

Avian taxonomic and functional diversity in early stage of longleaf pine (*Pinus palustris*) stands
restored at agricultural lands: Variations in scale dependency

Running Head: Longleaf pine restoration and avian diversity

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Abstract

In agricultural landscapes, the Longleaf Pine Initiative (LLPI) and the Bobwhite Quail Initiative (BQI) aim to restore longleaf pine forests and early successional habitats, respectively. The early stage of longleaf pine stands and grass and forb vegetation produced by a combination of both restoration programs (LLPI-BQI) may form habitat conditions favorable to early successional bird species and other birds, increasing avian diversity. We investigated how the LLPI and BQI programs affected taxonomic and functional diversity of birds and abundance of early successional birds (grassland and scrub/shrub species), and what environmental characteristics were associated with the diversity and abundance of birds. Our study was performed at 41 fields in Georgia, USA, during 2001-2002 by considering environmental characteristics at two spatial scales: local-scale vegetation features and restoration program type (LLPI or LLPI-BQI) and landscape-scale vegetation features and landscape heterogeneity. Functional evenness, species richness, and abundance of grassland and scrub/shrub species did not show a clear association with local- or landscape-scale variables. Shannon-Wiener diversity was slightly influenced by restoration program type (local-scale variable) with higher value at LLPI-BQI stands than at LLPI stands despite no significant differences in local vegetation features between those stands. Functional divergence was strongly positively associated with landscape-scale variables. That is, niche differentiation increased with increasing shrub coverage within a landscape, reducing competition between abundant bird species and others. Our results suggest that although a combination of BQI and LLPI program may have a positive effect on avian taxonomic diversity,

it is important to consider shrub vegetation cover within a landscape to improve functional diversity.

Key words: early successional habitat, functional diversity, landscape-scale variables, longleaf pine, restoration program, vegetation

Implications for Practice:

- In agricultural landscapes, potential bias in the assessment of effectiveness of restoration programs on avian diversity can be reduced by considering both taxonomic and functional diversity.
- Landscape context should be taken into account in the decision on the enrollment of agricultural lands that would be qualified for longleaf pine restoration program.
- Although allowing the enrollment of agricultural lands in multiple restoration programs may have some positive effects on avian diversity, further considerations are needed to improve local habitat conditions to maximize benefits from each program.

Introduction

Longleaf pine (*Pinus palustris*) forests are one of the most biologically diverse and unique ecosystems other than the tropics (Jose et al. 2006). Nearly 600 endemic plant species are found in the forests (Walker 1998) and 300 animal species use longleaf pine forests as habitat

(NRCS 2017). Although longleaf pine forests were historically prevalent across the Southeast, USA, approximately 97% of their original extent was lost due to urbanization, agricultural intensification, and changes in forest practices including fire suppression (Van Lear et al. 2005; Mitchell & Duncan 2009). In particular, during the past several decades, much of the reduction has been caused by logging and conversion to a large-scale plantation of slash (*P. elliottii*) and loblolly pine (*P. taeda*), which has dense canopy cover with little ground layer vegetation (Croker 1987; Jackson 1988; Landers et al. 1995). These changes have negative effects on many endemic species in the longleaf pine forests that maintain “an open, park-like” structure and create heterogeneous habitat mosaics (Landers et al. 1995). The loss of the early successional stage of the longleaf pine-grassland habitats has also contributed to the widespread decline of early successional bird species associated with grasslands, abandoned farmland, and shrub thickets (Heard et al. 2000). Many of these species have been consistently declining over the last 50 years in North America (Sauer et al. 2013) largely due to loss of grassland and associated habitats as well as habitat fragmentation and degradation by agriculture and silviculture (Brennan & Kuvlesky 2005).

To restore longleaf pine to its native range, particularly on privately-owned, unproductive crop fields, the National Longleaf Pine Conservation Priority Area (also called the Longleaf Pine Initiative; LLPI, hereafter) was established in 1998, aiming to re-establish up to 101,200 ha of longleaf pine forests (Heard et al. 2001). In 1999, Georgia allowed LLPI properties to be enrolled in Georgia’s conservation (or restoration) program, the Bobwhite Quail Initiative (BQI)

that aims to restore nesting and brood rearing habitat for primarily Northern Bobwhite (*Colinus virginianus*) in agricultural landscapes. The key components of BQI practices are winter disking and managing or creating field borders (even at interior) with native grasses and forbs. In particular, winter disking is important to promote heavy-seeded annual plants that are main fall and winter food sources for both Northern Bobwhite and grassland obligates (Thackston 2007). The restored habitat is also expected to be used by other birds and wildlife (Thackston & Tomberlin 2010). The LLPI stands have lower tree densities than typically found in other pine stands, facilitating the growth of ground layer vegetation. As plant succession progresses, the LLPI stands can provide nesting and escape cover. The core practice for the early stage LLPI stands is centered on longleaf pine establishment; however, supporting practices such as invasive/exotic plant control and early successional habitat development are also included in the LLPI. Thus, a combination of both programs (LLPI-BQI, hereafter) may benefit birds beyond targeted species or early successional species. This was the primary assumption behind the expansion of BQI enrollment.

However, it has rarely been explored whether the LLPI-BQI could improve overall avian diversity. Little attention has also been paid to determine spatial scale (e.g., local/stand scale vs. landscape scale) and environmental features associated with avian diversity in the early stages of these longleaf pine forests. In pine forest, structural diversity of vegetation, and understory and ground vegetation cover within the forest patch or stand are considered important factors affecting biodiversity (Dickson et al. 1993; Wilson & Watts 2000; Sallabanks & Arnett 2005;

Bergner 2015; Lee & Carroll 2018). These features are largely determined by age, canopy cover, and basal area of trees within the pine forest (Melchior 1991; Dickson et al. 1993). For example, previous studies reported a decline in neotropical migratory birds at 7-11 year old stands due to reduction in hardwood (< 2m tall) and forb cover compared to young brushy and mature stand (Dickson et al. 1993) and greater avian diversity at pine stands with low levels of basal area due to heterogeneous vegetation structure (Lee & Carroll 2018). Some studies also found strong effects of environmental features surrounding a stand, especially in pine plantations, e.g., the degree of human land use (urbanization or agriculture), the amount of non-pine forest within 500m and 1km circular area, and landscape heterogeneity defined by stand age within 250m and 500m circular area (Loehle et al. 2005; Lee & Carroll 2014). These variations in scale dependency among studies suggest that consideration of multiple spatial scales is critical to understanding the species-environment or diversity-environment relationship as widely discussed in ecology (Wiens 1989; Cushman & McGarigal 2002; Mayor et al. 2009). Determining the relative importance of environmental features occurring at different scales is also crucial to make spatially-explicit decisions for conservation management.

The objective of this study was to identify spatial scale (local vs. landscape) and environmental factors associated with avian diversity at the early successional stage of longleaf pine stands newly established in agricultural landscapes. We used functional diversity as a trait-based measure of diversity to complement taxonomic diversity, i.e., species richness and Shannon-Wiener index. Functional diversity estimates the dissimilarity in multiple traits such as

morphological, physiological, behavioral, and ecological traits among species or organisms, which directly influence ecosystem functioning and the species-environment relationship (Tilman 2001; Hooper 2005). Unlike an ecological guild approach based on single trait, functional diversity can deal with multiple traits simultaneously. There are a growing number of biodiversity studies adopting functional diversity indices to investigate effects of human land use, hardwood forest management, and land-use planning (Luck et al 2013; Murray et al. 2017; Cannon et al. 2019).

We expected a positive relationship between avian diversity and grass and forb cover at both local and landscape scales given the findings from previous studies (Bergner et al. 2015; Lee & Carroll 2018). However, it is possible that taxonomic diversity and functional diversity would show different patterns. Increasing grass and forb cover may enhance taxonomic diversity due to an increase in species using grasses and forbs (e.g., more ground foragers or grassland species). However, trait similarity among species may also increase, lowering functional diversity. If increasing grass and forb cover is coupled with decreasing woody cover, this pattern will be more conspicuous. We also expected that landscape heterogeneity would have a positive effect on avian taxonomic and functional diversity because it can provide complementary resources or other types of habitats that may be used by birds, as often assumed in the relationship between diversity and habitat/landscape heterogeneity relationship (Benton et al. 2003; Tews et al. 2004; Fahrig et al. 2011).

Methods

Study area

Our study sites were located in Dodge, Emanuel, Laurens, and Sumter counties in the Upper Coastal Plain of Georgia, USA (Fig. 1). We used Natural Resource Conservation Service and Georgia Department of Natural Resources data and aerial photographs to identify a total of 41 privately-owned longleaf pine stands enrolled in LLPI or LLPI-BQI: 40 stands (14 LLPI-BQI and 26 LLPI stands) in 2001 and one additional LLPI stand in 2002. The ages of the longleaf pine stands ranged from 0.5 to 2.5 years and the height of most longleaf pines was ≤ 1 m. The size of stands ranged from 6.4 to 53.9 ha (mean = 16.2 ± 10.3 SD ha). Each stand was previously row crop agriculture or pasture land.

Bird surveys

We conducted breeding bird surveys within each stand three times during 4 June - 14 July in 2001 (40 stands) and three times during 13 May -10 June in 2002 (41 stand), using the line transect method (Bibby et al. 2000). Bird surveys were conducted at sunrise and continued for up to 3 hours but not performed in adverse weather conditions (Robbins 1981). We randomly oriented a 250 m line in each stand at least 50 m from the edge of the field. An observer started at one transect line endpoint and walked the line at 1.5 km/hr pace toward the other endpoint. While walking the line, the observer recorded bird species and perpendicular distance from the observer to the bird detected either aurally or visually. To account for variation at either start

point, we alternated start points for every other survey. We also alternated observers between stands and between visits to minimize observer effects. To reduce observer bias, we ensured that observers had strong bird identification skills. In our preliminary DISTANCE analysis using relatively abundant species, observers had no influence on detectability (Gates 2008). We only counted birds that actively used the stands for foraging, nesting, perching, or singing/calling, excluding birds that flew over the stands but including aerial foragers such as swallows and swifts that caught preys in the stands.

Vegetation surveys and local-scale variables

We conducted vegetation surveys on the same day as bird surveys for each respective stand, resulting in a total of 6 surveys (3 surveys for 1LLPI stand added in 2002) across 2 years. We placed five 1-m² plots alternately at 25, 75, 125, 175, and 225 m from the starting point along the 250m transect. We placed each plot 5 m from the line center. Within a plot, the percent coverage of grasses, forbs, debris (litter; fallen leaves, twigs, and other unclassified matter), bare ground (exposed soil and rocks), and woody plant species (including saplings) were visually estimated. A Robel pole was used to measure the height of vegetation, including both longleaf pines and other plants (Robel et al. 1970). One observer held a pole divided in 5 cm increments in the center of the plot while another observer kneeled from 4 m away, and read height from the north, west, south, and east. We determined height by the topmost increment obstructed by vegetation. To reduce bias, the same observer estimated all Robel pole and percent cover

measurements. Mean percent cover of each category and mean vegetation height across all surveys were calculated for each stand.

As local-scale variables for analysis, we focused on vegetation features, i.e., mean vegetation height and mean percent cover of grasses, forbs, woody plants, and debris. To account for low to moderate correlations among these features, we performed a principal component analysis and selected 3 principal components (PC) that explained 84% of total variation in the data (Table S3): PC1 = increasing grass cover with decreasing forb cover; PC2 = increasing debris cover and decreasing vegetation height; PC3 = decreasing woody cover and vegetation height. In addition to the 3 PCs, log-transformed stand size and restoration program type (i.e., LLPI-BQI or LLPI) were considered as local-scale variables.

Landscape-scale variables

To characterize landscape features surrounding each sample stand, we used the 2001 National Land Cover Database (NLCD). Within a 1-km radius surrounding the center of the line transect, we calculated the percentage of each of the four land cover types: agricultural land, shrub, grassland, and forest (including pine, deciduous, and mixed forest). Among these cover types, percent cover of agricultural land and forest were highly correlated (Pearson correlation, $r = -0.87$). Given that our study was centered on semi-natural and natural vegetation features at both local and landscape scale, we excluded the percent cover of agricultural land and focused on the other three. Landscape heterogeneity (Shannon-Wiener diversity) was calculated based on 6

vegetation types: shrub, grassland, 3 forest types, and wetland woody vegetation. The percent cover of LLPI-BQI and LLPI stand, and the type and age of pine stands within a landscape may influence avian diversity; however, we could not include them due to lack of information on the locations of all LLPI stands and no classification of pine type and age in the NLCD.

Taxonomic and functional diversity of birds

Species richness (number of species) and Shannon-Wiener diversity were used as indices representing avian taxonomic diversity. We pooled 2 years of data (1 year of data for 1 LLPI stand in 2002) and used the maximum number of individuals observed throughout all visits as an estimate of abundance. We performed DISTANCE analysis on 12 species abundant enough to determine a cut-off distance where detection probability started to decline (Buckland et al. 2000). Those 12 species showed decreasing detection probability between 25 m and 60 m. Thus, for analysis, we included species observed at least once within 60 m perpendicular distance to the center of transect, resulting in a total of 40 species (Table S1 for species list).

We used functional evenness (FEve) and functional divergence (FDiv) as a measure of functional diversity. These two indices are considered as “better multi-trait indices for analyzing ecosystem functioning” (Gagic et al. 2015). They were independent of species richness ($-0.3 < r \leq 0.3$ for both). Although functional richness is also commonly used, we did not include the index as it was highly correlated with species richness ($r = 0.86$), which has been found in other studies (Mouchet et al. 2010; Pla et al. 2012). FEve describes the regularity of species’

abundance in functional space (Mason et al. 2005; Villéger et al. 2008). FDiv represents the distribution of abundance, especially how abundant species are distributed in the volume of functional space (Mason et al. 2005; Villéger et al. 2008). FEve decreases when functional space is unevenly filled, indicating that resource may be underutilized. FDiv increases as the functional traits of the most abundant species are far from the center of the trait space, increasing niche differentiation and decreasing competition in a community.

For functional diversity, we considered 5 traits: body mass, diet type, foraging strategy (foraging behavior and location), migratory status, and habitat preference (Table S1 and S2). The first three traits are strongly associated with resource use and acquisition (Luck et al. 2012). We compiled data on body mass from Dunning (2008) and the other traits from The Birds of North America online database (BNA 2005) and Ehrlich et al. (1988). Some of the habitat preference data were compiled from Lee & Carroll (2014). FEve and FDiv were calculated following a common approach described by Villéger et al. (2008) using dbFD function in package FD (Laliberté et al. 2014; See Table S2 for detail processes).

Data analysis

As response variables, we used species richness, Shannon-Wiener diversity, FEve, FDiv, abundance of grassland species (i.e., sum of each grassland species' abundance), and abundance of shrub species (i.e., sum of each shrub species' abundance). Our study was centered on overall avian diversity; however, we included abundance of grassland and scrub/shrub bird species to

assess the suitability of habitat that both programs, particularly BQI aims to restore, considering their close association with early successional habitat (Table S1 for the list of grassland and scrub/shrub species).

Using 5 local-scale and 4 landscape-scale explanatory variables, we constructed a generalized linear model (glm) with a Poisson distribution for species richness and abundance, a glm with a gamma distribution for Shannon-Wiener diversity, and a linear model with beta distribution (beta regression model) for FEve and FDiv. The relative importance of local and landscape features on avian diversity was determined using model selection based on Akaike's Information Criterion (AIC). We built four models: Null model (intercept only model), Full model (including all variables), Local model (5 local variables), and Landscape model (4 landscape variables). We used adjusted AIC (AICc) due to a small sample size compared to the number of explanatory variables. According to Burham & Anderson (2002), models with $\Delta AICc$ (AICc difference from the best model) < 2 are considered as substantially plausible models and models with $\Delta AICc > 10$ have essentially no empirical support. Thus, we included all models with $\Delta AICc \leq 10$ in a set of candidate models for model averaging to take into account uncertainties in model selection and parameter estimates (Burham & Anderson 2002). Relationships between response variables and explanatory variables were determined based on estimates from the model averaging. Overdispersion of each model was also examined with $c\text{-hat}$. If overdispersion was found ($c\text{-hat} > 1.1$), we used Quas AICc (QAICc), an adjusted AICc with an overdispersion parameter, $c\text{-hat}$. When the Null model was the best model, we concluded

that there was no strong relationship between the response variable and the environmental variables at any scale and no further analysis was performed. However, when ΔAICc of the subsequent model was < 2 , we conducted a likelihood ratio test on the model (Burham & Anderson 2002). If $P < 0.05$, we considered the model different from the Null model and performed model averaging.

We also examined spatial dependency with Moran's I test (package "spdep", Bivand & Piras 2015), the homogeneity of variance with Leven's test (package "car", Fox & Weisberg 2011), and multicollinearity with the variance inflation factor (VIF; package "car"). We did not find spatial dependency in our data ($p < 0.05$), satisfying one of main assumptions in regression analysis, i.e., the independence of residuals. The assumption of the homogeneity of variance was not violated ($p < 0.05$) and multicollinearity could be ignored ($1 < \text{VIF} < 1.5$ in all cases). All other analyses were conducted in R (R Core Team 2017), using package "betareg" for beta regression model (Cribari-Neto & Zeileis 2010) and package MuMIn for model selection and averaging (Bartoń 2016).

Results

Of the 40 species detected, 20 were early successional species: 2 open forest species and all of 6 grassland and 12 scrub/shrub species (Table S1). Northern Bobwhite was most commonly found among grassland species, observed at least once during surveys at over 45% of

sample stands. Two scrub/shrub species (Blue Grosbeak [*Passerina caerulea*] and Mourning dove [*Zenaida macroura*]) occurred at over 70% of sample stands.

Local vegetation features between LLPI and LLPI-BQI stands were similar (Fig. 2). The mean percent cover of woody vegetation, grasses, and forbs did not differ between LLPI and LLPI-BQI stands based on 95% confidence interval (CI). However, the mean percent cover of debris and bare ground were higher at LLPI-BQI stands and at LLPI stands, respectively. Vegetation height and stand size did not differ between the two restoration programs: mean vegetation height, LLPI = 19.5 ± 1.9 SE cm (95% CI, 15.4-23.4 cm) and LLPI-BQI = 22.7 ± 2.7 cm (16.8-28.5 cm); mean stand size, LLPI = 14.8 ± 1.5 ha (11.7-17.9 ha) and LLPI-BQI = 18.9 ± 3.7 ha (10.8-26.9 ha).

Most of the 6 response variables except FDiv and Shannon-Wiener diversity did not show a clear association with the environmental variables considered; the Null model was often the top model selected (Fig. 3 and Table S4). However, compared to the Local model or the Full model, the Landscape model showed lower AICc in FEve, FDiv, abundance of grassland species, and abundance of scrub/shrub species, indicating that the Landscape model was the more plausible than the other two models (Table S4). In particular, the Landscape model was selected as the top model in FDiv (Fig. 3 and Table S4). The Landscape model explained variations in FDiv over 20 times ($0.782/0.037$) better than the Local model, suggesting a strong association between FDiv and landscape variables. Although the Local model of Shannon-Wiener diversity

was also close to the top model, i.e., the Null model ($\Delta \text{AICc} = 1.82$), the result of likelihood ratio test indicated that the Local model and the Null model differed ($p < 0.05$).

FDiv increased as shrub vegetation cover increased within a landscape (Table S5; estimate of shrub vegetation = 0.19, $p < 0.01$). That is, with increasing shrub vegetation, trait dissimilarity between abundant species and other species increased, facilitating niche differentiation, and consequently reduced competition between those species. Although the explanatory power of the Local model for FDiv was trivial, FDiv was positively related to stand size in the Full model and thus in the model averaging results (estimate of stand size = 0.27, $p < 0.05$). Shannon-Wiener diversity was affected by the type of restoration program, i.e., whether the LLPI stand was enrolled in BQI or not (Table S5). Shannon-Wiener diversity was higher at LLPI-BQI stands than at LLPI stands: 0.54 at LLPI-BQI stands and 0.47 at LLPI stands, $p < 0.05$. Other environmental variables, such as landscape heterogeneity and local vegetation features (PC1, PC2, and PC3), did not have an impact on FDiv and Shannon-Wiener diversity or other diversity indices and abundance variables (Table S5, $p > 0.05$).

Discussion

Our results suggest that avian diversity-environment relationships can be complex at the early stage of longleaf pine stands restored in agricultural landscapes, depending in part on the aspect of diversity being considered. The spatial scale and environmental variables associated

with avian diversity differed between taxonomic and functional diversity although there were variations in the strength of the association among diversity indices.

It is well known that ecological processes and patterns are scale dependent (Wiens 1989; Levin 1992). That is, patterns we observe are strongly affected by the spatial (and temporal) scale at which variables are measured in the study. This scale dependency influences our understanding of diversity-environment relationships and ultimately conservation decision making. In pine forests, stand or local scale environmental characteristics such as stand age and vegetation structure and cover within a stand significantly influence avian diversity and occupancy (Melchior 1991; Turner et al. 2002; Luck & Korodaj 2008; Lee & Carroll 2014; Bergner et al. 2015; Lee & Carroll 2018). However, strong effects of environmental features at the landscape scale have also been reported, especially in pine plantations (Mitchell et al. 2001; Loehle et al. 2005; Mitchell et al. 2006; Lee & Carroll 2014). For example, the amount of hardwood forest and heterogeneous stand age within a landscape, and proximity to non-pine forest cover such as riparian vegetation can positively affect avian species richness and occupancy in pine plantations. Our results are consistent with the findings of other studies given that functional divergence was strongly associated with the amount of shrub vegetation within a landscape and the Landscape model showed higher AICc weight than the Local model or the Full model.

However, vegetation features at the local scale did not have an effect on any of diversity indices or abundance. In our sample stands, we found several plants including croton (*Croton*

spp.), butterfly pea (*Centrosema virginianum*), common lespedeza (*Kummerowia striata*), Johnsongrass (*Sorghum halepense*), partridge pea (*Chamaecrista fasciculata*), and common ragweed (*Ambrosia artemisiifolia*). These plants can provide food for abundant early successional species in our study such as Blue Grosbeak, Eastern Kingbird (*Tyrannus tyrannus*), Field Sparrow (*Spizella pusilla*), and Mourning Dove (Dickson et al. 1993; Miller & Miller 1999). But, many of the stands we surveyed also contained agricultural pests such as sicklepod (*Senna obtusifolia*) or exotic forage grass, e.g., bermudagrass (*Cynodon dactylon*), with less important native forbs (Gates 2008). Most early successional species including Northern Bobwhite avoid areas dominated by exotic grasses (Szukaitis 2001; Cook 2004; Martin et al. 2015). Due to lack of detail compositional data of vegetation, our study could not consider native and non-native plants separately. It is uncertain whether percent cover of native and non-native grasses and forbs varied across our sample stands. However, it is possible that LLPI stands may have more non-native vegetation cover than LLPI-BQI stands. We noticed that most LLPI stands were rarely managed as required by the LLPI during our study period, e.g., no prescribed burn and mowing. Some LLPI stands also had a slightly different land use history: all sites should have been row crop fields previously, but some sites were also used as pastures after crop rotation. These situations make it difficult to control non-native plants, especially pasture grasses such as bermudagrass that could impede the growth of longleaf pine trees and potentially beneficial grasses and forbs (D'Antonio and Vitousek 1992).

The situations could partly explain higher Shannon-Wiener diversity at LLPI-BQI stands than at LLPI stands. Among local-scale variables, only the type of restoration program had some effect on Shannon-Wiener diversity. Given little differences in major vegetation features between LLPI and LLPI-BQI stands, we cannot clearly identify environmental characteristics related to the pattern. It could be associated with characteristics not measured by our vegetation surveys, e.g., proportion of native and non-native plants. We need a further investigation on variations in vegetation composition between LLPI-BQI and BQI stands as well as management and land use history at those stands.

The most significant pattern found in our study was the positive relationship between functional divergence and the amount of shrub vegetation at the landscape scale. Functional divergence is related to the degree of niche differentiation; it increases as dissimilarity between abundant species and other species increases (Mason 2005; Schuleter et al. 2010), which reduces resource competition between those species (i.e., high niche differentiation; Mason 2005; Mouchet et al. 2010). Among 40 species, there were 8 species for which each species' abundance was > 5% of total abundance (See Table S1 for the list of 8 species and their traits). None of them were either foliage gleaners, open-forest, or grassland species and all species except Morning Dove were insectivores. Five of those 8 species were also shrub species that was the most abundant group of species. Increases in shrub vegetation may increase resources available to these species, e.g., foods and nesting sites available to insectivores and shrub species,

respectively. This can lower resource competition and elevate dissimilarity between them and less abundant species, allowing these species to coexist.

Functional evenness indicates under/over utilization of resources in the space (Mason 2005). High functional evenness suggests efficient resource use in a community. However, a community with low functional evenness has empty niches in the functional space by leaving unexploited resources (Mouchet et al. 2010), which may increase a chance for invaders, especially non-native species to colonize successfully by using the resources as predicted from the empty niche hypothesis (Elton 2000). In our study, the insignificant pattern of functional evenness reveals that environmental variables we considered did not affect the resource utilization in a community. However, higher values of functional evenness (≥ 0.6 in all stands, mean 0.76 ± 0.09 SD) may indicate relatively low amount of unexploited resources with fewer empty niches throughout our study sites.

Among landscape-scale variables, the insignificant effect of landscape heterogeneity on avian diversity was somewhat unexpected. Habitat/landscape heterogeneity has often been emphasized as a crucial factor for the conservation of biodiversity in agricultural landscapes (Benton et al. 2003; Fahrig et al. 2011). One recent study reported that landscape heterogeneity can positively affect functional diversity of birds in agricultural landscapes where some croplands are managed to restore early successional habitats (Lee & Martin 2017). In managed pine-dominant landscapes, landscape heterogeneity is primarily determined by stand age and its positive impact on avian diversity is often reported (Turner et al. 2002; Loehle et al. 2005;

Mitchell et al. 2008). The main reason we did not find effects of landscape heterogeneity could be related to low variability of landscape heterogeneity across stands. Mean value of landscape heterogeneity was 1.34 (\pm 0.13 SD) and the value ranged from 1.09 to 1.60, suggesting that landscape heterogeneity among stands did not considerably differ.

In conclusion, the strong effect of shrub cover at the landscape scale on functional divergence indicates the importance of landscape context in habitat restoration program for birds as emphasized in other studies that assessed the effectiveness of similar practices in agricultural landscapes (Lee & Martin 2017) and in recent BQI management (Thackston & Tomberlin 2010). The positive relationship between Shannon-Wiener diversity and a combination of both LLPI and BQI also suggests that BQI can be slightly effective to improve taxonomic diversity. However, insignificant effect of local-scale vegetation features raises a question about potential factors associated with the positive relationship and habitat conditions created by the programs. We discussed that vegetation composition (i.e., native vs non-native plants), which could be linked to land use and management history of the stands, may affect the patterns. We again emphasize a need for future study to test the possibility. Lastly, to increase the effectiveness of restoration programs for avian diversity conservation, we recommend considering vegetation features surrounding fields in the decision on the LLPI or BQI enrollment of agricultural lands, e.g., prioritizing fields in a landscape with higher amount of shrub vegetation, and verifying the establishment of beneficial grasses and forbs within a stand.

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Figure Legend

Figure 1. Land cover map of study sites located at four counties (grayed areas in an inset map) in Georgia, USA. The numbers on the map represent the number of stands monitored on each site.

Figure 2. Comparison of vegetation features at the local scale between stands enrolled in the Longleaf Pine Initiative (LLPI) and both LLPI and the Bobwhite Quail Initiative (LLPI-BQI). Bare indicates bare ground. Error bars represent $\pm 95\%$ CIs. When 95% CIs were not overlapped between two restoration programs, it was considered that there was an effect of BQI on the response variable.

Figure 3. The relative AICc weights of each of four models considered. The Local model with five environmental variables at the local scale; the Landscape model with four variables representing landscape features; the Full model including all variables of Local and Landscape model; the Null model with intercept only. Abbreviation: FEve, functional evenness; FDiv, functional divergence; Richness, species richness; Shannon, Shannon-Wiener diversity; Grassland, abundance of grassland species; Shrub, abundance of scrub/shrub species.

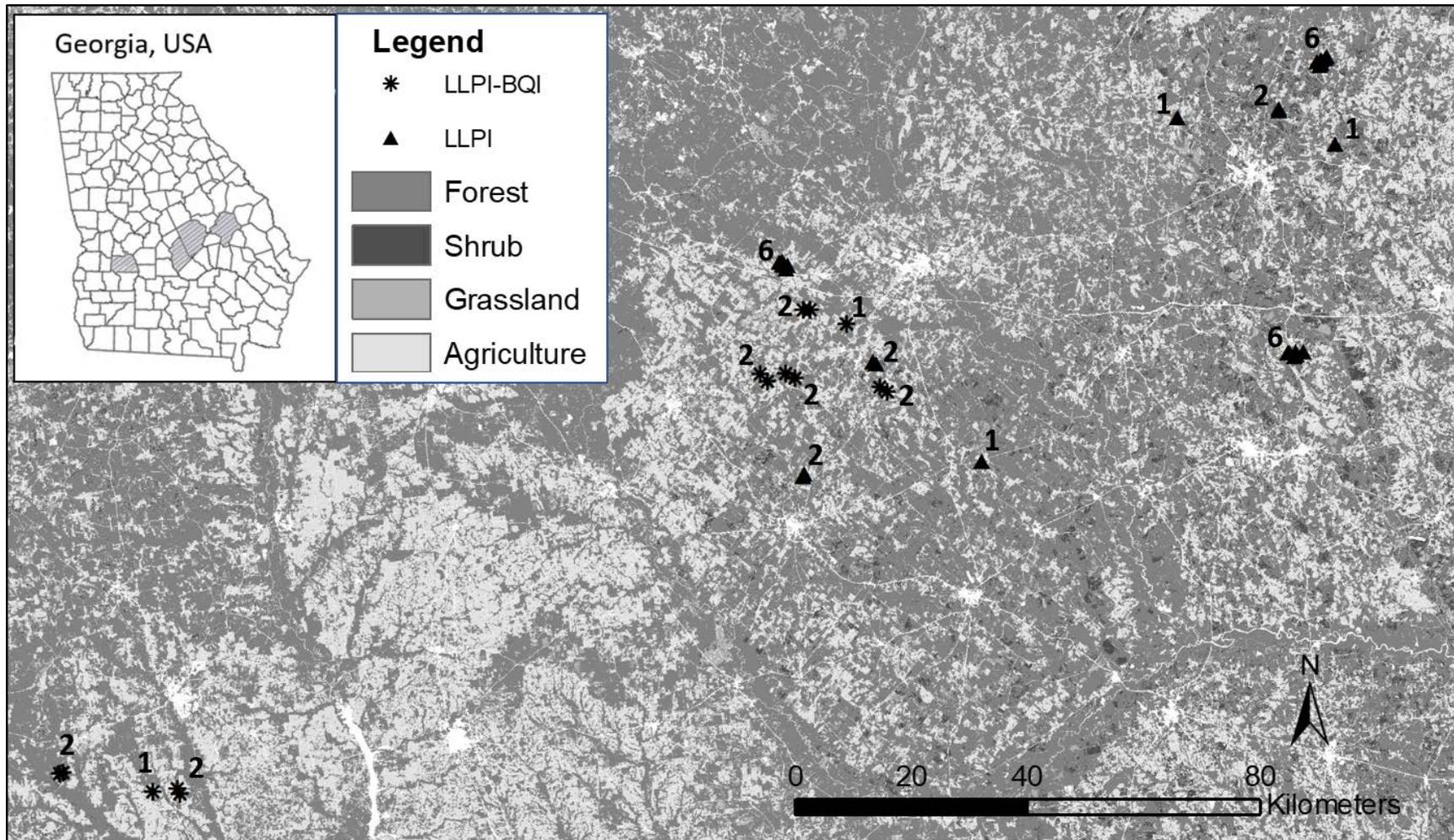


Figure 1

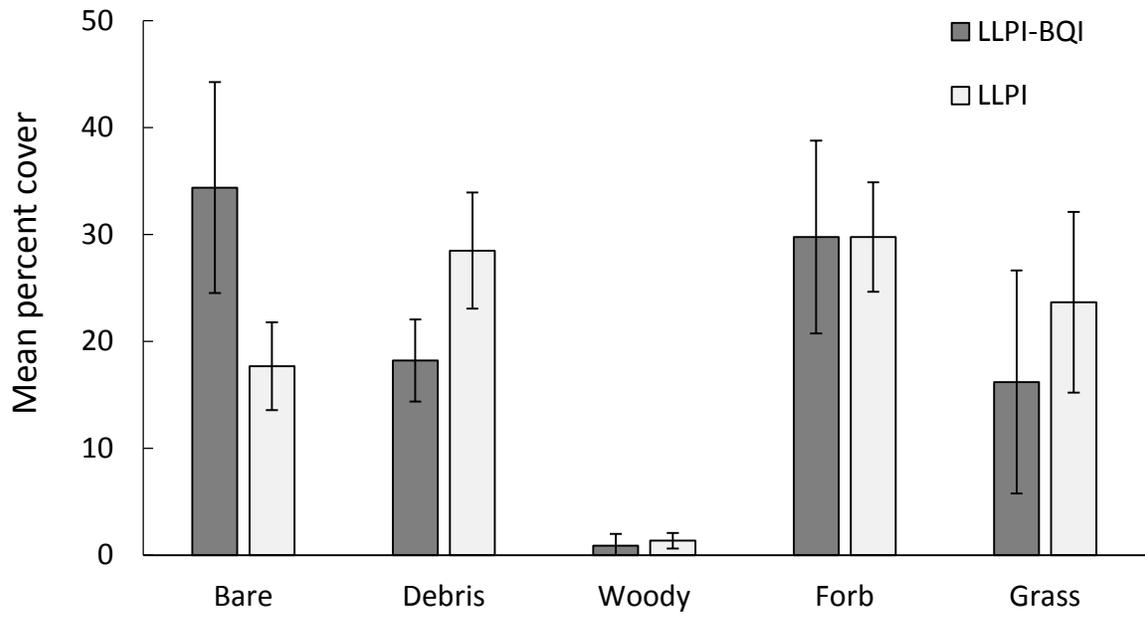


Figure 2

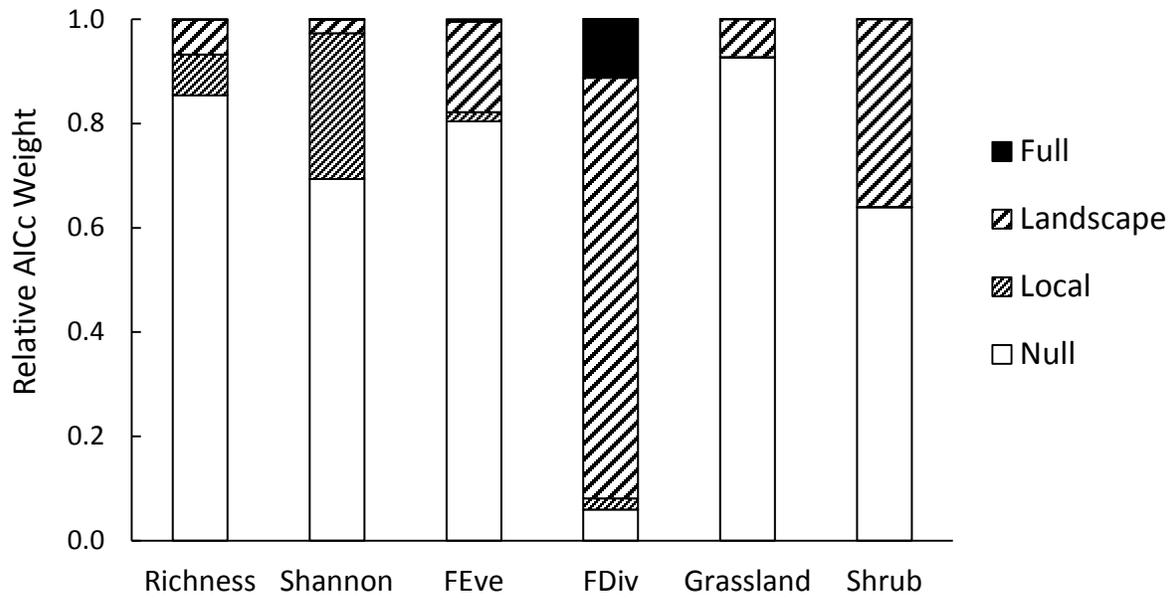


Figure 3

Table S1. List of species and their traits used for analysis. Diet type: Din, insectivore; Dsd, granivores; Dom, omnivores. Foraging behavior and location: Fflg, foliage gleaners; Fgr, ground foragers; Faer, aerial foragers. Migrant status: Mres, residents. Habitat preference: HFop, open forest species; HSh, scrub/shrub species; HGra, grassland species; Hoth, other species.

Common Name	Scientific Name	Body mass	Din	Dsd	Dom	Fflg	Fgr	Faer	Mres	HFop	HShr	HGra	Hoth
American Crow	<i>Corvus brachyrhynchos</i>	474	0	0	1	0	1	0	1	0	0	0	1
American Goldfinch*	<i>Carduelis tristis</i>	12.5	0	1	0	1	0	0	1	0	1	0	0
Barn Swallow [†]	<i>Hirundo rustica</i>	19.2	1	0	0	0	0	1	0	0	0	0	1
Brown-headed Cowbird [†]	<i>Molothrus ater</i>	38.1	1	0	0	0	1	0	1	0	0	0	1
Blue Grosbeak* [†]	<i>Guiraca caerulea</i>	27	1	0	0	0	1	0	0	0	1	0	0
Blue Jay	<i>Cyanocitta cristata</i>	88	0	0	1	0	1	0	1	0	0	0	1
Bobolink*	<i>Dolichonyx oryzivorus</i>	29.2	0	1	0	0	1	0	0	0	0	1	0
Brown Thrasher	<i>Toxostoma rufum</i>	68.8	0	0	1	0	1	0	1	0	1	0	0
Common Ground-Dove*	<i>Columbina passerine</i>	37	0	1	0	0	1	0	1	0	1	0	0
Chipping Sparrow	<i>Spizella passerine</i>	12.2	0	1	0	0	1	0	0	1	0	0	0
Chimney Swift	<i>Chaetura pelagica</i>	23.6	1	0	0	0	0	1	0	0	0	0	1
Cliff Swallow	<i>Petrochelidon pyrrhonota</i>	21.6	1	0	0	0	0	1	0	0	0	0	1
Common Grackle	<i>Quiscalus quiscula</i>	92.2	0	0	1	0	1	0	1	0	0	0	1
Common Yellowthroat*	<i>Geothlypis trichas</i>	9.2	1	0	0	1	0	0	0	0	1	0	0
Eastern Bluebird* [†]	<i>Sialia sialis</i>	27.5	1	0	0	0	0	1	1	0	1	0	0
Eastern Kingbird* [†]	<i>Tyrannus tyrannus</i>	41.6	1	0	0	0	0	1	0	0	1	0	0
Eastern Meadowlark*	<i>Sturnella magna</i>	76	1	0	0	0	1	0	1	0	0	1	0
Eastern Phoebe	<i>Sayornis phoebe</i>	19.7	1	0	0	0	0	1	1	1	0	0	0
Eastern Towhee*	<i>Pipilo erythrophthalmus</i>	38.8	0	0	1	0	1	0	1	0	1	0	0
Field Sparrow* [†]	<i>Spizella pusilla</i>	12.5	1	0	0	0	1	0	1	0	1	0	0
Great-crested Flycatcher	<i>Myiarchus crinitus</i>	32.1	1	0	0	0	0	1	0	1	0	0	0
Grasshopper Sparrow*	<i>Ammodramus savannarum</i>	18.4	1	0	0	0	1	0	0	0	0	1	0
House Finch	<i>Haemorhous mexicanus</i>	21.4	0	1	0	0	1	0	1	0	0	0	1
Horned Lark*	<i>Eremophila alpestris</i>	32.2	0	1	0	0	1	0	0	0	0	1	0
Indigo Bunting*	<i>Passerina cyanea</i>	14.5	1	0	0	1	0	0	0	1	0	0	0
Loggerhead Shrike*	<i>Lanius ludovicianus</i>	47.7	1	0	0	0	0	1	1	0	1	0	0

Common Name	Scientific Name	Body											
		mass	Din	Dsd	Dom	Fflg	Fgr	Faer	Mres	HFop	HShr	HGra	Hoth
Mourning Dove* [†]	<i>Zenaida macroura</i>	115	0	1	0	0	1	0	1	0	1	0	0
Northern Bobwhite*	<i>Colinus virginianus</i>	178	0	1	0	0	1	0	1	0	0	1	0
Northern Cardinal*	<i>Cardinalis cardinalis</i>	41.8	0	1	0	0	1	0	1	0	1	0	0
Northern Mockingbird	<i>Mimus polyglottos</i>	48.5	1	0	0	0	1	0	1	0	0	0	1
Northern Rough-winged Swallow	<i>Stelgidopteryx serripennis</i>	15.9	1	0	0	0	0	1	0	0	0	0	1
Orchard Oriole	<i>Icterus spurius</i>	19.9	1	0	0	1	0	0	0	1	0	0	0
Painted Bunting*	<i>Passerina ciris</i>	15	0	1	0	0	1	0	0	0	1	0	0
Purple Martin	<i>Progne submis</i>	54.1	1	0	0	0	0	1	0	0	0	0	1
Red-headed Woodpecker	<i>Melanerpes erythrocephalus</i>	71.6	0	0	1	0	0	1	0	1	0	0	0
Red-winged Blackbird [†]	<i>Agelaius phoeniceus</i>	39.5	1	0	0	0	1	0	0	0	0	0	1
Savannah Sparrow*	<i>Passerculus sandwichensis</i>	17.1	1	0	0	0	1	0	0	0	0	1	0
Summer Tanager	<i>Piranga rubra</i>	28.2	1	0	0	1	0	0	0	1	0	0	0
Yellow-billed Cuckoo	<i>Coccyzus americanus</i>	25.4	1	0	0	1	0	0	0	0	1	0	0
Yellow-breasted Chat*	<i>Icteria virens</i>	64	1	0	0	1	0	0	0	1	0	0	0

* Early successional species, including all grassland and scrub/shrub species, and two open forest species

[†] Eight species for which their abundance was > 5% of total abundance

Table S2. Traits used to quantify functional diversity of birds. To calculate two functional diversity indices, these raw traits were converted to new traits following a common approach described by Villéger et al. (2008) and using dbFD function in package FD (Laliberté et al. 2014). First, we constructed a trait matrix of 41 species. dbFD function converted it into a dissimilarity matrix with Gower distance given our data included both continuous and categorical data and performed the principal coordinate analysis (PCoA) on the dissimilarity matrix, creating new traits (PCoA axes). Three PCoA axes that explained 72% of the variation in the matrix were adopted as new traits to calculate the values of FEve and FDiv.

Trait type	Trait categories	Value type
Body mass	Body mass	Continuous
Diet	Insectivore (insects), granivore (seed/grains), omnivore (various items)	Categorical
Foraging strategy	Foliage gleaner, ground forager, Aerial forager	Categorical
Migratory status	Resident	Binary
Habitat preference	grassland, scrub/shrub, open forest, others	Categorical

Table S3. Principal component (PC) factor loadings of environmental variables at local scale. We selected the first three PC components based on the criterion, i.e., retention of components accounting for $\geq 80\%$ of total variance, and used as local-scale variables. PC1 = increasing grass cover with decreasing forb cover; PC2 = increasing debris cover and decreasing vegetation height; PC3 = decreasing woody cover and vegetation height.

	Factor loading				
	PC1	PC2	PC3	PC4	PC5
Grass	0.5453	-0.3684	0.1535	-0.3987	0.6200
Forbs	-0.5765	-0.2713	-0.0540	0.4312	0.6365
Woody	0.3339	0.2527	-0.8624	0.2021	0.2000
Debris	-0.3348	0.6908	0.0302	-0.5328	0.3548
Vegetation Height	-0.3831	-0.4995	-0.4783	-0.5747	-0.2111
Eigen value	2.1398	1.2270	0.8714	0.5248	0.2368
Cumulative Proportion	0.4252	0.6687	0.8444	0.9484	1.0000

Table S4. Summary of model selection results. Due to overdispersion, QAICc (adjusted AICs with c-hat) was used for Grassland and Shrub. Model: Null with intercept only; Local with 5 local-scale variables; Landscape with 4 landscape variables; Full with both local-scale and landscape-scale variables.

	Response Variable	Model	df	logLik	AICc	Delta AICc	AICc weight
Diversity	Richness	Null	1	-101.743	205.6	0	0.854
		Local	6	-97.955	210.4	4.79	0.078
		Landscape	5	-99.475	210.7	5.08	0.067
		Full	10	-95.595	218.5	12.94	0.001
	Shannon	Null	2	-13.757	31.8	0	0.694
		Local	7	-8.13	33.7	1.82	0.279
		Landscape	6	-11.982	38.4	6.61	0.026
		Full	11	-6.206	43.5	11.69	0.002
	FEve	Null	2	44.343	-84.4	0	0.804
		Landscape	6	47.883	-81.3	3.07	0.173
		Local	7	47.092	-76.8	7.58	0.018
		Full	11	52.692	-74.3	10.09	0.005
	FDiv	Landscape	6	61.296	-108.1	0	0.807
		Full	11	67.645	-104.2	3.93	0.113
Null		2	53.617	-102.9	5.2	0.060	
Local		7	59.087	-100.8	7.34	0.021	
Abundance	Grassland	Null	1	-59.59	97.135	0	0.927
		Landscape	4	-58.06	102.23	5.095	0.073
		Local	6	-53.61	112.661	15.526	0.000
		Full	9	-52.99	117.584	20.449	0.000
	Shrub	Null	1	-98.87	163.83	0	0.640
		Landscape	4	-97.4	164.98	1.15	0.360
		Local	6	-94.79	177.62	13.79	0.001
		Full	9	-92.21	187.03	23.2	0.000

Table S5. Summary of parameter estimates from model averaging. All bird species were used to calculate FDiv (functional divergence) and Shannon (Shannon-Wiener diversity). Note that stands enrolled in Longleaf Pine Initiative (LLPI) only are set as a reference, which is represented by an intercept. R^2 (pseudo- R^2) value of the Full model (including both local and landscape variables) was used because there is not a proper method to calculate R^2 value for an averaged model, especially beta regression. Values in parentheses represent standard error. Significance level: *, $P < 0.05$; **, $P < 0.01$. Local-scale explanatory variables: LLPI-BQI, stands enrolled in both LLPI and the Bobwhite Quail Initiative; PC1, increasing grass cover with decreasing forb cover; PC2, increasing litter cover and decreasing vegetation height; PC3, decreasing woody plant cover and vegetation height. Landscape scale explanatory variables: Forest_veg, percent cover of forest; Shrub_veg, percent cover of shrub; Grassland_veg, percent cover of grasses and forbs; LandH, landscape heterogeneity.

Response variable	Explanatory variable										R^2
	Intercept	LLPI-BQI	Stand size	PC1	PC2	PC3	Forest_veg	Shrub_veg	Grassland_veg	LandH	
Shannon	0.47 (0.05)	0.07* (0.03)	0.02 (0.02)	0.01 (0.01)	0.02 (0.01)	0.01 (0.01)	-0.01 (0.01)	-0.02 (0.01)	-0.1 (0.1)	-0.02 (0.11)	0.29
FDiv	0.50 (0.68)	-0.16 (0.14)	0.27* (0.10)	0.02 (0.03)	-0.08 (0.05)	-0.05 (0.06)	-0.06 (0.04)	0.19** (0.05)	0.02 (0.06)	0.55 (0.45)	0.44