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Implications of sea level rise for bee communities in rural eastern Virginia coastal habitats

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ABSTRACT: In the coastal mid-Atlantic region of the USA, landscapes are a mosaic of upland habitats (woodland, grassland, old fields and farmland) and low-lying coastal salt marsh. Flooding and salinization of coastal areas due to sea-level rise results in the conversion of upland habitats to salt marsh, and changes the relative proportion of habitat types surrounding coastal farmland. This has the potential to influence population sizes of organisms living in this area and could alter the ecosystem services, such as pollination, that these habitats provide. To examine the potential outcome of these habitat conversions, we used blue vane traps at 14 sites along the Eastern Shore of Virginia (USA) to compare the bee communities of salt marsh, old fields and agricultural fields. Although there was no difference among habitat types for total bee abundance per site, we found that the coastal marsh is depauperate in bee species relative to old fields and agricultural fields, and that the bee species using the marsh habitat tend to be specialists of plant families that are common in the marsh (Asteraceae and Malvaceae) but are relatively uncommon in local agriculture. Thus, the transition of upland areas to marsh not only has the potential to impact agricultural productivity directly through salt water intrusion, ultimately it may also may reduce the species richness of native bees available to provide pollination services to coastal agriculture.

Keywords: sea level rise, bees, salt marsh, agriculture, bee habitat, land cover change, abundance

Introduction

In the coastal mid-Atlantic region of the USA, landscapes are a mosaic of upland habitats (woodland, grassland, old fields and farmland) and low-lying coastal salt marsh, which together provide habitat for wildlife, including pollinators. This habitat mosaic, however, is undergoing rapid change. In this region, sea-level rise rates are 4.28-5.37 mm yr^{-1} (Mariotti et al. 2010, NOAA 2019), more rapid than anywhere along the US coastline except the Gulf Coast (2.13-9.65 mm y^{-1}, NOAA 2019). As a consequence of sea-level rise, mid-Atlantic upland habitats are converted to salt marsh vegetation when soils are flooded and salinized (Nicholls and Leatherman, 1995). In the Chesapeake Bay region, 400 km^2 have been converted from upland habitat to salt marsh since the beginning of the 19th century (Schieder *et al.*, 2018). Globally, agricultural lands are disproportionately exposed to projected sea-level rise effects (Feng *et al.*, 2018). For instance, on the Eastern Shore of Virginia in Accomack County, 20 ha of cropland is salinized and taken from cultivation each year to become old fields or high salt marsh (Titus *et al.*, 2009). Similar habitat conversions from farmland to old field or salt marsh are reported in coastal Maryland, USA (Epanchin-Niell *et al.*, 2016). The result is a proportional shift in habitat and soil types surrounding the coastal agricultural areas that remain, and this is likely to affect the populations of organisms living in those habitats, including some that contribute to agricultural productivity.

Wild bees contribute greatly to agriculture through pollination (Garibaldi *et al*., 2011; Winfree *et al*. 2008), but their populations frequently rely on quality habitat adjacent to agricultural lands rather than the agricultural lands themselves (Benjamin *et al*., 2014; Carvell *et al*., 2006; Kremen *et al*., 2007; Winfree *et al*., 2008). In light of recent declines in native bee populations, it is imperative to document their abundance and species richness in a variety of habitats to understand their current distribution across space and time and predict how their populations may change as habitats change (Harrison *et al*. 2018).

The increase in saltmarsh habitat due to sea level rise is likely to affect bee populations through a reduction in both floral resources and suitable nesting sites (Harrison *et al*. 2018). The saltmarsh plant community is dominated by five wind-pollinated grass species (Silberhorn and Harris, 1977) that likely provide little food to pollinators. Only a small, albeit persistent, proportion of the marsh community is composed of insect-pollinated plants, including *Aster tenuifolius* Nesom, *Sabatia stellaris* Pursh, *Limonium carolini anum* Britton, *Hibiscus moscheutos* L., *Kosteletzkya pentacarpos* Ledeb, and to a lesser extent *Atriplex patula* L. and *Atriplex arenaria* Nutt (Christian and Blum, 2017) (Table 1). While proportionally sparse, these plant species provide resources across the entire growing season. Like food resources, nesting opportunities may also be reduced in marsh habitat relative to upland. Periodic inundation with saline water (Elsey-Quirk *et al.*, 2011) is likely to prevent bees from successfully nesting in either the ground or plant stems unless the bees are adapted to live and forage in wet environments (Cane 1991; Cane *et al.*, 1996). Thus, the abundance and diversity of native bees in salt marshes may be less than in nearby old fields and agricultural fields where floral resources may be more diverse and suitable nesting sites more abundant.

Few studies have been carried out on native bees in saltmarsh habitats. Pojar (1973) examined pollination by *Bombus terricola occidentalis* (Grne) of saltmarsh plants in Vancouver Island, Canada. Zarillo and Stoner (2019) compared bee species richness of saltmarsh, beach dune and scrub habitat in an estuarine preserve in coastal Connecticut (USA), and found the saltmarsh relatively depauperate. In that study the fauna of the saltmarsh was only 78% as rich as the scrub and 63% as rich as the dune habitats.

The current study seeks to answer the question: How well does coastal marsh support native bee abundance and diversity relative to old fields and agricultural fields? We selected these three landcover (habitat) types because farmland (560 km^2) and salt marshes (460 km^2) represent the two largest landcover types in coastal Virginia's Accomack and Northampton counties (https://coast.noaa.gov/ccapatlas/), and because old fields (56 km^2) have more diverse plant communities than other land cover types (Table 1). The motivation for asking this question is that reduction in bee abundance and diversity during conversion of old fields to salt marsh might be detrimental to maintenance of bee species diversity in local upland habitat and to the productivity of nearby farmland that relies on native bees for pollination (Kremen and M'Gonigle, 2015). We hypothesized that native bee abundance and diversity would be lowest in high salt marsh habitat compared to agricultural fields or old fields. We further hypothesized that the abundance and diversity of native bees will be greater in old fields than in agricultural fields.

Materials and methods

Study Sites and Sampling Methods

We carried out sampling from July 11th to August 5th, 2016. The study included 14 field sites along the Eastern Shore of Virginia, USA. Potential field sites were identified first on a map of the peninsula, selected based on accessibility and having a land cover type classified as either agricultural, old field, or high marsh. All sites were at least 600 m apart, which limited the possibility of the same bees moving between study sites (Greenleaf *et al.*, 2007). In the end, five high marsh sites, five old field sites, and four agricultural sites, including corn, tomato, melon, and soybean fields, were selected within a 100-kilometer stretch of land (Fig. 1).

In each field, one blue vane trap (SpringStar Inc., Woodinville, WA, USA) was hung from PVC pipe at vegetation height (approximately 45-63cm above soil), and filled with a 1:1 (vol:vol) mixture of water and propylene glycol (Buchanan *et al.*, 2017). The traps were placed as far from wooded areas, roads, and walkways as possible. Each blue vane trap was sampled every seven days for four weeks (once each in the weeks of July 11th, July 18th, July 25th, and August 1st), resulting in a total of four samples from each site. The content of the blue vane traps was strained and placed in whirl pack plastic bags with 70% ethanol solution, and placed on ice for return to the laboratory. In the laboratory, samples were frozen at -20 °C until they were processed. Processing comprised straining the contents of each sample bag through a fine mesh strainer, washing the contents with warm water and soap to remove residual propylene glycol and ethanol, and rinsing thoroughly with tap water. A blow dryer was used to dry specimens for pinning and identification. Of all bee specimens captured, 6026 were identified to species, 211 *Lasioglossum* (subgenus Dialictus, Family Halictidae) individuals were identified to subgenus, and 35 specimens of *Andrena, Ceratina, Melissodes, Agapostemon,* and *Megachile* were in too poor a condition to identify beyond genus. An additional 67 specimens could not be identified to genus. Reference specimens for the study are deposited in the insect collection of the University of Virginia's field station at Blandy Experimental Farm.

Statistical Analysis

The four weekly samples per site were pooled and treated as a single collection for analyses. For all analyses except total bee abundance, data were limited to specimens identified to species. Spatial autocorrelation in community composition was tested using a mantel test comparing the Pearson correlation coefficient of the community dissimilarity matrix for all sites with a site by distance matrix using the function mantel in the VEGAN package in R (Oksanen *et al.*, 2018). Finding no spatial autocorrelation (p=0.796), analysis of variance was used to compare the mean number of specimens among habitats (species abundance), diversity (Shannon's H'), and equitability (Shannon's E_H) among the three habitat types. When a difference was found, a post-hoc Tukey's test was run to determine which habitat types differed from each other. Because bee species richness was not normally distributed, a Kruskal Wallis one-way ANOVA test on ranks was run, followed by a Dunn's post-hoc test to determine habitat main effects.

Species diversity for each sample location was calculated as:

$$H' = -\sum_{S=1}^{S} p_i \cdot \ln p_i$$

Where H' = species diversity; S = total number of species, i = proportion of total number of species; and p_i = total number of species. This index, Shannon's H, accounts for both abundance and evenness of the species present (Pielou, 1984; Beals et al., 1999).

Species equitability (evenness) for each sample location was calculated as:

$$E_H = \frac{H'}{\ln(S)}$$

Where E_H = equitability, H' = Shannon's diversity, and S = total number of species (i.e., H_{max}), and equitability assumes a value between 0 and 1 with 1 being complete evenness (Pielou, 1984; Beals et al. 1999).

In addition to comparing realized species richness among habitats using the pooled samples within sites, we compared species accumulation curves for the habitats. Species accumulation curves were drawn using the 'specaccum' function in the R package VEGAN. The "random" method was used for choosing the order in which replicates were drawn. The sites of each habitat type were treated as replicates for habitat type in drawing the accumulation curve.

Non-metric multidimensional scaling was used to compare species composition among habitat types. We used the ‘metaMDS’ function in the R package VEGAN to plot Bray-Curtis dissimilarities among communities. Based on stress values for goodness of fit, we reduced the overall dataset to 3 dimensions for representation (stress value=0.115). The degree of separation among community types was estimated using the function 'vegdist' to calculate a community dissimilarity matrix and the function ‘anosim’ to test for a significant difference among community types.

The proportion of all individuals captured in each habitat that were pollen specialists was compared using a one-way analysis of variance following confirmation of data normality. This test was carried out because the main floral sources used by pollinators in the marsh belong to two plant families (Asteraceae and Malvaceae) that are known to be visited extensively by specialist bee species and could host a disproportionately specialist insect fauna. Specialization was determined for all identified species using Krombein *et al.* (1979) and checked with ecological literature on individual species (Rust, 1980; Cane 2017; LaBerge 1961). The proportion of individuals that were stem nesters in each habitat was compared using a one-way analysis of variance following a log transformation to normalize the dependent variable. This test was carried out because the nesting substrate in the marsh least likely to be affected by inundation is the upper portion of plant stems. Nesting habit was determined for all identified species following Krombein (1967), Michener (2000), and McCravy et al. (2019).

Results

In four weeks of sampling, 6339 specimens (6026 identified to species) were collected in blue vane traps across the 14 field sites (Table 2). The marsh samples contained a total of 28 bee species from 1480 specimens, while farms and old fields contained 37 and 39 species from 2457 and 2402 specimens, respectively. Bee species richness was lower in marsh sites than farm field sites (Kruskal-Wallace statistic H=2.851, p=0.013), but there were no detectable significant difference among habitats in abundance, diversity, or evenness (Fig. 2).

Using species accumulation curves rather than simple comparisons of detected species, the marsh habitats added species at a much slower rate than the farm and old field habitats and showed some evidence of reaching a plateau after only five sites (Figure 3). The 95% confidence levels were distinct between the marsh habitat and the other habitats after only three collections, while there was no separation in species accumulation curves between the farm and old field habitats. No attempt was made to extrapolate total species richness per habitat type given the lack of a plateau in accumulation rates in the farm and old field samples.

Species composition by site clustered significantly by habitat type (anosim statistic R=0.289, p=0.028), with the old field community overlapping both (Figure 4). The most dominant species in the farm fields were *Agapostemon virescens* Fabricius (821 specimens), *Ptilothrix bombiformis* Cresson (562), *Melissodes bimaculatus* Lepeletier (395), *Bombus impatiens* Cresson (111), and *Bombus griseocollis* DeGeer (68). The dominant species in the old fields were *A. virescens* (625), *P. bombiformis* (616), *M. bimaculatus* (386), *Ceratina dupla* Say (177), and *Svastra obliqua* Say (99). The dominant species in the marshes were *P. bombiformis* (971), *M. bimaculatus* (83), *Melissodes comptoides* Robertson (82), *C. dupla* (41), *B. impatiens* (34), and *Svastra obliqua* Say (51).

The proportion of each community that consisted of individuals from specialist species varied across habitat types (F=4.119, p=0.046). More than two thirds of the individuals sampled from high marsh sites were specialist species, while just a third of individuals collected from agricultural and old field sites were specialists (Fig. 5). The most abundant specialist species overall was *P. bombiformis*, which collects pollen only from Malvaceae (Rust, 1980). It accounted for nearly 70% of all samples in high marsh sites, 23% of agricultural field samples, and 27% of old field samples. Other prominent specialists included two that specialize on Asteraceae (*Svastra obliqua* and *Melissodes trinodis* Robertson) which together accounted for 4.8% of marsh individuals, 4.9% of old field individuals and 1.1% of farm individuals. The only other prominent specialist was the *Cucurbita* specialist *Peponapis pruinosa* Say, which occurred almost exclusively on farm and old field sites. There was not a significant difference among habitats in the proportion of stem nesting individuals (F=1.946, p=0.189, Fig. 6). Stem nesting individuals comprised three species of the genus *Ceratina* (*C. calcarata* Robertson, *C. dupla* and *C. floridana* Mitchell), as well as *Hylaeus ornatus* Mitchell. Over 97% of bees captured in each habitat nest primarily in the ground, either as ground excavators or ground cavity nesters (bumble bees).

Discussion

The summer bee fauna of the high salt marsh of eastern Virginia is depauperate relative to old field and agricultural areas (Fig. 2 & Fig. 3). Its composition is also distinct from that of agricultural areas (Fig. 4), a difference generated primarily by abundant specialist species that find their host plants among marsh vegetation. The most abundant bee in the marsh habitat, *Ptilothrix bombiformis*, is a specialist pollen collector of plants in the Malvaceae. Although it has a prominent floral host in the marsh (the seaside mallow, *Kosteletzkya pentacarpos*), it has few common hosts in old fields or agricultural land. The only agricultural plants in that family grown commonly in North America are cotton and okra, both of which are grown commercially, but not widely, in this region (https://www.nass.usda.gov/AgCensus/FAQ/2017/index.php). However, cotton was grown adjacent to the tomato field sampled in this study. Because *P. bombiformis* builds its nests underground, its prominence in collections from the old field and agricultural sites where cotton is not grown likely reflects its foraging commute from inland nesting areas to foraging areas in the marsh. The other prominent specialist bee species in the marsh, (*Melissodes trinodis* and *Svastra obliqua*) collect pollen primarily from Asteraceae. The Asteraceae are well represented in old field habitat but are not commonly cultivated as crop plants in this area (Table 1). These bees also are ground-nesting species that are likely nesting inland and foraging in the marshes. Thus, rather than the natural habitat of the marsh subsidizing pollinator services of coastal agricultural areas, it may be that old fields and undisturbed areas within agriculture are subsidizing marsh pollination by providing dry nesting substrate in upland areas. If plants such as cotton and sunflowers were commonly grown as crops in the region, then the specialist pollinators found in the marsh would likely play a stronger role in local agriculture.

Coastal marsh is likely a poor habitat for pollinators to overwinter in the soil, due to winter-time flooding during which standing water is always present. There may be potential for emergent plant stems in the marsh to serve as reliable nesting substrate if they remain above the level of the water year-round. In this study, however, there was not a disproportionate amount (as proportion or simple abundance) of stem nesting bees in the marsh habitat relative to old fields and agricultural sites. If the bees foraging in the marsh primarily nested there as well, then we should have detected an overabundance of stem nesters.

Our finding that bee species richness is lower in saltmarsh than in adjacent habitats is similar to Zarrillo and Stoner (2019), who compared saltmarsh to beach dune and scrub habitats. Although that study captured more species in saltmarsh (40) than were found in the current study (28), that study took place over two years instead of one and over a longer portion of the growing season (April - September) than the current study (July - August). It also used two capture methods (pan traps and targeted net collecting), which are known to be complementary (Wilson *et al.*, 2008), instead of the one used in this study. A distinct difference between the two studies is that pollen specialists were rarely encountered by Zarrillo and Stoner (representing 3 out of 3928 individuals), while they represented between one third and two thirds of all specimens collected in the current study, depending on habitat. Two of the most prominent specialists in the current study (*P. bombiformis* and *Svastra obliqua*) have distributions primarily south of Connecticut (Mitchell, 1962) and those species were not encountered in that study. The one specialist encountered in both studies, *Melissodes trinodis*, was not prominent in the other study but it also was not considered a specialist in that study, despite it being considered one by Laberge (1961).

Sea level rise will likely change the relationship between land cover types as coastal systems are forced to move inland or be submerged when the ecosystem can no longer adapt to increased inundation (Schieder *et al.*, 2018). As agricultural land is abandoned to old field and, in turn, old fields transition to high salt marsh, the boundaries between habitat types and the proportion of upland to marsh area will change. Changes in land cover patterns are contextual and difficult to predict, but marsh extent has persisted over the last century in the Chesapeake Bay, as upland farm fields, old fields, and forests transition to salt marsh (Schieder *et al.*, 2018). These changes in land cover patterns have the potential to reduce plant diversity at marsh-upland boundaries as marsh plants replace upland vegetation due to soil salinization and inundation (Fagherazzi *et al.*, 2019) thereby reducing the proportion of land suitable for ground nesting bees.

Our focus on native bee abundance and diversity is a first step towards understanding how potential changes in the coastal landscape influence the relationship between habitat types in providing agricultural pollination services in the mid-Atlantic region and how changes in native bee communities might impact local economies. Various studies have shown that unmanaged native bees frequently make important contributions to agriculture, as they can be both more numerous than honey bees in agricultural fields and more effective as pollinators of certain crops (Garibaldi *et al.*, 2011; Julier and Roulston, 2009; Winfree *et al.* 2008). Environments that offer diverse floral resources and abundant high-quality nesting sites are associated with high native bee abundance and species richness (Kremen *et al*., 2007), and farm fields closer to more natural habitat cover tend to receive more pollination services, indicating that the surrounding habitats provide essential resources to native pollinators (Benjamin *et al*., 2014; Winfree *et al*., 2008). Not all unmanaged habitats, however, are likely to contribute equally to maintaining pollinator populations that contribute to agriculture. Habitats supporting highly specialized, low diversity, low abundance bee communities may be less likely to provide suitable pollinators to agricultural crops. For instance, extensive deciduous forests in eastern North America support less diverse and abundant bee populations than agricultural, suburban and urban landscapes (Winfree *et al*., 2007a), and may make smaller agricultural contributions as they occupy larger proportions of the landscape. We find that saltmarsh, which forms an extensive habitat type in coastal regions, may similarly support a relatively narrow portion of the regional bee fauna.

Overall, our study indicates that in the coastal region of eastern Virginia, in areas where sea level rise results in the conversion of old field and agricultural habitats into high salt marsh, the availability of pollinators to the adjacent, unconverted habitats will likely be reduced due to a reduction in nesting substrate and by the presence of forage that serves mainly to attract bees that are scant contributors to agricultural systems.

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Table 1. Plant species of farm fields, salt marshes, and old fields in Accomack and Northampton counties on the Eastern Shore of Virginia. Species listed for a habitat type were not necessarily found in all replicates of that habitat type. *Distichlis spicata* (L.) Greene, *Juniperus virginiana* L., *Phragmities australis* (Cananilles) Trinius Ex Steudel, and *Sporobolus pumilus* (Roth) P.M. Peterson & Saarela were the only species that were common between the salt marsh and old field habitats. Superscripts indicate species with synonymous names. Weed species are not listed for the farm fields because suppression of weeds for these crops stringent (cultivation, pesticides, and black plastic mulch).

Farm Field

Cucurbita pepo L.
Glycine max (L.) Merr.
Gossypium sp. L.
Solanum lycopersicum L.
Zea mays L.

Salt Marsh

Aster tenuifolius L.[1]
Atriplex arenaria Nutt[2]
Atriplex patula L.

Borrichia frutescens (L.) A.P. deCandolle
Cyperus esculentus L.
Distichlis spicata (L.) Greene
Fimbristulis spadicea (L.) Vahl
Hibiscus moscheutos L.
Iva frutescents L.
Juncus gerardii Loisel.
Juncus roemerianus Scheele
Juniperus virginiana L.
Kosteltzkya pentacarpos L.
Limonium carolianum (Walter) Britton
Myrica cerifera L.[3]
Phragmities australis (Cananilles) Trinius Ex Steudel
Pluchea odorata (L.) Cassini
Sabatia stellaris Pursh
Salicornia bigelovii Torrey

Old Field

Acer rubrum L.
Ambrosia artemislifolia L.
Apocynum cannabinum L.
Asclepias incarnate L.
Asclepias tuberosa L.
Aster pilosus Willd.[7]
Baccharis halimifolia L.
Campsis radicans L.
Celtis occidentalis L.
Chamaecrista fasciculata (Fernald) C.F. Reed
Distichlis spicata (L.) Greene
Diospyros virginiana L.
Duchesnea indica (Andr.) Focke
Eupatorium capillifolium (Lamarck) Small
Ilex opaca Aiton
Ipomoea hederacea Jacq.
Ipomoea lacunose L.
Juniperus virginiana L.
Ligustrum sinense (Loureiro)
Liquidambar styraciflua L.
Lonicera sempervirens L.
Melothria pendula L.
Morus rubra L.
Myrica cerifera L.[3]
Nyssa sylvatica Marshall
Oxalis stricta L.
Panicum virgatum L.

Salicornia virginica L.	*Parthenocissus quinquefolia* (L.) Planch.
Sarcocornia pacifica Standl.	*Phragmities australis* (Cananilles) Trinius Ex Steudel
Satatia stellaris Pursh	*Phytolacca americana* L.
Schoenoplectus americanus Persoon	*Pinus taeda* L.
Setaria geniculata (Wild.) P. Beauv., nom. Illeg.	*Prunus serotina* Ehrhart
Sporobolus alterniflorus (Loisel.) P.M. Peterson & Saarela[5]	*Quercus sp.* L.
	Rosa multiflora (Rehder & E.H. Wilson) L.H. Bailey[8]
Sporobolus pumilus (Roth) P.M. Peterson & Saarela[6]	*Rubus cuneifolius* Pursh
	Rubus strigosus (Michx.) Focke
Typha sp.(L.)	*Setaria parviflora* (Poiret) Kerguélen
	Smilax rotundifolia L.
	*Solidago sp.*L.
	Sporobolus pumilus (Roth) P.M. Peterson & Saarela[6]
	Toxicodendron radicans L.
	Traxacum officinale F.H. Wigg
	Vicia angustifolia L. ex Reichard
	Vitis rotundifolia Michx,
	Vitis sp. L.
	Xanthium strumarium L.

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[1] *Symphyotrichum tenuifolium* (L.) G.L. Nesom

[2] *Atriplex mucronate* Raf

[3] *Morella cerifera* L.

[4] *Setaria parviflora* (Poir.) Kerguélen5

[5] *Spartina alterniflora* Loisel.

[6] *Spartina patens* Roth

[7] *Symphyotrichum pilosum* (Willd.) Nesom

[8] *Rosa cathayensis* ((Rehder & E.H. Wilson) L.H. Bailey

Table 2. Identity and abundance of bee species captured in three habitats sampled.

	No. of Specimens		
Species	**Farm Fields**	**Old Fields**	**Salt marshes**
Agapostemon sericeus (Forster)	5	2	3
Agapostemon splendens (Lepeletier)	55	14	2
Agapostemon virescens (Fabricius)	821	625	21
Apis mellifera Linnaeus	39	7	3
Augochlora pura (Say)	3	3	5
Augochlorella aurata (Smith)	5	6	21
Augochloropsis metallica metallica (Fabricius)	0	0	1
Bombus bimaculatus Cresson	14	27	8
Bombus fervidus (Fabricius)	0	1	0
Bombus griseocollis (De Geer)	68	31	7
Bombus impatiens Cresson	111	56	34
Bombus pensylvanicus (De Geer)	5	13	6
Ceratina calcarata Robertson	8	53	25
Ceratina dupla Say	32	177	41
Ceratina floridiana Mitchell	1	4	1
Halictus ligatus Say	15	40	1
Halictus parallelus Say	1	1	0
Halictus rubicundus (Christ)	2	2	2
Hylaeus ornatus Mitchell	1	1	0
Lasioglossum bruneri (Crawford)	7	5	1
Lasioglossum callidum (Sandhouse)	0	2	2
Lasioglossum forbesii (Robertson)	4	11	0
Lasioglossum hitchensi Gibbs	0	1	0
Lasioglossum imitatum (Smith)	1	1	0
Lasioglossum oblongum (Lovell)	3	2	3
Lasioglossum pectoral (Smith)	1	1	0
Lasioglossum pilosum (Smith)	36	1	0
Lasioglossum tegulare (Robertson)	1	1	0
Lasioglossum versatum (Robertson)	1	0	0
Lasioglossum zephyrum (Smith)	0	1	0
Megachile campanulae (Robertson)	5	0	1
Megachile exilis Cresson	1	0	0
Megachile mendica Cresson	2	0	0
Megachile sculpturalis Smith	0	1	0
Megachile texana Cresson	0	1	0
Melissodes bimaculatus (Lepeletier)	395	386	83
Melissodes comptoides Robertson	55	40	82
Melissodes nr *communis*	4	0	0
Melissodes trinodis Robertson	12	18	20
Peponapis pruinose (Say)	36	21	3

Ptilothrix bombiformis Cresson	562	616	971
Svastra atripes (Cresson)	2	3	8
Svastra obliqua Say	15	99	51
Xylocopa virginica (Linnaeus)	4	7	6
TOTAL SPECIMENS	**2337**	**2281**	**1412**
TOTAL No. of SPECIES	**37**	**39**	**28**

List of Figures

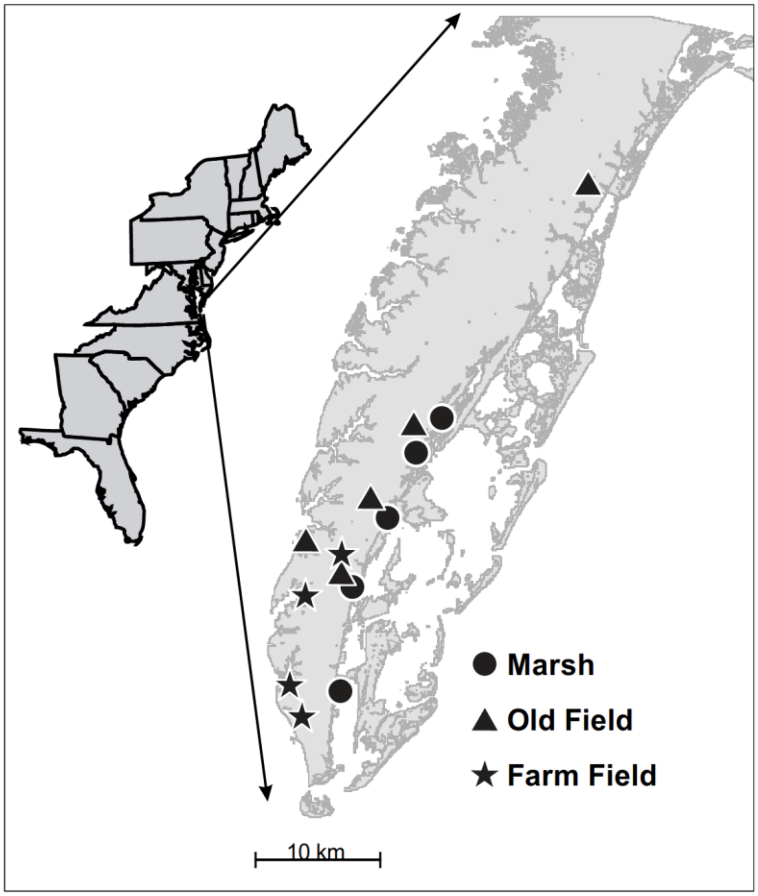
Figure 1. Upland and marshes are shaded in grey in maps of the Eastern US Atlantic Coast (upper left) and the Eastern Shore of Virginia. Three habitat types were sampled at fourteen locations total, indicated on the map of the lower Delmarva Peninsula (Eastern Shore of Virginia). A total of four agricultural sites, five old fields, and five high salt marsh sites along the mainland of the Eastern Shore sampled in this study are shown by symbols; agricultural sites are represented by stars, old fields by triangles, and marshes by circles.

Figure 2. Comparison of bee samples collected by blue vane trap across habitat types. A. Number of specimens captured in each habitat type. B. Number of species collected in each habitat type. Bars not sharing letters are statistically different from each other. C. Species diversity in each habitat type. D. Equitability of bee species in each habitat type. Number of replicates was four farm fields, and five marshes and old fields. Error bars are one standard error of the mean.

Figure 3. Species accumulation curves for total species richness per habitat type in farm field (n = 4 sites), old field (n = 5) and marsh (n = 5). Error bars are 95% confidence intervals.

Figure 4. NMDS plot showing bee community similarity across habitat types. Red crosses represent individual species, circles represent individual sites, and ovals represent habitat type.

Figure 5. Proportion of bee communities that are specialists, by habitat type



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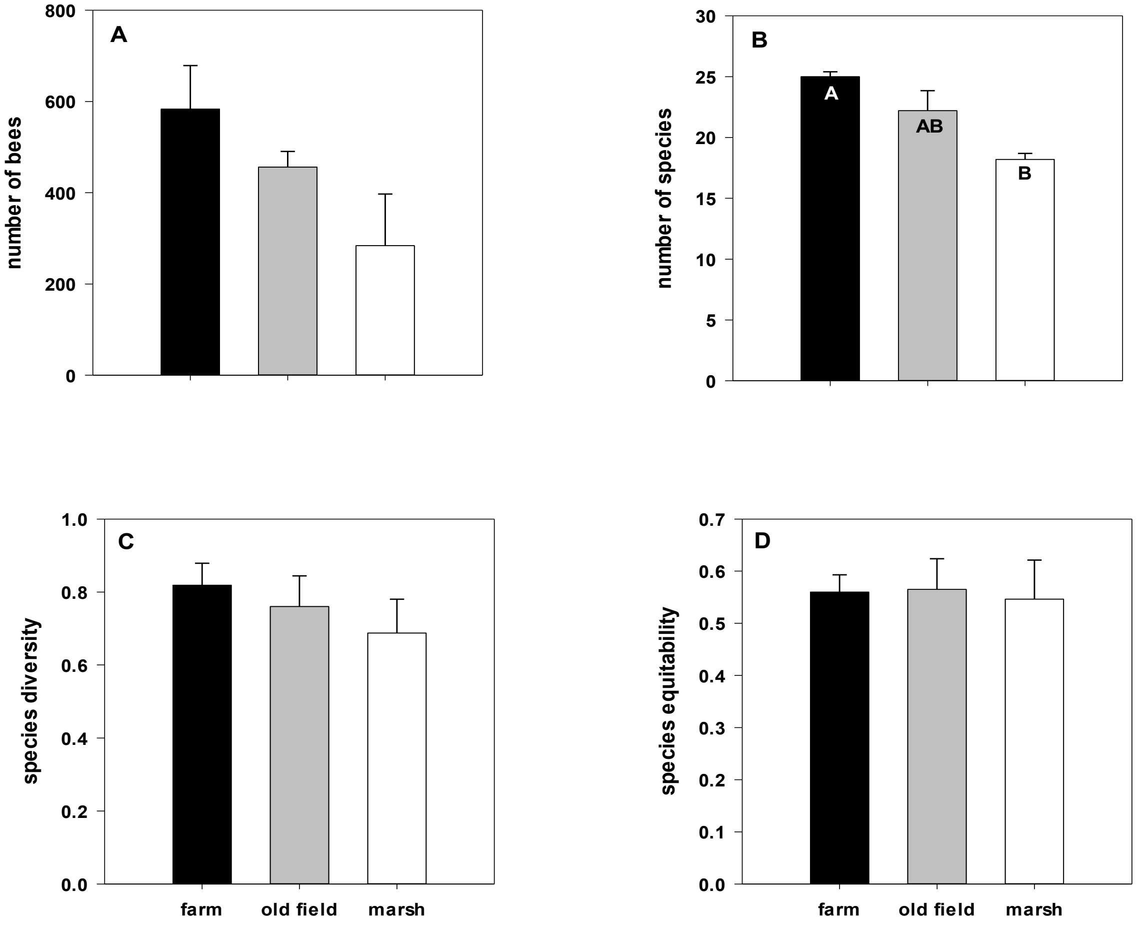

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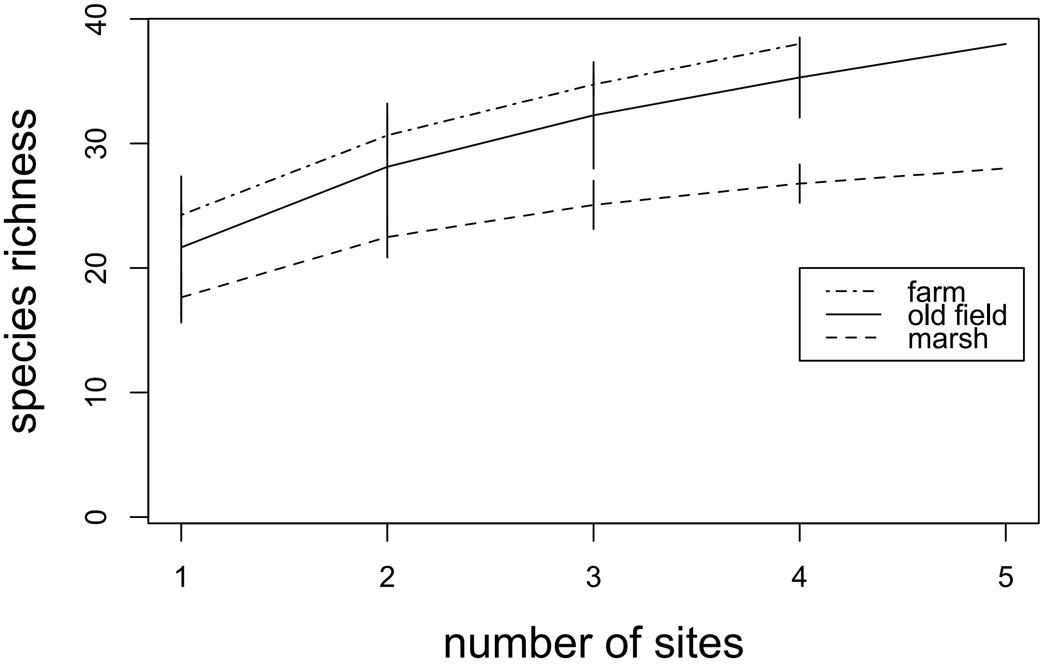

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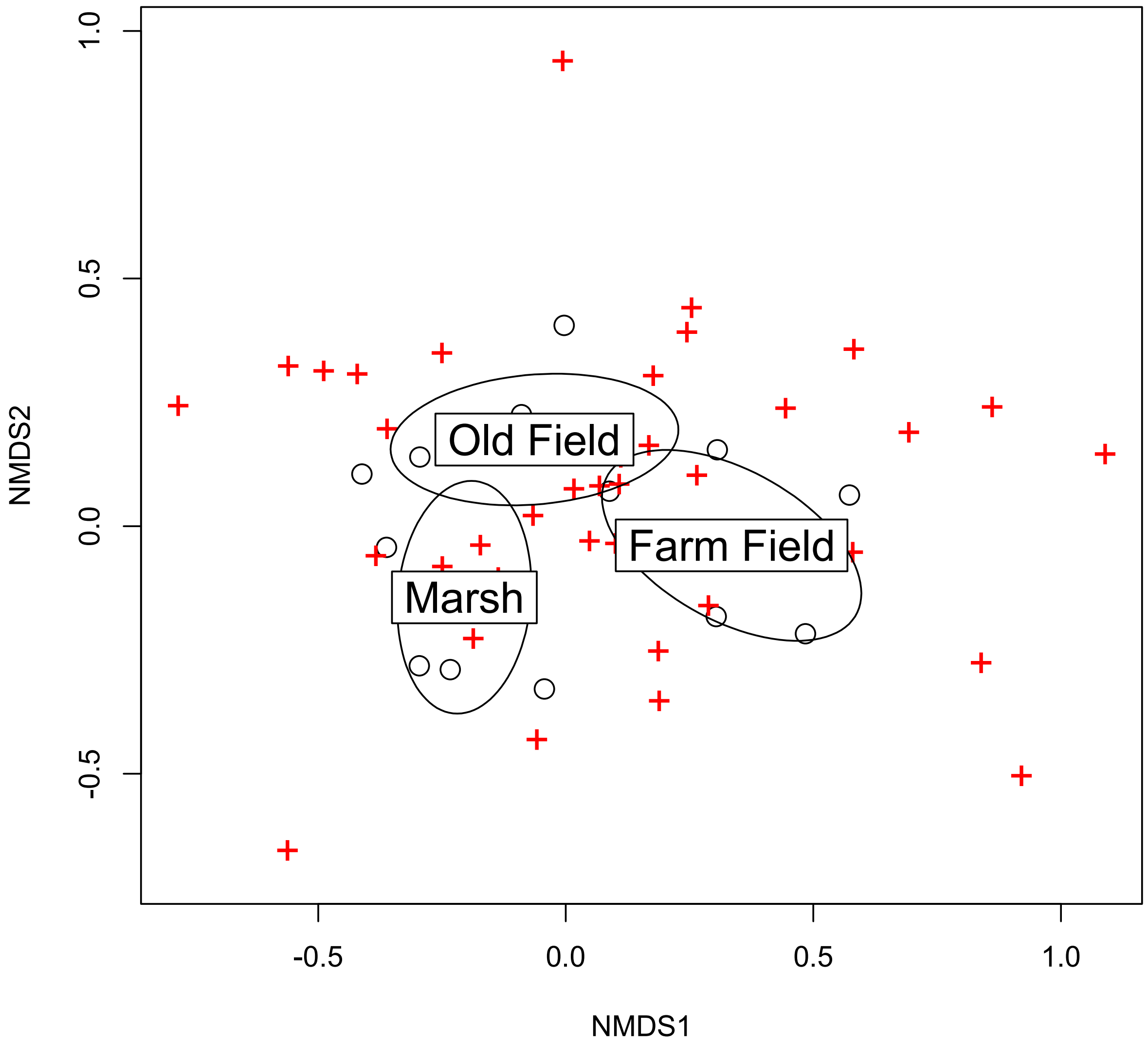

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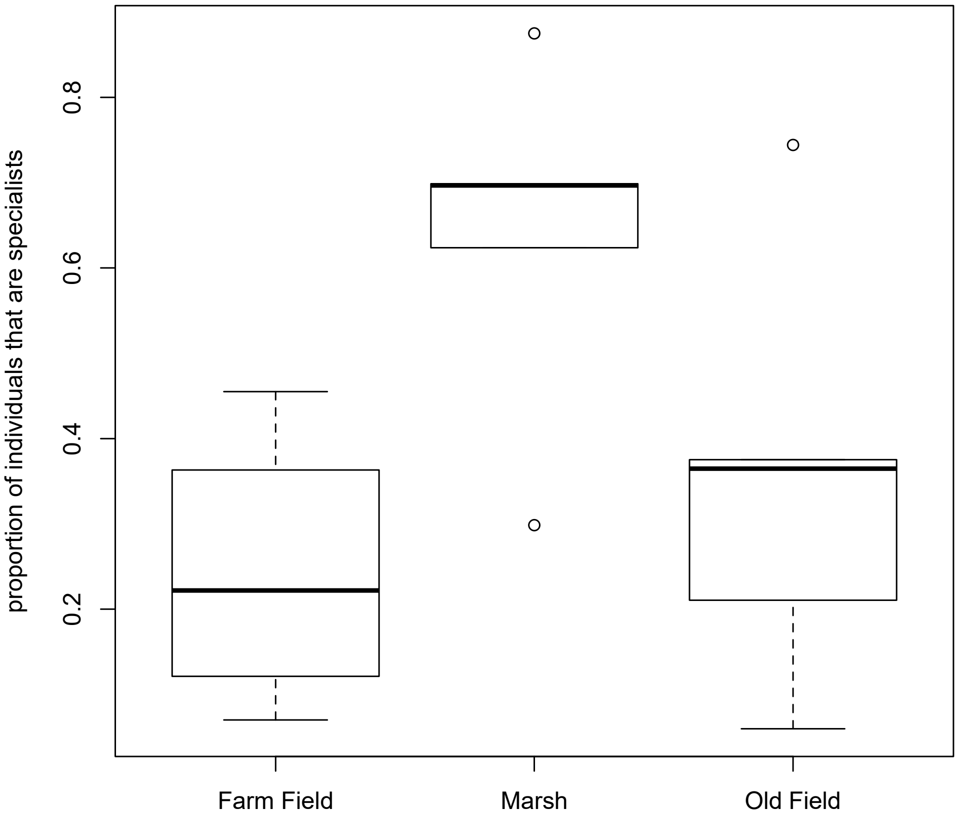


Figure 5. Proportion of bee communities that are specialists, by habitat type

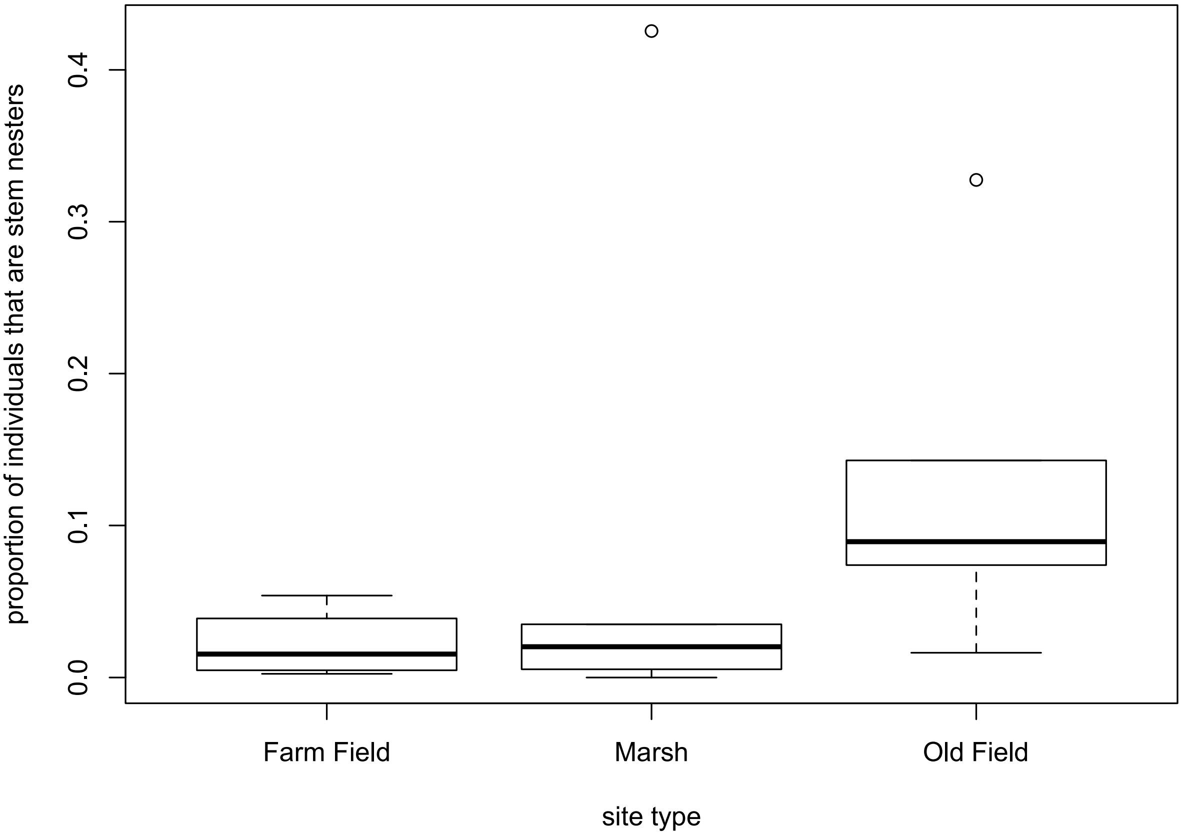
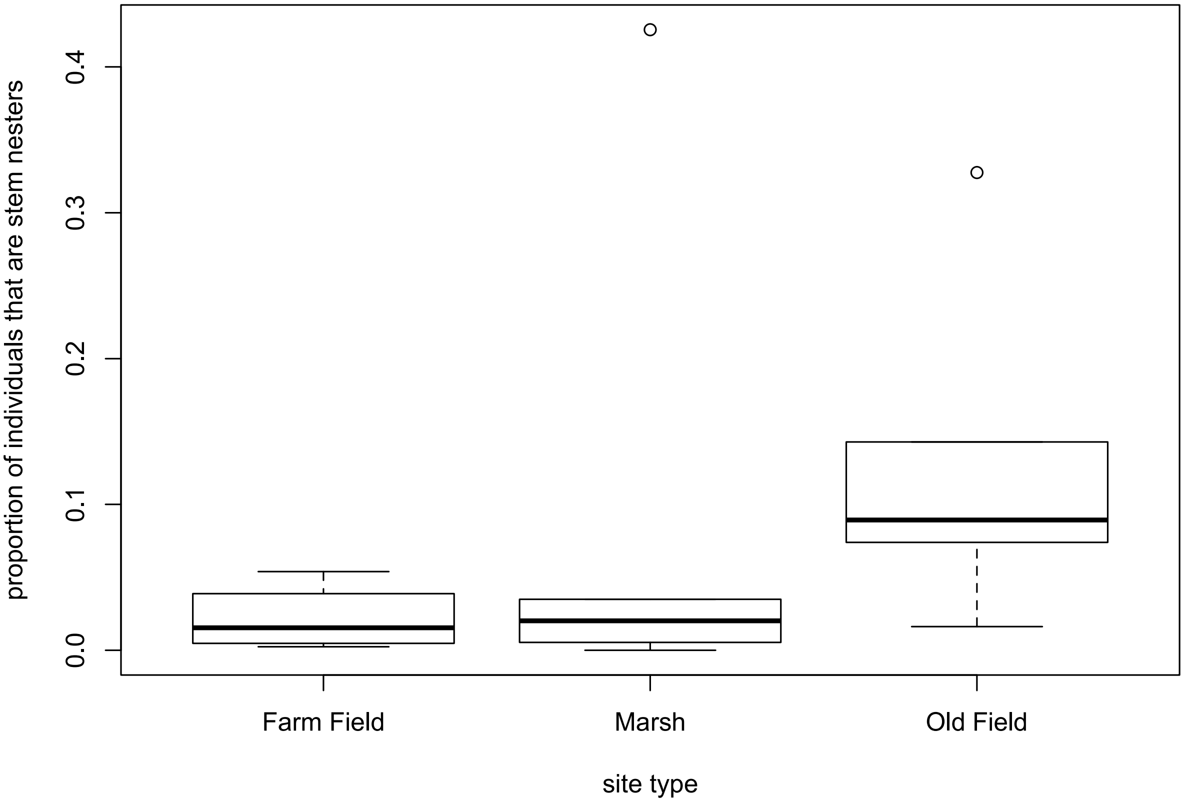


Figure 6. Proportion of bee communities that nest in herbaceous stems.



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