversity and latitude. Secondly, we simulated occurrence patterns along latitudinal base–tip for individual Florida species from observations. For each species, we computed its mean occurrence counts of cells occupied across latitude using a 1o moving window, such that for each 0.5o of latitude, mean count in a window (± 0.5o) was extracted for that 0.5o latitude band. Huisman-Olff-Fresco (HOF) models (Figure 2) were used to simulate each species’ occurrence distribution along latitudinal gradients. HOF models are a set of five hierarchical logistic regression models and they are simplified in a pre-determined order: (V) skewed, (IV) symmetric, (III) plateau, (II) monotonic, (I) flat response (Oksanen & Minchin 2002). Starting with the most complex model (V), the best model is selected based on the likelihood ratio test of residual deviance with P = 0.05 (Oksanen & Minchin 2002).

Geometry hypothesis of peninsular effect predicts a decline in population density along peninsula, thus HOF model type V with a southern skewness (i.e. model maxima south of latitudinal center of range) is regarded as evidences supporting peninsula geometry hypothesis.

Other HOF model types were regarded not being affected by the peninsula geometry. There are many endemic species in Florida, especially southern Florida and they are sparsely distributed across its small ranges within Florida. Therefore they were not included in HOF model simulation but referred to as endemic species in further analysis as well as not being affected by the peninsula geometry. We define endemic species are species, geographic ranges of which span less than 5 latitudinal degrees. This small range is set by the HOF model for model accuracy reason.

Data were extracted and managed using PostgreSQL 9.6.1 (PostgreSQL Global Development Group, 2017). All statistical analyses were performed in R version 2.12.1 (R Development Core Team, 2010).

# 3. Results

Figure 1 shows the richness pattern across latitudes for all 252 inventoried tree species in the eastern 31 states. Tree diversity exhibits a humped-shape pattern with latitude, where the highest diversity is located around latitude 35 degree (central eastern U.S.) and diversity decreases in both directions with a lowest in southern Florida (12 species). The decreasing trend in southeastern U.S. contradicts the general LGD pattern, but is coherent with the predicted pattern of peninsula effect in Florida where richness linearly increases from 12 at tip to 118 at base (latitude 31°). In peninsula alone, 113 tree species (representing 29 taxonomic families and 62 genus) have been observed in this recent FIA inventory. Species richness was significantly and positively related to latitude as indicated by a linear regression (adjusted R2 = 0.97, P < 0.001; Figure 3). Therefore, peninsula effect is supported for tree species in Florida, which is consistent with some previous estimation of diversity at different scales (Jenkins et al. 2015; Fan and Waring, 2009; Watson et al. 2015).

Occurrence data of tree species in Florida exhibit a variety of HOF model response types. Of all the model types, type V (skewed) was the most common latitudinal pattern in occurrence observed and this type accounted for 43 species (38%) (Table 1, Appendix S1). 15 of them had their peak occurrence locating south of the latitudinal center of range, and the greater proportion of this type (22%) had peak occurrence significantly skewed toward northern latitudes. HOF model II (Monotonic) and IV (Gaussian response) accounted for 21 and 15 species, respectively. 9 species (10%) had a flat response (type I) and the least popular type is type III (4 species, 4%).

Provide some exemplary species; pair them with conceptual models

# 4. Discussion

4.1 Discussion about the observed patterns at group of species level

Our results suggested that tree species diversity decreases with distance from the mainland and thus supported peninsular effect. Most species (92 of 113 species) exhibit an occurrence pattern aligning with its regional latitudinal trend across its entire range rather than displaying any abrupt decrease at the peninsula-mainland boarder as expected by the geometry hypothesis. Therefore, immigration–extinction hypothesis could be inferred as an underlying factor for tree diversity pattern in Florida. Among the 92 species, 73 species progressively become extinct in terms of occurrence towards the south and this single species decreasing trend of occurence could well have contributed to the decreasing diversity patterns in the peninsula. Therefore, we concluded that geometry gradient alone proposed by Simpson’s (1964) failed to explain the majority of tree species’ diversity patterns in Florida.

Some previous work found dual patterns for studied species: species with a northern affinity decreased in richness towards the south, vice versa for species with a southern affinity. Examples include patterns for lizards and snakes by Seib (1980) and for betlets (textbook). He argued that ecological and historical deterministic factors appear to explain the patterns better than the SPH

4.2 patterns comparing to studies on woody plant species in other regions

Woody plant species have been tested for peninsular effect in in North America (Milne and Forman 1986; Schwartz 1987); tropical riparian forests in Belize and Venezuela (Tackberry and Kellman 1996); Italy (Feoli and Lagonegro 1982). richness peaks midway between the mainland and the tip of the peninsular (Feoli and Lagonegro 1982).

An absence of evident gradients along the axis of peninsulas was still considered ‘peninsula(r) effect’ by Schwartz (1988), who did not observe a reduction in woody flora richness from North to South Florida. This pattern may reveal the peninsular effect as it also follows the expected increase of species number towards the tropics (latitudinal gradient; Schall and Pianka 1977; Willig et al. 2003). Different groups of temperate species in Florida, including hammock and non-hammock species, evergreen and deciduous species, understory and over story species. They concluded that the similarity in range termini patterns between suggests that Wamer's (1978) observation of structural change in the vegetation along the length of Florida is not caused by the loss of species employing a particular life history strategy. The structural changes in vegetation along peninsular Florida observed by Wamer (1978) could be caused by either a change from temperate to tropical species pool, or changes in relative occurrences within species pools; this study does not account for occurrence.

Trees have never been tested for peninsular effect, thus this study fills the taxonomic gap for cross-taxon generality. and necessitates more quantitative analysis taxa with actively dispersal ability or highly vagile are more likely to exhibit a peninsular effect? Peninsular patterns have been shown to differ among regions and species groups primarily focused on Baja California (14 studies, 38%) and Florida (7 studies, 19%), faunas (33 studies, 89%) accounted for the most studied taxonomic groups with a few on floras (4 studies, 11%). but (see a recent review by Battisti, 2014).

4. 3 Infer the underlying factors

Peninsula Florida spans a nearly 6o range in latitude, characterized by regular winter frosts in the north and frost-free winters in the south (Fernald, 1981), and the community structures change from southern mixed hardwood forest of north peninsular and panhandle Florida and transition into the tropical forest in southern Florida (Greller 1980).

In this study, this choice of using latitudinal gradients as a surrogate for geometry gradients is justified by the north-south orientation of peninsula. In the region, habitats change from a warm temperate regime in the north to subtropical climate in the south, such that this climatic variation is also reflected in the latitudinal gradients of peninsula. Florida’s geological history is relatively simple and stable since the early Pliocene (Myers & Ewel 1990), and this long environmental stability can be assumed to minimize the impact of past climatic or geological events, i.e. glacier, on current distribution of tree species. So the most-widely know hypotheses, habitat, geometry and history, cannot fully explain the diversity patterns for tree species along Florida peninsula.

Occurrence is greatly affected by abrupt changes reflecting sudden disruption within the geometric shape of the peninsula. Distribution of occurrence across geographical ranges In other words, occurrence patterns for species often vary gradually in a predictable manner by spatial autocorrelation (Fortin et al. 1989; Legendre 1993) only if the geometry of peninsula affects population dynamics.

The tree species richness of an area will largely depend on the amount of area as stated by “area-per se hypothesis” (Preston 1960). Larger tracts of forest can support larger populations and attract new species with greater resource and habitat availability. Extinction rates are lower in large habitats as population sizes are better supported by larger habitats. Tree species richness within the Peninsular could be strongly influenced by the amount of the forested area.

Species having small ranges are also predicted to have greater vulnerability to extinction because they have a narrower tolerance for environmental conditions and more readily show decrease in occurrence over even minor changes in habitats (Wilson et al. 2004; Schwartz et al. 2006; Ohlemu¨ller et al. 2008). Species with small ranges and low occurrence within the Florida peninsula may be evidences of their history with low immigration and high extinction rates.

Small-ranged species have consistently been found to be more prone to extinction (Schwartz et al. 2006; Payne & Finnegan 2007; Gaston & Fuller 2009); occurrenceSpecies with small ranges and low occurrence may be particularly susceptible to stochastic factors.

Similar to one problem that LDG studies face, peninsular-effect research has been biased toward taxa with actively dispersal ability or highly vagile species whose behavior mechanism (e.g. habitat selection) may have exclusively lead to this pattern, in such case peninsular effect is only specific to this group of taxa. But before such a claim be made, studies of taxa with passively dispersal mechanisms will illuminate this issue at the heart of peninsular study. Species richness

In addition, Carrascal and Diaz (2003) suggested that the occurrence distribution of single bird species could influence the species richness patterns at community levels. Schwartz (1988) compared range termini patterns of species groups exhibiting different growth characteristics and they found very similar patterns.

4.4. Inference of species which indeed exhibit strong peninsular effect

monitor; future analysis/study

# 5. Conclusions

Tree species in Florida exhibits a linear decline with distance from the mainland (113 species) to the tip (12 species). 15 species (~13%) showed a significant decline of occurrence level in the peninsula comparing with the mainland, but the majority did not display any declining trend which could be attributed to the peninsular geometry. Our analysis suggested that immigration-extinction dynamics is insufficient to explain the observed peninsular effect of tree species in the region.

**Figure captions**

**Fig.1**. Approximate Forest Inventory and Analysis plot locations (black points) bounded by Florida longitudinal extent (red dashed lines) in the eastern United States.

**Fig.2**. Proportion of Florida tree species by HOF model types.

**Fig.3**. Species richness patterns of different groups of tree species in Florida.

**Fig.4**. Decline of tree species richness in Florida.

**Table 1** HOF model results