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Andriana Miljanic April 5, 2017

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by

Andriana Miljanic

Berry Brosi
Adviser

Environmental Sciences

Berry Brosi

Adviser

Christopher Beck

Committee Member

John Wegner

Committee Member

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Andriana Miljanic

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An abstract of
a thesis submitted to the Faculty of Emory College of Arts and Sciences
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Abstract

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Land-use change in agricultural landscapes is believed to be a major driver of pollinator declines. In the United States, expansion of the biofuel industry is expected to cause extensive land-use change. Increasing energy demands have led the US Department of Energy to enact mandates to increase cellulosic biofuel production, which will require extensive cultivation of fast-growing trees as feedstock. Managed forests and tree plantations can support rich biodiversity. While we know that local management regimes often can impact plantation wildlife, we know little about how changes in the surrounding landscape, such as those brought about by the rapid expansion of biofuel plantations, impact resident communities. Furthermore, we know little about how local management and landscape context interact to affect biodiversity. I examined the effects of forestry management practices associated with cellulosic biofuel production – both local-level forest management (pine plantations, clearcuts, natural longleaf forests, and cornfields) and landscape management – on bee communities in 85 sites in Alabama, Georgia, and Florida. I explored the interactions between local management and landscape context, and their effect on bee abundance and richness. I found that both landscape composition and configuration impact both bee abundance and richness. Percent tree cover, landscape richness, landscape Shannon's diversity, and patch shape had significant main effects on both bee abundance and richness. There was an interactive effect between local and landscape management, and these interactions may have been driven by

differing impacts of landscape heterogeneity based on the quality of local habitats. Landscape heterogeneity may be more important for bees in low-quality or disturbed local habitats. Future studies should explore how landscape context and the interactions of local and landscape management impact bee community composition and beta-diversity. Understanding how land use changes will impact pollinators on both a local and landscape scale is critically important to maintaining biodiversity and ensuring resilience of these ecosystems.

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INTRODUCTION

Pollinators have been substantially declining in recent years (Potts et al. 2010). These declines are particularly concerning as pollinators are critically important for agricultural production. They are responsible for producing food that provides about one-third of global calories consumed and a disproportionate amount of the important vitamins, minerals, and other nutrients in our diet (Klein et al. 2007; Eilers et al. 2011). Pollinators are also essential for the reproduction of many native plants, including about 90% of angiosperm species (Burd 1994; Kearns et al. 1998; Ollerton et al. 2011).

Bees are an important group of pollinator insects and have suffered declines due to land use change (Potts et al. 2010). Agricultural expansion causes extensive landscape change often to the detriment of biodiversity, because crop fields often are dominated by one or few annual crop species, and thus lack the habitat complexity and heterogeneity needed to support high biodiversity (Kareiva et al. 2007). In addition, bee biodiversity has been reduced due to habitat disturbances (Winfree et al. 2009) and reduced connectivity to natural habitat (Ricketts et al. 2008). A meta-analysis of existing studies on the impacts of human disturbances on bee declines found a significant negative effect of habitat loss and fragmentation on bee abundance and richness in systems where little natural habitat remains (Winfree et al. 2009). Agriculture is a major driver of these landscape changes (Kareiva et al. 2007), and the intensification of agriculture and forestry is a major cause of biodiversity loss (Tscharntke et al. 2005).

In terms of land-use changes related to agriculture and forestry, biofuel cultivation is likely to become an important cause of land use change in the United States. As energy demands continue to rise, pressure for more sustainable alternatives to fossil fuels is increasing. Biofuels, which are produced from biomass (plant matter), have the potential to reduce our dependence on fossil fuels in some contexts (Hill et al. 2006; Fargione et al. 2008; Charles 2009), and could reduce our reliance on imported petroleum (Demirbas 2009; Langholtz et al. 2016). These potential benefits have led the United States Department of Energy to enact mandates to increase levels of liquid biofuel use in the United States (Sissine 2007). The Renewable Fuel Standard, an important part of the Energy Independence and Security Act of 2007, mandates that the US produce 21 billion gallons of advanced biofuel by 2022, of which 16 billion gallons are cellulosic biofuel (U. S. Congress 2007). Cellulosic biofuels are made from fibrous or woody plant materials that are broken down into sugars and then converted to ethanol or other liquid fuels (Carroll and Somerville 2009). Cellulosic biofuels have some advantages compared to biofuels made directly from plant-produced sugars or starches as they can—at least in some contexts—yield higher net energy gains (Yuan et al. 2008), require less water and fertilizer (Evans and Cohen 2009), may have greater resistance to pests and disease (Hinchee et al. 2011), can be grown on lands unsuitable for agriculture (Carroll and Somerville 2009), and may compete less with food crops for land (Landis and Werling 2010; Yuan et al. 2008). However, it is considerably more difficult to degrade cellulosic biomass into sugars, so sugar and starch-based biofuel feedstocks have been substantially more utilized to date (Rubin 2008). Cellulosic biofuel technologies are available, but not yet commercially scalable (Langholtz et al. 2016). Once this scalability is achieved, which could occur on a relatively short timeframe (Langholtz et al. 2016), a rapid increase in cellulosic biofuel cultivation is likely, which will result in potentially dramatic land use changes.

In terms of land use change driven by biofuels in the US, the United States Department of Agriculture expects that approximately 49% of biofuels produced to fulfill these mandates will come from the southeastern US (Bittleman et al. 2010). The forestry community has identified loblolly pine plantations to be a top candidate for contributing to meeting these biofuel mandates (Kline and Coleman 2010). There are thirteen million hectares of pine plantations in the southeastern US and 600,000 hectares are being planted each year (Kline and Coleman 2010). Additionally, this species has broad genetic potential and better productivity than most hardwoods on the same sites (Kline and Coleman 2010). These well-developed operations and the rapid growth rate of loblolly pine in southeastern climates make it an ideal candidate for biofuel production.

Intensified cellulosic biofuel cultivation will necessarily require changes in land use, which has generated concerns about biodiversity impacts (Fargione et al. 2009). While clearing natural remnant vegetation for biofuel crops poses an obvious ecological threat, simply changing how human-modified lands are utilized also can shape biodiversity. For example, Fletcher et al. (2011) examined the effects of increased biofuel cultivation on vertebrate biodiversity at two scales, (i) across landscapes and (ii) within-fields or stands. On a landscape-level, land-cover change, overall composition of land use changes, and placement of biofuel crops alter the availability and connectivity of habitat for wildlife and pollinators (Fletcher et al. 2011; Meehan et al. 2010; Scott and Tiarks 2008; Fahrig et al. 2011). At the stand-level, increases in chemical applications and changes in harvesting techniques have been correlated with biodiversity loss (Fletcher et al. 2011). In addition, changing crop types also influences biodiversity. Pine stands have been found to have greater abundance and diversity of bees relative to cornfields, though specific management practices for cultivated forests such as thinning and rotation timing have relatively little effect (Gruenewald 2014). Nevertheless, forest harvesting practices, such as the treatment of woody residues accrued during harvest, may increase bee abundance but decrease species diversity (Gruenewald 2014). Evidently, local management conditions can have significant impacts on bee diversity and abundance.

While the impacts of management regimes on plantation biodiversity have been studied to some extent, less is known about more general landscape-level factors that may drive biodiversity change (Lindenmayer et al. 2006). In particular, we have a very limited understanding of how landscape context surrounding individual biofuel plantations impacts resident bee communities. Characteristics of surrounding landscapes can significantly impact local populations (Turner et al. 2001); therefore, it is important to consider landscape context when attempting to understand local ecological processes. The potential effects of landscape context surrounding biofuel cultivation plots on bee biodiversity are dependent on landscape composition, configuration, and connectivity. For example, landscapes with higher compositional heterogeneity may provide a greater diversity of resources for breeding, feeding, and nesting (Benton et al. 2003). This diversity of habitat quality may support higher bee diversity. Landscapes with higher configurational heterogeneity may increase the probability that different resources will be in close proximity (Dunning et al. 1992; Flick et al. 2012). This is closely related to landscape connectivity, which has been shown to be positively correlated with bee diversity (Diekötter et al. 2008), as connectivity may allow insects to move among and utilize a greater number of resource patches (Haddad and Kingsolver 1999).

Despite the potentially large effect of the surrounding landscape on local diversity, existing studies on the impacts of forestry management tend to focus on local scale effects of management (Gruenewald 2014) or patch size (DeLong 2007), with considerably less work on landscape context (Lindenmayer et al. 2006). Some research has begun to explore the influence of landscape context on pollinator diversity (Steffan-Dewenter et al. 2002); however, our understanding of the interactions between local management and landscape context remains poor. To effectively protect pollinator diversity, it is important to identify the effects of both local and landscape management and their interactions. In addition, it is essential to understand the implications of biofuel cultivation and management of these plantations on both a local and landscape scale (Robertson et al. 2008), and how these different scales interact (Holzschuh et al. 2007).

In this paper, I examined the effects of forestry management practices associated with cellulosic biofuel production – both local-level forest management and landscape management – on bee communities. I compared pine plantations and recently clearcut plantations to natural reference longleaf pine forests and cornfields (an alternative biofuel feedstock). I studied the effects of the landscape context surrounding each site to determine how bee communities (specifically, abundance and species richness) will respond to intensification of biofuel cultivation, and explored the interaction between local and landscape management on bee abundance and richness. I hypothesized that more heterogeneous landscapes will support a greater abundance and diversity of bees. I expected a more diverse landscape composition and configuration to increase bee abundance and richness. I expected the impacts of local management to be dependent on landscape context.

METHODS

STUDY SITES

OVERVIEW: This study was conducted as part of a larger USDA-funded project examining how biofuel cultivation will impact bird, bat, bee, and reptile communities.

SITES: This study was conducted between April 2013 and July 2015 in pine plantations, pine forests, and cornfields in eastern Alabama, northern Florida, and southern Georgia. We surveyed sites on the southeastern coastal plain, a region historically dominated by longleaf pine (*Pinus palustris*) (Christensen 2000). Much of the longleaf pine forests have been cleared and converted to pine plantations with faster growing loblolly pine (*Pinus taeda*) (Wear and Greis 2002). We sampled a total of 85 sites across three states (Figure 1). We sampled bee communities in Newton County, GA, in the spring and summer of 2013. In spring and summer of 2014, bees were sampled in Alabama (Butler, Conecuh, Escambia, and Monroe counties), Florida (Jefferson, Liberty, and Wakulla counties), and Georgia (Decatur and Thomas counties). In spring and summer of 2015, we sampled bees in Alabama (Butler and Covington counties), Florida (Alachua, Columbia, Gilchrist, Levy, Marion, and Suwannee counties), and Georgia (Mitchell county). All sites were spaced at least 2500 m apart to ensure independent replicates.

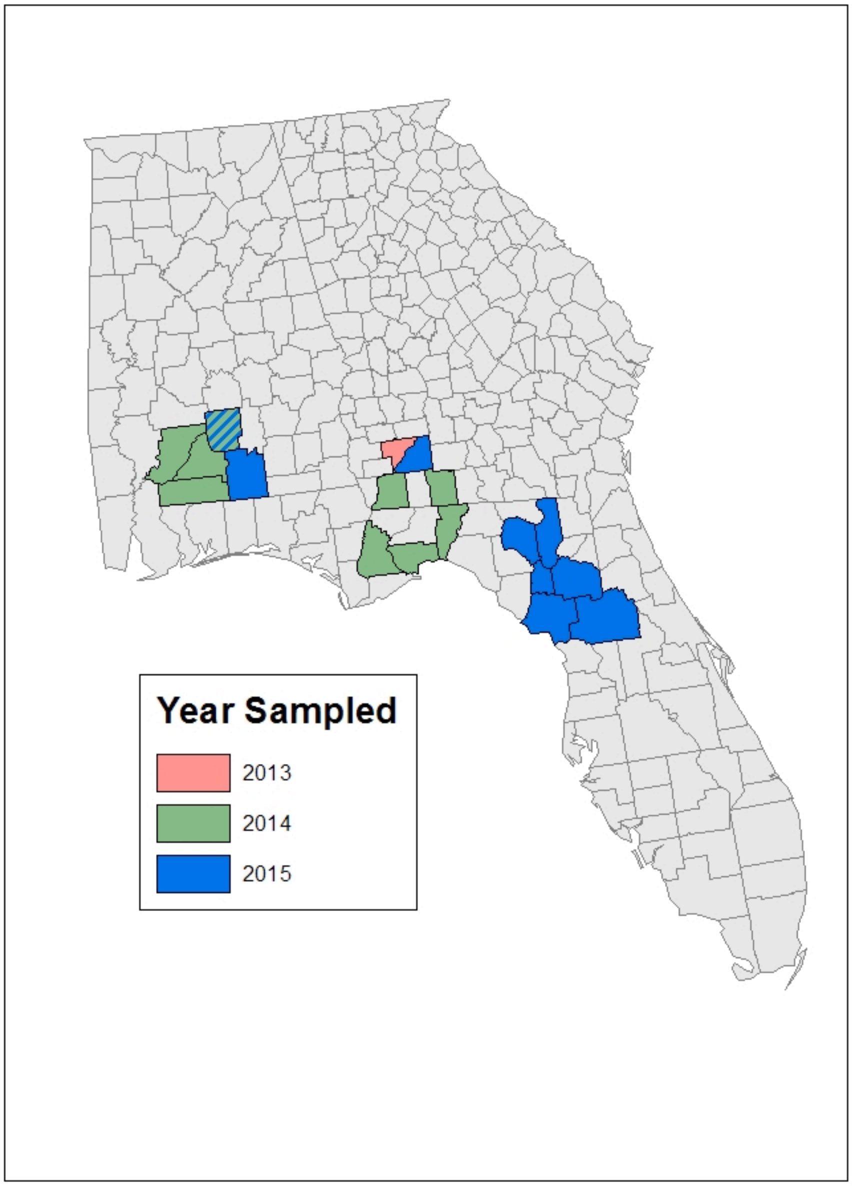

Figure 1. Map of counties surveyed. Colors denote year surveyed.

LOCAL MANAGEMENT: To explore the interaction between local and landscape level management we compared four different local management practices: plantation forest, clearcut, natural longleaf forest, and cornfield (an alternative biofuel crop) (Table 1). Previous work focused on comparing biofuel management with traditional pine plantation practices in the southeastern US found no differences in bee abundance, richness, and community composition among the different plantation types (Gruenewald 2014), so we have aggregated them here.

Table 1. Description of local management practices

Management Style	Description	Number of sites
Plantation forest	Loblolly pine trees, managed for cultivation	47
Clearcut	All trees removed recently	21
Natural forest (longleaf)	Longleaf pine trees with low degree of disturbance and management	10
Cornfield	Corn monoculture, crop present and growing during study	7

TRANSECT DESIGN: We set up two 200m x 2m transects, an interior and an edge, in each site. The edge transect was placed 50m from the edge of the tree stand, bordering non-tree land use (row-crop, grass, or urban). In corn sites, we placed the edge transect 50m from the edge of the cornfield, which bordered land not in corn cultivation (forest, grass, urban, or non-corn row-crop). We placed the interior transect so that it was surrounded with a minimum radius of 150m of the management type being studied. Interior transects were placed using ArcGIS and satellite data from National Land Cover Database 2011.

BEE SAMPLING

OVERVIEW: We collected bees from mid-April to late-July in 2013, 2014, and 2015. Each site was sampled four times, once every three to four weeks. We sampled bees from both the edge and interior transects at each site.

PASSIVE SAMPLING: We used pan traps to passively sample bees. Pan traps were 104mL plastic Solo cups (Model P325) painted with blue, white, or yellow UV reflective paint to attract bees (Kearns and Inouye 1993; Westphal et al. 2008). We filled the painted cups with approximately 76mL of soapy water, which has reduced surface tension, so that bees would sink to the bottom and drown (Kearns and Inouye 1993). We set pan traps approximately 40cm above the ground using Vigoro plant props (Model #611872). Fifteen pan traps were evenly distributed along the middle 100m of each transect. We alternated pan trap colors, generating a total of 5 blue, 5 yellow, and 5 white traps (Westphal et al. 2008). We collected bees from pan traps 24 hours after they had been set. We washed, pinned, and labeled bees the same day they were collected.

ACTIVE SAMPLING: Aerial netting was conducted to actively sample bees in each site. A field team member walked along the 200m transect line searching for bees for 30 minutes. Timers were paused while handling bees. Sampling was conducted between 10am and 11am. We pinned and labeled bees the same day they were collected.

BEE IDENTIFICATION: We identified bees to the species level or lowest possible taxonomic category based on morphological characteristics. We used interactive keys from DiscoverLife to identify bees. Bees were identified with assistance from Emily Dobbs, Dave Gruenewald, Sam Droege (USGS), and Ismael Hinojosa (UNAM).

DATA ANALYSIS

OVERVIEW: All statistical analyses were conducted in R (R Core Team 2016). We analyzed how bee abundance and species richness changed with local management (whether a study site was in a natural (longleaf) forest remnant, pine plantation, clearcut or cornfield) as well as various landscape context metrics (Tables 1 and 2).

LANDSCAPE METRICS: The condensed set of landscape metrics used in this study were: percent tree cover, landscape richness, landscape Shannon diversity, Aggregation Index, mean patch shape, mean patch core area and mean effective mesh size (Table 2).

Landscape configuration may be described in terms of constituent patch attributes, such as shape, core area, subdivision, and dispersion. I selected one landscape metric for each factor. I selected mean shape index to describe patch shape because it is normalized to prevent a size dependency problem (e.g., circles of differing area have different edge to area ratios; this metric prevents that) and it is not overly sensitive to sites with only a few patches. I used mean patch core area, because core area is a better predictor of habitat quality than total area

(Temple 1986). I chose effective mesh size to describe the subdivision of the landscape because it takes into account all patches according to their size, and it is more sensitive to fragmentation than other subdivision metrics. I described dispersion of the different land classes in the landscape with the aggregation index. This metric tells us how spread out or dispersed the land classes are, and it is scaled to account for the maximum possible number of like adjacencies given the abundance of land classes.

I included percent tree cover, patch richness, and Shannon's Diversity Index as metrics to describe the landscape composition (Table 2). I selected percent tree cover to understand how pine plantation expansion may affect bees. Patch richness tells us the number of land classes in a landscape and is the simplest measure of landscape composition. Shannon's Diversity Index takes both richness and evenness into account, and is more sensitive to rare patch types. Shannon's Diversity Index is a popular measure of diversity in community ecology (Hill 1973).

Table 2. Landscape metrics

Landscape Metric	**Description**
Composition	
Percent Tree Cover	Percent of tree cover in the landscape
Patch Richness	Number of land classes in the landscape
Shannon's Diversity Index	Measure of richness and evenness of land classes
Configuration	
Mean Shape Index	Normalized perimeter to area ratio, describes shape
Mean Patch Core Area	Area of patch comprised of core, describes edge depth
Mean Effective Mesh Size	Probability that two points in a region will be connected, describes subdivision
Aggregation Index	Percentage of like adjacencies given the proportion of each class in the landscape

Landscape metrics were calculated using SDMTools (VanDerWal et al. 2014) based on LANDSAT remote sensing data (30-m spatial resolution) with automated classification from the National Land Cover Database (Homer et al. 2015). The NLCD classifies land cover into sixteen landscape classes, and we grouped these into nine landscape classes: water, tree cover, row crop, grassland, urban, barren, shrub, pasture, and wetland. The remote sensing data were collected in 2011. We assessed each landscape metric at four buffer radii: 500, 1000, 2000, and 5000 m.

RICHNESS AND ABUNDANCE: Because the probability of species detection increases with sampling effort, we used the iNEXT package (Chao and Jost 2015) to construct rarefaction curves of species richness, bootstrapping 50 times to estimate site species accumulation at the third sample. For bee abundance, we used the mean per-sample abundance in each site. We analyzed the responses of both bee abundance and rarefied richness with linear models that included local management, landscape metrics, and all local x landscape interactions (but not landscape x landscape interactions).

MODEL SELECTION: We constructed models of all combinations of constituent factors and ran automated AIC (Akaike's information criterion) model selection (R-package: MuMIn). AIC model selection balances model fit with model complexity (Goodenough et al. 2012). We included any model within two delta AICc points of the model with the lowest AICc in the best set of models. Models with the smallest AIC values are estimated to best explain the observed data, and two delta AIC points suggest substantial support of the model (Burnham and Anderson 2002). After model selection, we measured multicollinearity among various landscape metrics with variance inflation factors (Zuur et al. 2010), using a stepwise approach to eliminate metrics above a threshold VIF of 5, to confirm that the set of best models did not include collinear explanatory variables. VIF cutoff values are typically 5 or 10 (Craney and Surles 2002), so we used the more stringent value in our analyses.

RESULTS

OVERVIEW: In total, 5758 bees representing 128 species were sampled: 1480 bees (82 species) in Alabama, 1756 bees (76 species) in Florida, and 2522 bees (78 species) in Georgia. Overall, the most abundant species were *Lasioglossum floridanum*, *Lasioglossum reticulatum*, and *Lasioglossum nymphale*. Details of most abundant bee species for each state are listed in Table 3.

Table 3. Most abundant bee species across all sites and by state

Most Abundant Bee Species	**Number of bees**
Overall	
Lasioglossum floridanum	958
Lasioglossum reticulatum	520
Lasioglossum nymphale	485
Alabama	
Lasioglossum floridanum	325
Lasioglossum pilosum	94
Melissodes trinodis	75
Florida	
Lasioglossum nymphale	471
Lasioglossum floridanum	251
Melissodes communis	122
Georgia	
Lasioglossum reticulatum	414
Lasioglossum floridanum	382
Lasioglossum puteulanum	351

BUFFER RADIUS: The best models for both bee diversity and abundance (within two delta-AICc values of the best model) used landscape metrics at the 2000 m scale. AICc values for bee richness and bee abundance at all buffer radii are listed in Supplemental Tables 1 and 2. Means of landscape metrics for the 2000 m buffer are summarized in Supplemental Table 3.

LANDSCAPE METRICS: Our analysis of variance inflation factors indicated that our best models for both bee diversity and abundance did not include any collinear explanatory variables, even at a threshold VIF of 5.

BEE ABUNDANCE: Two models with very similar AICc values showed that percent of tree cover, Shannon's Diversity Index, mean shape index, and management had significant main effects on bee abundance (Table 4). In terms of main effects, there was a trend toward increasing bee abundance as percent of tree cover increased. Increases in Shannon's Diversity Index appear to be correlated with increased bee abundance. As mean shape index increased (patch shape became more complex), bee abundance appears to increase. Patch richness had a significant effect on bee abundance in the best model, but not the second best model (Table 4). While these metrics appear to have main effects, the interaction responses varied.

In both top models, the interactions between percent tree cover and management, Shannon's Diversity Index and management, and mean shape index and management had significant effects on bee abundance (Table 4). In natural forest sites and cornfields, bee abundance appears to increase as the percent of tree cover increased (Figure 2). In plantation forests, there is a trend toward a slight decrease in bee abundance as the percent tree cover increased (Figure 2). As Shannon's Diversity Index increased, bee abundance in cornfields and clearcut sites seems to increase (Figure 3). However, as Shannon's Diversity Index increased in natural forest sites, bee abundance appears to decrease (Figure 3). Abundance of bees in plantation forest sites did not appear to be significantly affected by Shannon's diversity. In both natural forests and cornfields, as mean shape index increased bee abundance appears to decrease (Figure 4). By contrast, in clearcut sites and plantation forests there is a trend toward increasing bee abundance as the mean shape became more complex (Figure 4).

BEE RICHNESS: For bee richness, seven models were within two delta AICc values. Across all seven models, percent tree cover, patch richness, and management had significant effects on bee richness (Table 5). Mean shape index had a significant positive effect in five of the seven models (Table 5). Shannon’s Diversity Index had a significant negative effect on bee richness in two models (Table 5). Aggregation index and mean patch core area each had a significant effect in just one model (Table 5).

In all seven top models for bee richness, there was an interaction between percent tree cover and management (Table 5). In natural forests, cornfields, and clearcut sites as percent tree cover increased bee richness appears to also increase (Figure 5). By contrast, in plantation forest, bee richness may slightly decrease as percent tree cover increased (Figure 5). In one of the seven models, there was an interaction between mean shape index and management for bee richness (Table 5). There was a trend toward decreasing bee richness with increasing mean shape index in cornfields and natural forest sites, while bee richness appears to increase with increasing shape complexity in clearcut sites and plantation forests.

Table 4. AIC model selection for bee abundance

Landscape Composition			Landscape Configuration	Local	Landscape and Local Interactions							
Percent Tree Cover	Patch Richness	Shannon's Diversity Index	Mean Shape Index	Management	Percent Tree Cover x Management Interaction	Shannon's Diversity Index x Management Interaction	Mean Shape Index x Management Interaction	df	logLik	AICc	delta	weight
261.87	3.66	168.91	47.08	+	+	+	+	18	-331.42	709.53	0	0.29
277.96		178.46	45.57	+	+	+	+	17	-333.82	711.06	1.52	0.13

Table 5. AIC model selection for bee richness

Landscape Composition			Landscape Configuration			Local	Landscape and Local Interactions						
Percent Tree Cover	Patch Richness	Shannon's Diversity Index	Aggregation Index	Mean Shape Index	Mean Patch Core Area	Management	Percent Tree Cover x Management Interaction	Mean Shape Index x Management Interaction	df	logLik	AICc	delta	weight
9.46	1.91			3.66		+	+		11	-206.28	438.83	0	0.08
3.68	2.19	-3.7		3.32		+	+		12	-205.18	439.48	0.64	0.06
10.01	1.69			7.11		+	+	+	14	-202.19	439.5	0.66	0.06
2.38	2.07	-4.29				+	+		11	-206.87	440.01	1.17	0.04
9.04	1.73					+	+		10	-208.31	440.12	1.28	0.04
8.22	1.87		14.41	4.13		+	+		12	-205.52	440.15	1.32	0.04
8.49	1.91			3.69	12.71	+	+		12	-205.83	440.78	1.94	0.03

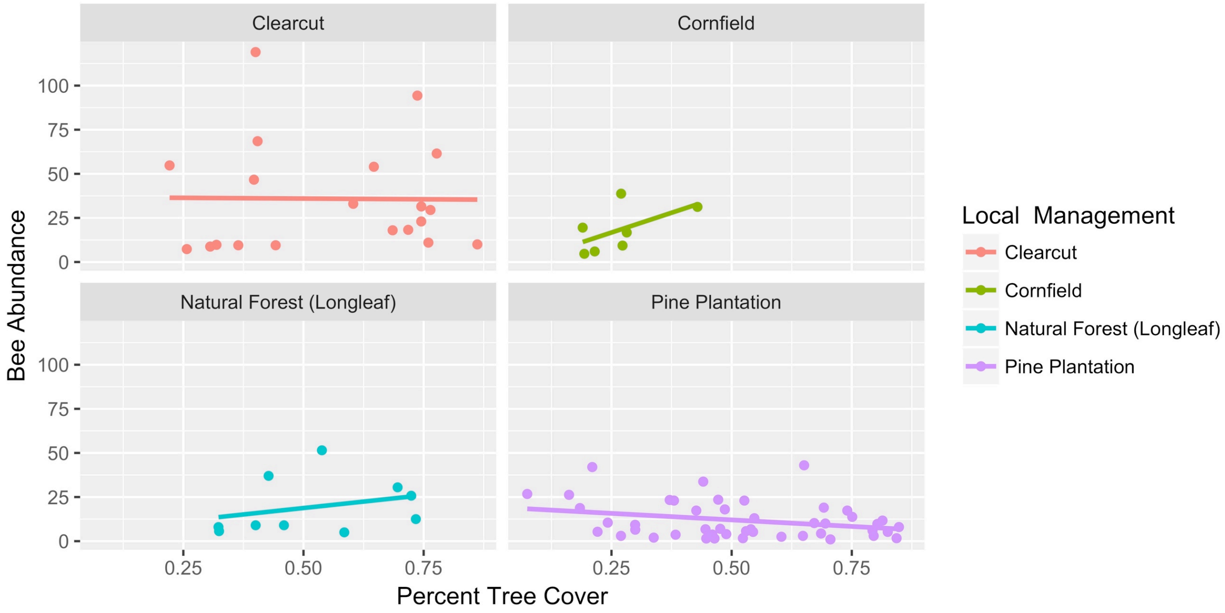

Figure 2. Interactive effects of local management and percent tree cover in the landscape on bee abundance.

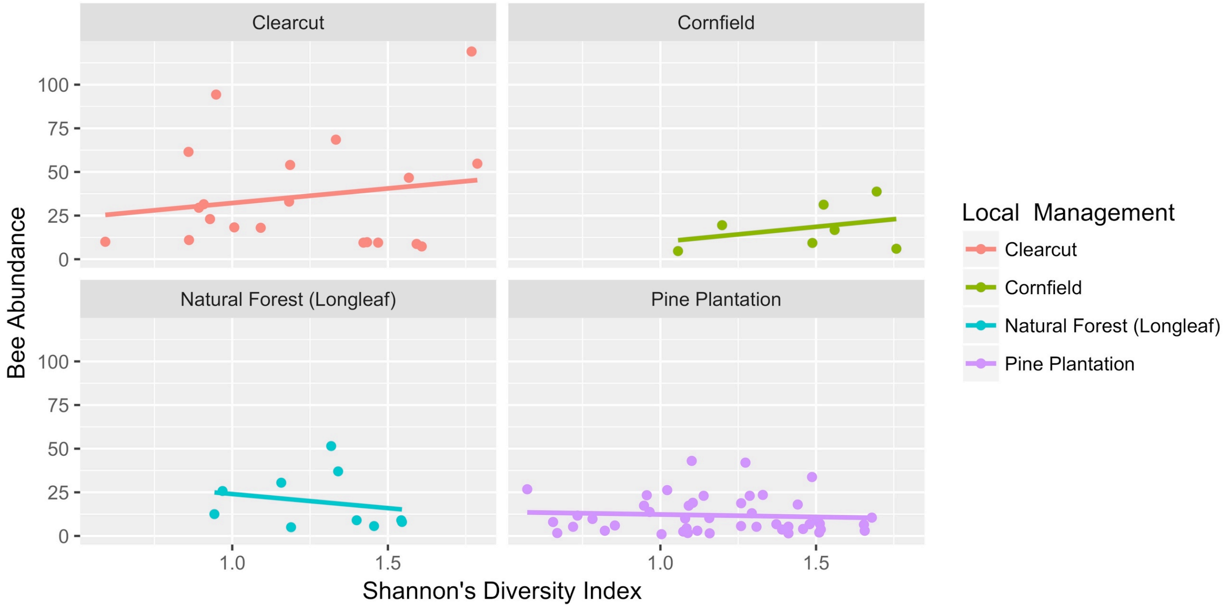

Figure 3. Interactive effects of local management and landscape Shannon's diversity on bee abundance.

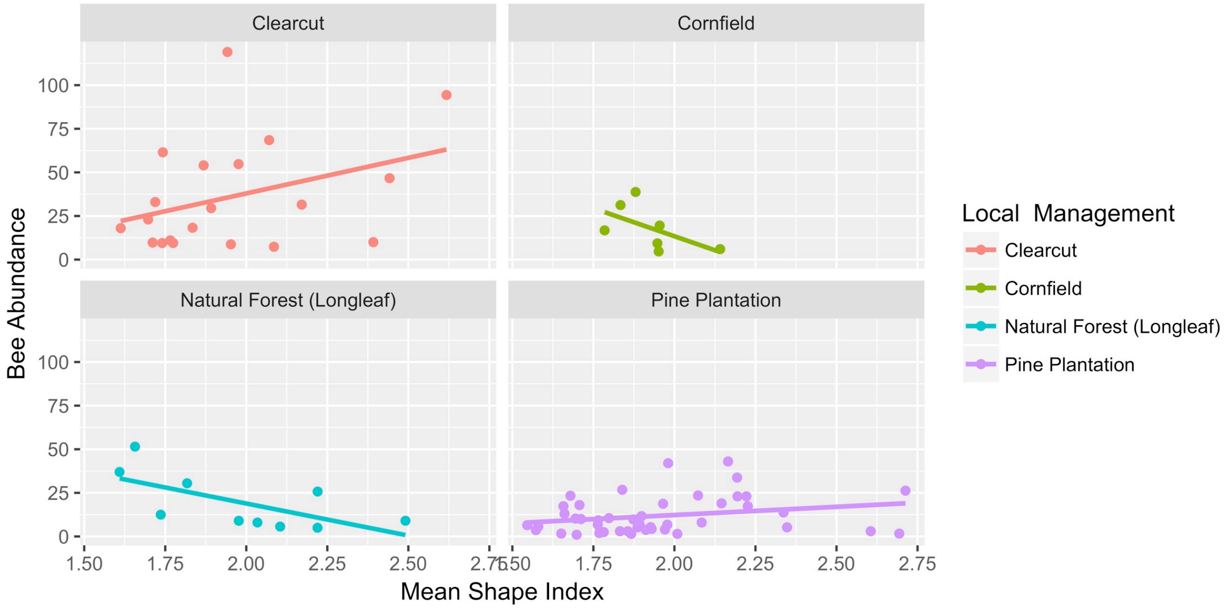

Figure 4. Interactive effects of local management and mean shape the land classes in the landscape on bee abundance.

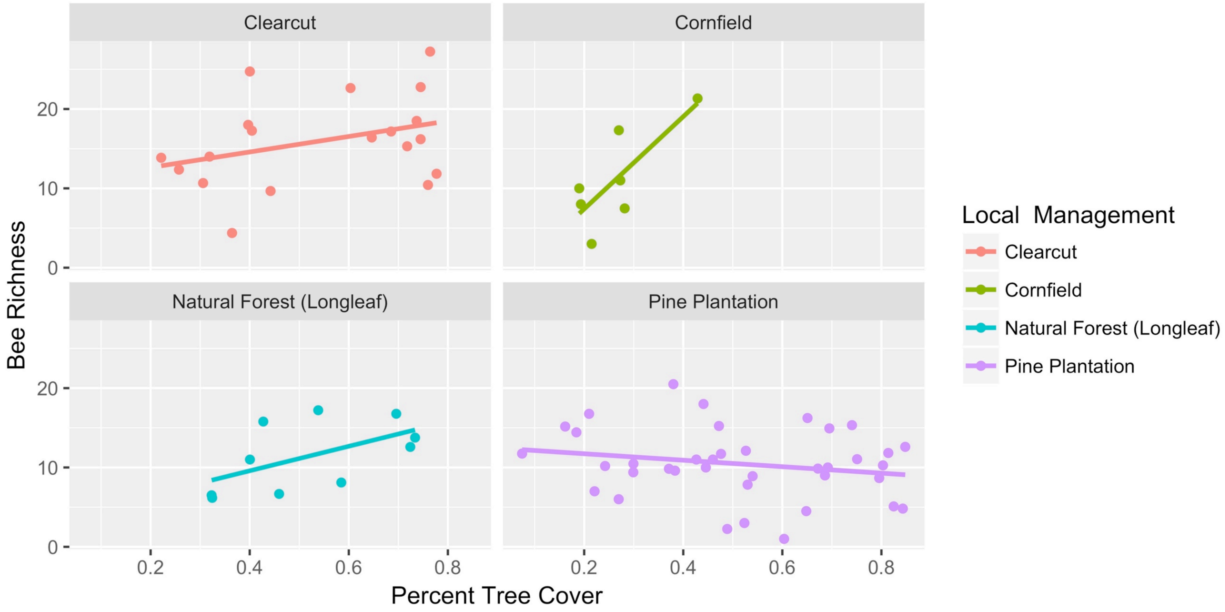

Figure 5. Interactive effects of local management and percent tree cover in the landscape on bee richness.

DISCUSSION

I examined the effects of local-level forest management practices and landscape context on bee communities to understand the implications of biofuel cultivation on bee diversity. I explored the interaction between local and landscape management on bee abundance and richness. Three primary findings emerge from my results. First, I found that both landscape composition and configuration are important for both bee abundance and richness. Second, there were interactions between the local-level management and the landscape context. Third, many of these interactions appeared to be driven by differing impacts of landscape heterogeneity based on the quality of local habitats. I discuss each of these findings in more detail in the following paragraphs.

LANDSCAPE COMPOSITION AND CONFIGURATION: Both landscape composition and configuration correlate with bee abundance and richness. All of the examined landscape composition metrics (percent tree cover, patch richness, Shannon’s Diversity Index) as well as mean shape index (a configuration metric) had significant effects on both bee abundance and richness. I found that the main effect of bee abundance and richness with increasing tree cover in the landscape trended toward an increase in bee abundance and richness, however the interaction responses varied. This main effect contrasts with findings by Winfree et al. (2007), that show decreasing bee diversity with increasing tree cover in the landscape. Tree cover reduces the amount of sunlight that can reach the forest floor, thereby in many cases reducing the density of flowering plants (important food resources for bees) (Jameson 1967). However, high proportions of tree cover may sometimes indicate more seminatural or noncrop habitat in the landscape, which has been associated with increased bee diversity (Holzschuch et al. 2010; Steckel et al. 2014). Both bee abundance and richness appear to increase as the number of land use classes in the landscape increased. Higher compositional heterogeneity may support higher bee diversity, because it may provide a greater diversity of resources for breeding, feeding, and nesting (Benton et al. 2003). Interestingly, as the Shannon Diversity of landscapes increased, bee abundance appears to increase while bee richness seems to decrease. Bee richness may decline with increasing landscape Shannon Diversity, as it could correlate with more habitat loss or fragmentation.

While previous research on agroecosystems found only weak effects of landscape configuration on wild bee pollinators in agroecosystems (Kennedy et al. 2013), I found strong effects of patch shape on bee richness. Both bee abundance and richness appears to increase as the shape of patches in the landscape becomes more complex (Tables 4 and 5). Increased configurational heterogeneity may increase the probability that different resources will be close to one another (Dunning et al. 1992; Flick et al. 2012), which may allow bees to more efficiently access and utilize a greater diversity of resources (Dunning et al. 1992).

The majority of pollination ecology literature does not distinguish between the effects of landscape composition and configuration (Hadley and Betts 2012). Although landscape composition and configuration are usually confounded (Fahrig 2003), it is important to separate composition and configuration because managed landscapes, such as these biofuel production plantations, can create landscape configurations that may conserve biodiversity (Hadley and Betts 2012).

LOCAL – LANDSCAPE INTERACTIONS: I found interactions between local-level management and landscape context. These interactions between local scales and landscape context are important to explore, as bee diversity responds to a large range of spatial scales (Holzschuch et al. 2007; Diaz-Forero et al. 2013). In terms of bee abundance, I found significant interactions between management and percent tree cover, Shannon's Diversity Index, and mean shape index (Figures 2, 3, 4). And in terms of bee richness, I found significant interactions between management and percent tree cover (Figure 5). Across clearcuts, cornfields, and natural forests bee richness appears to increase with increasing percent tree cover in the landscape (Figure 4). Higher proportions of tree cover may indicate more seminatural habitat within the landscape, which has been found to increase bee richness (Holzchuch et al. 2010; Steckel et al. 2014). However, in plantation forests, bee richness appears to slightly decrease with increasing tree cover in the landscape. Too much tree cover in the landscape and local habitat may reduce compositional heterogeneity and provide a limited variety of resources. Also, bee richness may be higher in disturbed landscapes as different bee species may utilize different resources from many patches experiencing different successional stages (Chesson and Huntly 1997). Highly homogeneous forested sites may lack resource heterogeneity, and may also not provide for disturbance-adapted bee species. Few studies have explored the interaction effects of local management and landscape context on pollinators (Rundlof et al. 2008; Kleijn and Langevelde 2006). These interactions between local and landscape scales emphasize the importance of considering both the local management as well as the landscape management associated with cellulosic biofuel production.

LOCAL HABITAT QUALITY AND LANDSCAPE CONTEXT: A key potential driver of the interactions between habitat type and landscape on bee abundance is that landscape heterogeneity may be more important for bees in low-quality or disturbed local habitats. I found a trend toward decreased bee abundance in natural forests as the composition and configuration became more heterogeneous, while bee abundance in cornfields and clearcuts appears to increase with increasing landscape heterogeneity. Bee abundance in clearcut sites and cornfields seems to increase as Shannon's Diversity Index of the landscape increases. As the composition in these landscapes becomes more heterogeneous, bees can access a larger variety of resources (Benton et al. 2003). However, bee abundance in natural longleaf forests and plantation forests seems to decrease as Shannon's Diversity Index increases. These local conditions are more natural and less disturbed than clearcuts and cornfields, suggesting that less compositional diversity in the landscape may allow for more seminatural landscape as one land class can dominate, and bees may prefer more seminatural landscape (Holzschuch et al. 2010; Steckel et al. 2014). Similarly, Kennedy et al. (2013) found that the beneficial effect of surrounding landscape composition decreased when local habitats were of high-quality. Compositional landscape heterogeneity may be more important for bees in low-quality or disturbed local environments.

Bee abundance in clearcut sites appears to increase as the shape of the habitat patches across the landscape becomes more complex. Increasing configurational complexity may allow bees in this highly disturbed local habitat to access a greater variety of resources as they may be in closer proximity (Dunning et al. 1992). I expected bee abundance to follow a similar trend in cornfields, as they are also highly disturbed habitats. However, I found that bee abundance in cornfields tends to decrease as the shapes in the landscape became more complex. A possible explanation for this result is that with greater landscape configurational heterogeneity, bees can more easily access other more favorable land classes. This may reduce abundance within cornfields even when landscape-level abundance remains unchanged. Bee abundance in pine plantations appears to slightly increase as patch shapes within the landscape become more complex, while bee abundance in natural longleaf forests seems to decrease with increasing shape complexity. Remnant forests may have different properties from mature pine plantations as the latter tends to be more recently disturbed and earlier in succession. Bees in a more natural environment may prefer less configurational heterogeneity, to maintain more continuous natural habitat. Configurational heterogeneity may be more important for bees in low-quality or disturbed local environments.

STUDY LIMITATIONS: As in all field studies, particularly those focused on landscape scales, there are a number of design and analysis trade-offs, some of which present important limitations to consider when interpreting our results. These include the level of landscape classification and temporal variation. I was unable to differentiate between pine plantation and natural forests in our classification of the landscape. A finer classification of the landscape may allow us to better understand the impacts of pine plantations on the landscape and the implications that may have for bee diversity. Additionally, my study was unable to account for temporal variation. My landscape characterization was based on data from 2011. Among other issues with this time lag, clearcut sites regenerate very quickly, so some of them may not have been cleared when the landscape data was collected. Hopefully, as research continues to move to understand ecological processes on a larger landscape scale and technology continues to advance, more current and finely characterized landscape data will become more available.

FUTURE WORK: My results underscore several areas in which future work is needed. There continues to be limited research on the effects of landscape context on bee diversity. Future research should address the limitations of my study, and explore the impacts of pine plantations on the landscape and the effects of temporal variation on bee communities. Future studies should explore the effects of landscape context on bee community composition (i.e., not just diversity and abundance), as community composition can significantly impact ecosystem processes (Tilman et al. 1997). To understand how we can increase biofuel cultivation while preserving bee biodiversity, we must consider beta-diversity (Karp et al. 2012). Studies have begun to document decreases in beta-diversity due to land use intensification (Karp et al. 2012). Future work also should explore how the interactions between local-level management and landscape context impact the community composition and beta-diversity. Diversity is essential to ecosystem resilience (Peterson et al. 1998), and we must understand the impacts of agricultural intensification so that we can best manage these biofuel production plantations and the landscape context in which they are placed.

CONCLUSION: Agricultural intensification is driving major landscape changes (Kareiva et al. 2007) and given the importance of maintaining biodiversity, we must understand how these changes will impact pollinators on both a local and landscape level. To meet our ever-increasing energy demands, biofuel cultivation will likely transform the southeastern United States. Intensified biofuel cultivation will cause changes to land use, and these changes will significantly impact bee communities. It is essential to maintain these bee communities to ensure resiliency of these ecosystems as well as food security. Management policies and guidelines must consider the landscape context in addition to the local-level management, and the interactive effects of these different spatial scales. The management of spatial heterogeneity of these biofuel cultivation landscapes is critical to the conservation of bee diversity. It is essential to understand how these land use changes will alter the landscape and impact bee diversity. Bees are continuing to decline (Potts et al. 2010), and we must slow, if not stop, their decline as we depend on these pollinators for more than one-third of the calories we consume (Eilers et al. 2011).

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Supplemental Table 1. AIC model selection for bee abundance. All models within two delta AICc points of the best model for landscape metrics at 500 m, 1000 m, 2000 m, and 5000 m.

500 m		**1000 m**		**2000 m**		**5000 m**	
AICc	delta	AICc	delta	AICc	delta	AICc	delta
716.372	0	711.791	0	709.539	0	726.335	0
717.813	1.441	711.894	0.102	711.060	1.521	726.401	0.065
718.269	1.896	711.974	0.182			727.804	1.469
		712.269	0.477			727.978	1.643
		713.382	1.590			728.010	1.674
		713.642	1.851			728.043	1.707
						728.188	1.853
						728.256	1.920
						728.273	1.938

Supplemental Table 2. AIC model selection for bee richness. All models within two delta AICc points of the best model for landscape metrics at 500 m, 1000 m, 2000 m, and 5000 m.

500 m		**1000 m**		**2000 m**		**5000 m**	
AICc	delta	AICc	delta	AICc	delta	AICc	delta
444.053	0	446.447	0	438.837	0	441.662	0
445.976	1.922	447.234	0.786	439.482	0.644	442.220	0.558
		447.551	1.103	439.504	0.667	442.351	0.688
		447.747	1.299	440.017	1.179	443.563	1.901
		448.036	1.588	440.123	1.286		
		448.235	1.787	440.158	1.320		
		448.303	1.855	440.781	1.943		

Supplemental Table 3. Mean ± standard error for each landscape metric at 2000m in each local management practice.

	Natural Forest	**Plantation Forest**	**Clearcut**	**Cornfield**
Percent Forest Cover (%)	52.1 ± 5.0	51.2 ± 3.0	55.0 ± 4.5	26.4 ± 3.1
Patch Richness (number of patch classes)	7.4 ± 0.266	7.659 ± 0.164	7.285 ± 0.156	8.428 ± 0.114
Shannon's Diversity Index	1.285 ± 0.068	1.188 ± 0.041	1.239 ± 0.075	1.468 ± 0.096
Aggregation Index (%)	80.472 ± 1.968	83.640 ± 0.598	84.346 ± 0.933	82.676 ± 1.233
Mean Shape Index (≥ 1)	1.986 ± 0.089	1.945 ± 0.040	1.943 ± 0.058	1.927 ± 0.043
Mean Patch Core Area (hectares)	1.66e+6 ± 2.64e+5	2.05e+6 ± 1.85e+5	2.20e+6 ± 2.17e+5	1.32e+6 ± 1.76e+5
Mean Effective Mesh Size (hectares)	2.90e+7 ± 1.10e+7	4.09e+7 ± 9.64e+6	2.60e+7 ± 1.29e+7	1.45e+7 ± 8.46e+6