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

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# Abstract

Patterns of tree species richness were examined in Florida (USA) in the context of peninsular effect for the first time using the most recent annual inventory by 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, absolute abundance of individual tree species was calculated at 20km by 20km grid level and its pattern along peninsula was constructed using Huisman-Olff-Fresco (HOF) models (Oksanen & Minchin 2002). Simulated abundance patterns showed that only 15 of the 113 tree species (~13%) experience significant abundance attrition in the peninsula comparing to their counterparts in the mainland, while the majority exhibits no or negligible difference. Thus this analysis suggested that diversity pattern of tree species cannot be attributed to the peninsula geometry alone in Florida. Rather, other factors, for example history and climate, should be considered as the underlying causes for the peninsular effect.

# 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. Among proposed suggestions, immigration-extinction hypothesis by Simpson (1964) (later also known as geometry hypothesis) has shown explanatory power for some taxa and assemblages of various peninsulas, and such examples included 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 discussed the decreased rate of immigration and increased rate of extinction toward the tip of a peninsula of 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, e.g. immigration and extinction, are closely related to population density distribution (Pimm et al. 1988; Gaston 2009; Sutton & Morgan 2009). Empirical studies from invasion ecology have shown high abundance (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 abundance has often been associated with high levels of extinction (Lavergne et al. 2006; Sutton & Morgan 2009). Therefore, current abundance 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 abundance when a species range enters a peninsula if the demographic process of this species is negatively impacted by peninsula geometry.

In this study, we examined abundance patterns of Florida tree species across its entire geographic range in eastern North America. Specifically, we compared each species’ abundance variations in the peninsula with its overall patterns in the mainland to look for abundance decrease, which may be attribute to peninsular geometry. Among the mixed records of peninsular effect, 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. To overcome these shortcomings, we used a comprehensive annual inventory with standardized sampling scheme from forested areas to analyze both observational qualitative (e.g. presence/absence of the species) and quantitative data (e.g. abundance). We also simulate abundance 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 annual forest inventory and has been the source for information about the extent, condition, status and trends of the forest resources in the country (Smith 2002). …(More introduction about FIA sampling)

In this study, we retrieved the most recent FIA annual inventories 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. A small proportion of costal Louisiana and Mississippi is of the same latitude with Florida, to avoid any potential confounding contribution to the comparison of abundance pattern, these regions were also excluded (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 was 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 abundance 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’ abundance 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.

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).

Of all the HOF models, type V (skewed) was the most common latitudinal pattern in abundance observed and this type accounted for 38% of the species (Table 1). Only 18 species (16%) had their peak abundance locating south of the latitudinal center of range, which supporting the geometry hypothesis. The greater proportion of type V species (22%) had peak abundance 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%).

**4. Discussion**

Our results suggest that tree species diversity decreases with distance from the mainland and support peninsular effect. But geometry gradient proposed by Simpson’s (1964) failed to explain such diversity pattern.

Schwartz (1988) compared range termini patterns of species groups exhibiting different growth characteristics and they found very similar patterns.

different groups of temperate species in Florida, including hammock and non-hammock species, evergreen and deciduous species, understory and overstory 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 abundances within species pools; this study does not account for abundance.

4.1 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).

Tree species in Florida display a variety of latitudinal abundance patterns and thus a wide range of influences

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?

have shown that peninsular patterns 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).

4.2 Carrascal and Diaz (2003) bird species progressively become extinct

4.2 underlying processes

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 on current distribution of tree species. In the region, habitat changes from a warm temperate in the north to subtropical climate in the south, this climatic gradient is partly reflected in the latitudinal gradients of the peninsula. re abundance is greatly affected by abrupt changes reflecting sudden disruption within the geometric shape of the peninsula. Distribution of abundance across geographical ranges In other words, abundance 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.

area gradients; normalized diversity over forested areas; inverse LDG

The tree species richness of an area will largely depend on the amount of area that can support large population which lowering extinction rate (Chisholm et al. 2013). The area-richness hypothesis observes greater levels of richness with larger habitats and explains the regional differences in species numbers. Preston (1960) was the first to develop the “area-per se hypothesis” which explains species richness as a function of immigration and extinction rates. The rate of immigration is dependent on the distance of the habitat to the population’s source while extinction rates are inversely proportional to the area size of the habitat. 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 study area may be strongly influenced by the amount of the forested area.

The forested area, shown in Figure 12, ranges from 1 to 21 plots per cell. The lower latitudes of the Florida peninsula have noticeably sparser forested areas of 1 to 7 plots than the rest of the study area. The southern half of the Florida peninsula contains many urban areas, such as Orlando and Miami, which likely limit forested areas. There are a few additional areas with lower forested area when compared to their surrounding areas, such as the area in northern Georgia which corresponds to the location of the metropolitan area, Atlanta. Regions of highly forested areas are seen in coastal areas, like the Florida panhandle, and further inland.

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 abundance 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 abundance 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); Species having small ranges are also predicted to have greater vulnerability to extinction due to range displacement tied to climate change because they have a narrower tolerance for environmental conditions and more readily show decrease in abundance over even minor changes in environmental gradients (Wilson et al. 2004; Schwartz et al. 2006; Ohlemu¨ller et al. 2008). Species with small ranges and low abundance at range peripheries may be particularly susceptible to range contraction (via regional extinction) at the trailing range edge and a diminished capacity to expand at the leading edge.

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 abundance distribution of single bird species could influence the species richness patterns at community levels.

# 4. Discussion

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).

# 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 abundance 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