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The effects of land use change on ant communities in New England

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Abstract

1. Urbanisation and agricultural expansion are two of the most prevalent and intense forms of land use change worldwide and can have dramatic consequences on biodiversity and biotic community structure.

2. Ants are extremely widespread, ecologically diverse and small ectotherms that are sensitive to changes from a wide range of environmental factors. Therefore, ants make an ideal study organism to examine the effects of anthropogenic land use change on biotic communities.

3. In this study, we examined differences in ant species richness and community composition between urban parks, farms and forest fragments, and related these differences to environmental factors that vary among each of these three habitat types.

4. We sampled 46 sites across Worcester County and found farms have significantly lower ant species richness than parks, and all habitat types had different ant community compositions. We also identified higher plant species richness is associated with higher ant species richness, and both plant species richness and air temperature are associated with differences in community composition.

5. Our findings support that habitats affected by human land use will host different assemblages of ant species compared to those found in nearby natural habitats, as seen in our New England forest fragments.

KEYWORDS
agroecosystems, ant communities, ant–plant interactions, forest fragments, species richness

INTRODUCTION

Urbanisation is one of the most severe and long-lasting forms of human land use change globally and will only continue to grow (Gao & O'Neill, 2020; Wagner et al., 2021). Habitat loss and fragmentation, decreased vegetation, decreased wind speed and increased land coverage of impervious surfaces, all contribute to increases in temperatures in urban spaces (i.e., the urban heat island; Cui & Shi, 2012; Kotze et al., 2011). These changes can result in reduced species richness and altered community composition within urban habitats when compared to less disturbed areas. However, urban green spaces, like urban parks and gardens, can be critical to maintaining species richness and communities within urban areas (Gaston et al., 2005; Koh & Sodhi, 2004; McDonnell & MacGregor-Fors, 2016).

Agricultural land covers approximately a third of the earth's habitable surface and has been expanding for the past three centuries (Ramankutty et al., 2018). Global land use change has progressed at a rate four times greater than previously estimated, with 17% of terrestrial land changing uses between 1960 and 2019 being attributed to agricultural disturbance (Winkler et al., 2021). Within this 17%, there has been a global net loss of 0.8 million km^2 of forest and agricultural land use has increased by 2 million km^2. Furthermore, agriculture is

associated with habitat destruction, the introduction of exotic species, loss of biodiversity, increased carbon output and contamination of air, soil and water (Ojima et al., 1994; Ramankutty et al., 2018).

Many arthropod communities, given their sensitivity to environmental factors and quick generation times, can provide valuable insight into the ecological impacts of land use (Chowdhury et al., 2023; Kotze et al., 2011). Urbanisation has been found to overall decrease the diversity and abundance of terrestrial arthropods and homogenise arthropod communities (Fenoglio et al., 2020; Kotze et al., 2011). The loss of arthropod biodiversity has the potential to have serious ecological consequences, as these organisms provide many essential ecosystem services such as pollination, nutrient cycling, biological pest control and decomposition (Fenoglio et al., 2020). Ants were our primary study organism, as they are ecologically diverse, provide a wide variety of ecosystem services and make up an astoundingly large amount of the earth's biomass (Schultheiss et al., 2022). Despite their abundance, ants are not immune to the global decline in insect diversity currently being caused by a wide range of human-mediated stressors, including urbanisation and agricultural disturbance (Del Toro et al., 2015; Wagner et al., 2021).

In New England, more than 350,000 ha of forest cover has been lost since 1985, reversing a 200-year trend of forest expansion, concentrated in suburban areas surrounding major cities (Olofsson et al., 2016; Thompson & McLachlan, 2007). Meanwhile, there has been little movement from urban and agricultural land back to forest in this same time frame (Olofsson et al., 2016; Thompson & McLachlan, 2007). In Northeastern temperate forests, ants play a role in seed dispersal, soil aeration, nutrient cycling and nitrogen availability through activities such as building subterranean nests and foraging in the leaf litter (Del Toro et al., 2012; Warren et al., 2021).

Anthropogenic land use can significantly disrupt ecosystem services provided by ants, as ants are sensitive to changes in temperature, humidity and soil compaction (Sanford et al., 2009). Furthermore, changes in plant community structure can have a profound effect on ant community composition (Ellison et al., 2005; Grevé et al., 2018). Human impacts on environments, such as urbanisation, habitat fragmentation and conversion to agricultural land and pastures, have been shown to decrease ant biodiversity (de Queiroz et al., 2020; Gómez et al., 2003) or at least significantly alter community composition (Cuautle et al., 2016). In areas where habitats have been disturbed or destroyed through anthropogenic land use, the ant community becomes dominated by generalist ant species, while less disturbed habitats foster an ant community with more specialist ant species (Buczkowski & Richmond, 2012; Cuautle et al., 2016; Uno et al., 2010). Additionally, because many exotic ant species tend to be opportunistic generalists, disturbed environments show an increased presence of non-native ant species, such as the tramp ant *Tetramorium caespitum* (Linnaeus 1758) (Buczkowski & Richmond, 2012). Furthermore, *T. caespitum* along with the native *Tapinoma sessile* (Say 1836) are considered to be urban exploiters, an ecological category of ant characterised by its reliance on human disturbance for food and shelter (Buczkowski & Bennett, 2008; Meissner & Silverman, 2001).

The dominance of introduced generalist species can lead to biotic homogenisation, which can lead to a loss of functional diversity. This loss in diversity can in turn lead to decreased community function and weakened ecosystem resilience (Olden et al., 2004).

To assess the effects that urbanisation has on ant assemblages, we focused on several environmental factors that are pertinent in shaping ant community structure. For example, high temperature can accelerate brood development and ant activity (Challet et al., 2005; Porter & Tschinkel, 1993). While these increases can be beneficial, they also create higher energy demand for the colony (Brian, 1973; Coenen-Stass et al., 1980). In New England forests, ant species have been found to vary significantly in their thermal tolerance (Oberg et al., 2011). Ants with the lowest thermal tolerance are most sensitive to abiotic environmental changes, and therefore, most vulnerable to local extinctions (Wittman et al., 2010). Knowing the presence and absence of different species will provide insight into how ant communities are changing in response to urbanisation, the UHI effect and agricultural expansion. We also investigated how factors like canopy cover, the presence and size of trees and plant species richness affect the structure of ant communities in New England. Forest succession impacts the structure of ant communities, as trees facilitate microclimates, affect leaf litter composition, temperature and humidity (Anderson & Toro, 2021). Soil compaction and soil temperature may also be impactful, as many species of ants in New England are ground nesting (Ellison et al., 2017).

In this study, we examined the effects of land use change on ant community structure and biodiversity by collecting ants and environmental data from forests, farms and urban parks around central Massachusetts. The objective of this study is to determine (1) how ant species richness and community composition differ between rural, urban and agricultural habitats and (2) what environmental variables may explain these differences. Broadly, we hypothesise that the disturbed urban and agricultural habitats will show a decreased level of species richness and an altered community composition when compared to rural/undisturbed habitats (McKinney, 2008). Furthermore, due to the complexity of how disturbance can impact species richness (Fox, 2013), we hypothesise that we will find relationships between ant species richness and the environmental variables that shape these habitats.

MATERIALS AND METHODS

Ant diversity and species richness survey

New England (the Northeastern United States) contains 30 genera of ants and at least 132 species (Ellison et al., 2017). To assess the effects of land use on ant species composition, we surveyed farms, forests and urban parks in central Massachusetts from June to October 2021 (Figure S1). Fifteen sites were selected for farm and forest habitat types, and 16 sites were selected for urban parks (n = 46) (Table S1). Forest fragments were primarily mixed hardwood forests between 4 and 267 ha in size. Urban Parks sites were between

3 and 32 ha, all of which contained a large open field for recreational use. We selected agricultural sites by contacting local farmers of pick-your-own orchards and small produce farms, which were between 0.5 and 101 ha (Table S1). We did not perform a longitudinal study of land use change, but instead used forest fragments to represent rural/undisturbed habitats. Urban parks and farms were considered as habitat types already having undergone the process of land use change.

During each survey, 200 m straight transects were placed by dividing a map of the area into a grid and using a random number generator to select where the transect began. In sites that were too small for this method to be practical, the transects were placed where they could fit best, with a preference for where they would be less likely to be disturbed, or at the discretion of the farmer. In cases where the 200 m transect could not be straight and continuous, which occurred primarily in urban parks and agricultural sites, the transect was modified into an 'L' shape or placed in two parallel shorter transects approximately 20 m apart from each other. We then created 10×10 m quadrats every 20 m along the transect. This sampling structure was modelled after similar studies (de Queiroz et al., 2020; Gotelli et al., 2011; Solar et al., 2016).

We used three collection methods (similar to Sabu et al., 2011) to obtain a representative sample of the ant community at each site. We placed pitfall traps in the centre of each quadrat, which consisted of a 118 mL plastic container filled approximately halfway with water, 2–3 g of salt and a drop of dish soap. A paper plate was propped above each pitfall to protect them from precipitation. We also placed two baited traps, using 1.5 mL microcentrifuge tubes containing either honey or tuna to a tree or shrub nearest to the centre of each quadrat at approximately chest height. Lastly, we sampled leaf litter ants by placing a 50×50 cm frame in the centre of the quadrat, gathered the leaf litter and organic detritus inside of it and extracted the arthropods over 48 h using a Berlese funnel (Sabu et al., 2011).

To investigate which environmental factors drive community differences, we installed iButtons (iButtonLink, USA) near each pitfall trap to measure ambient temperature and relative humidity. Additionally, we measured the soil temperature of each quadrat with a digital thermometer (ThermaPro, USA) and soil compaction with a penetrometer. To investigate the relationship between plant and ant communities, we measured plant species richness, tree diameter at breast height (DBH), tree abundance (when DBH was >7 cm) and canopy cover within each quadrat. Plant species richness was performed by counting morphospecies of vascular plants in the field. Mean ambient temperature, humidity, soil temperature, soil compaction, canopy cover, plant species richness per quadrat abundance of trees per quadrat and DBH of trees per quadrat were calculated for each site.

Statistical analyses

We calculated species richness using all of the above-described sampling methods to ensure an accurate measurement of the ants in these habitats. Due to the large number of predictor variables collected, we first categorised variables into groups (vegetation variables and environmental variables), then tested for multicollinearity using Pearson's correlation to identify any correlated variables within the groups and selected variables for our analysis (Philpott et al., 2020). When variables were correlated, we chose to include only one within our analysis. We also included variables that were not correlated with any other variables. Based on the Pearson's correlations, we included plant species richness, soil compaction, soil temperature, air temperature, canopy cover and mean DBH in our analysis and removed humidity and tree count (Table S2). We then ran a linear model using the 'aov' function in base R (R Core Team, 2021) with habitat type coded as a categorical fixed effect, while our environmental factors were included as continuous fixed effects. Because correlation coefficients are pairwise comparisons, we ensured that there was no remaining collinearity within our model by checking the variance inflation factor (VIF) in the model using the *vif* function in the *car* package version 3.0-12 (Fox & Weisberg, 2011; Philpott et al., 2020). We found canopy cover was collinear with other variables. We then removed this variable from our global model where all remaining VIF scores were below 2.9 (Table S3). When significant differences were found between location types in a model, we performed Tukey's post hoc tests using the 'TukeyHSD' function in R. The final model utilised the response variables of habitat type, air temperature, soil temperature, soil compaction, plant species richness and mean DBH. Finally, to ensure that the differences observed throughout these results were not caused by geographic variation, we conducted mantel test.

To examine whether ant community composition differs by habitat type, we performed a non-parametric multidimensional scaling (NMDS) analysis (in the *vegan* package in R, Oksanen et al., 2022), a non-parametric ordination technique that iteratively locates positions on the axes to minimise the stress of the configuration (Kruskal, 1964; McCune & Grace, 2002). For this analysis, we used the presence/absence of ant species within each site. We then created ordination plots using Jaccard distance metrics in two dimensions for the presence/absence data set. To compare the differences in ant community composition using habitat type, plant species richness and air temperature as response variables, we performed a permutational analysis of variance (PERMANOVA) in the *vegan* package in R with the adonis2 function using the Jaccard method for the presence/absence data and 10,000 permutations (Martinez Arbizu, 2020). All analysis were performed in R (4.2.1; R Core Team, 2021).

RESULTS

We collected a total of 5487 ants, including 61 individual species from 46 sites (Table S2 and S4). The most common species we found in forests were *Aphaenogaster picea* (Wheeler 1908), *Camponotus nearcticus* (Emery 1893), *Camponotus pennsylvanicus* (De Geer 1773), *Formica neogagates* (Viereck 1903) and *Lasius alienus* (Foerster 1850) (Table S4). The most common species we found in farms were *Prenolepis imparis* (Say 1836), *T. caespitum*, *L. alienus* and *F. neogagates* (Table S4). The most common species we found in urban parks were *T. caspitum*, *L. alienus*, *Myrmica detritinodis* (Emery 1921), *F. neogagates* and *C. pennsylvannicus* (Table S4).

We found ant species richness varied significantly based on habitat type ($p = 0.004$; Table 1 and Figure 1a). In particular, farms have significantly lower ant species richness than parks ($p = 0.003$; Table S5) and had nearly significantly lower ant species richness compared to forests ($p = 0.052$; Table S5). Ant species richness was not different when comparing forests and parks ($p = 0.587$; Table S5). Furthermore, we found that increased plant species predicted ant species richness ($F = 6.659$, $p = 0.014$; Table 1, Figure 1b). Our mantel test for species richness was non-significant (observation $= -0.025$, $p = 0.559$), indicating that site proximity did not predict ant species richness.

Our multidimensional scaling ordination revealed that the ant community composition of forests and parks do not overlap, while forests and farm habitats overlap very little (Figure 2). We also found that the ant community composition of parks is nested within the farm habitats. Additionally, we found that the ant communities differ significantly by habitat type ($F = 4.076$, $p < 0.0001$; Table 2 and

Figure 2). Post hoc tests demonstrate that community composition of each habitat type was different from the others in the study ($p < 0.0007$; Table S6). We also found that ant communities differ significantly based on plant species richness ($R^2 = 0.034$, $p = 0.021$; Table 2) and air temperature ($R^2 = 0.030$, $p = 0.040$; Table 2).

DISCUSSION

Overall, we found that land use type does have a significant effect on ant species richness, with farm habitats having a lower species richness than parks. Furthermore, our NMDS analysis demonstrated that ant species composition differs based on habitat type but also provided us with an interesting result in that park communities appear to be a subset of the species that exist in farms.

While we do not see that forests have a significantly higher species richness than human-mediated habitat types (Figure 1a), all three habitat types have a very distinct community composition (Table 2). Indeed, the forest ant community overlaps far less with the park and farm ant communities than they do with each other (Figure 2). This demonstrates that land use change from forest to human-mediated environments like urban parks and farms causes a homogenisation of the ant community, and that in urban areas, there is a subset of ants that are excluded from park habitats that can normally thrive in farm habitats. Additionally, the ant communities in park and farm habitat types both demonstrated a similar response to anthropogenic land use change, moving in the same direction from the forest habitat community (Figure 2). Farm and park ant communities both have a greater presence of the exotic urban exploiter *T. caespitum* ants that have been known to pose a significant danger as an invasive species (Ellison et al., 2017; Wetterer, 2011). Concerningly, *Myrmica rubra*

TABLE 1 Generalised Linear Model results comparing species richness of the combined sampling methods and the environmental variables recorded.

	Df	Sum Sq	F value	Pr(>F)
Habitat type	**2**	**145.45**	**6.494**	**0.004**
Air temperature	1	14.37	1.283	0.265
Soil temperature	1	1.26	0.113	0.739
Soil compaction	1	0.05	0.004	0.947
Plant species richness	**1**	**74.58**	**6.659**	**0.014**
Mean diameter at breast height	1	25.16	2.246	0.142

Note: Significant relationships are bolded.
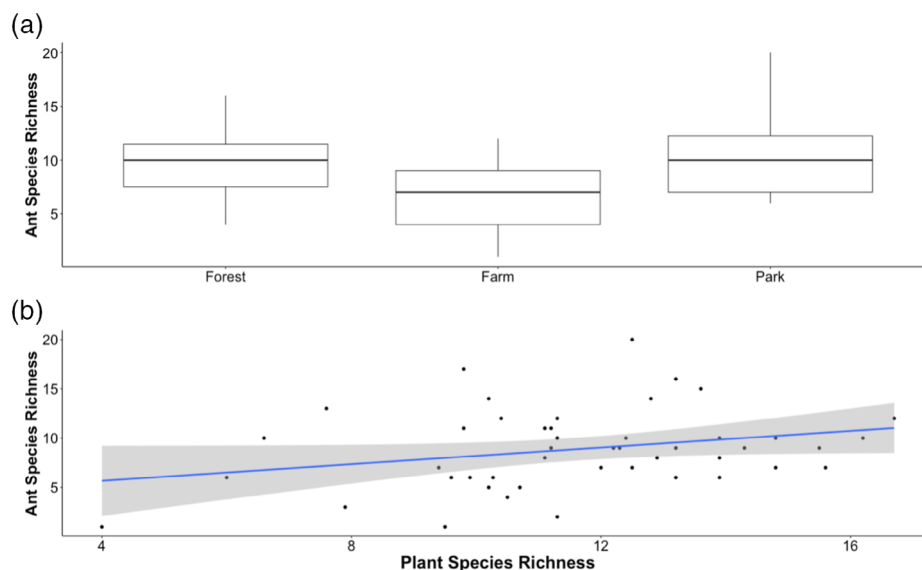
FIGURE 1 (a) Boxplot displaying the median and interquartile range of the species richness of ants collected from. Error bars denote minimum and maximum of the quartile range, and bold line represents the median. Dots represent outliers. (b) Scatterplot demonstrating the relationship between species richness and plant species richness.

was found in all habitat types, with the highest presence in forests. *Myrmica rubra* is the most aggressive ant invasive species found in New England, with wide-reaching deleterious ecological impacts on the invertebrate community, is even capable of killing small mammals (Garnas, 2004) and negatively affecting the growth rates of ground-nesting birds (DeFisher & Bonter, 2013).

Many of the species that characterised the forest community, such as *A. picea*, *C. nearcticus* and *Myrmecina americana* (Emery 1895), are known to nest in forest habitats (Ellison et al., 2017). Additionally, acorn nesting ants, such as *Temnothorax curvispinosus* (Mayr 1866), and leaf litter ants, such as *Stenamma diecki* (Emery 1895) and *Stigmatomma pallipes* (Haldeman 1844), were exclusively found in forests. This highlights the ecological niches that trees provide for ants through creating leaf litter and nesting sites in the leaf litter itself, acorns and loose bark.
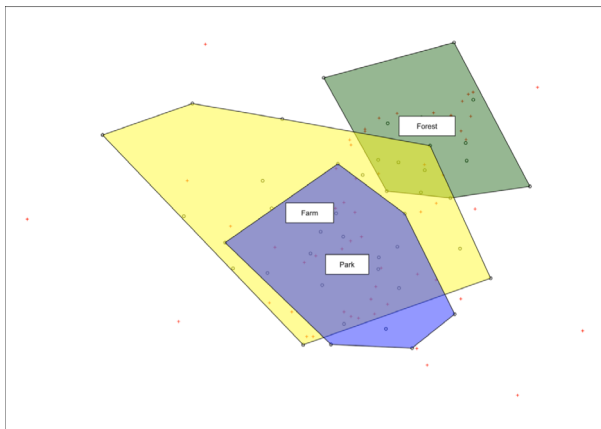
Across the environmental factors investigated, plant species richness showed the strongest effect on ant species richness. We found ant and plant species richness to be positively correlated. Plant biodiversity has been shown to have a positive relationship to arthropod diversity and a stabilising effect on food webs (Haddad et al., 2009, 2011). In the context of our sites, those that had a higher number of plant morphotypes likely provided a wider array of ecological niches for ants, allowing for more ant species to exist in an area. Indeed, plant species richness also explains differences in community composition within our study. This highlights the importance of promoting biodiversity in human-managed habitats, which has indeed been shown to benefit to insect communities (Egerer & Philpott, 2022). Air temperature was another factor that explains differences in ant community composition, indicating that ant assemblages can experience impacts from small changes in microclimates at a local scale. As a result, urban and agricultural areas may be at higher risk of experiencing greater damage to their biodiversity within the context of climate change.

Whether it be urbanisation or agricultural development, areas affected by human land use lead to lower organismal diversity (Wagner et al., 2021). Plant diversity was found to be the most influential factor in differences in ant species richness, thus the effect land use change has on the relationship between plant and ant communities should be further studied. *Myrmica rubra* is a growing concern in New England, and while it was most common in our forest sites, this invasive ant was also present in the farms and parks we surveyed. Therefore, it is important to continue to monitor *M. rubra* populations and the native ants it may be displacing, as well as learn more about the environmental factors associated with human land use that may facilitate or hinder their dispersal. Overall, the more we learn about the impacts of anthropogenic land use on arthropod communities and the subsequent impacts on ecosystem services, the better prepared we will be to face future challenges like climate change, deforestation and human food security.

FIGURE 2 Plot of Non-metric multidimensional scaling (NMDS) ordination of presence/absence data. Species are red crosses, and locations are black circles. Blue (park), green (forest) and yellow (farm) polygon overlays represent the three different habitat types. Stress = 0.2.

AUTHOR CONTRIBUTIONS

Amelia K. L. Curry: Conceptualization (equal); Methodology (equal); Investigation (lead); Writing – Original Draft Preparation (lead). **Joseph A. Nelsen**: Investigation (supporting); Writing – Original Draft Preparation (supporting). **Dale R. Stevens**: Formal Analysis (lead), Writing – Original Draft Preparation (supporting); Writing – Review & Editing

TABLE 2 PERMANOVA results for the model comparing ant species presence/absence data and habitat type, plant species richness and air temperature.

	Df	Sum Sq	R^2	F	Pr(>F)
Habitat type	**2**	**2.385**	**0.158**	**4.076**	**<0.001**
Air temperature	**1**	**0.474**	**0.031**	**1.621**	**0.040**
Soil temperature	1	0.369	0.024	1.261	0.170
Soil compaction	1	0.323	0.021	1.105	0.307
Plant species richness	**1**	**0.515**	**0.034**	**1.759**	**0.021**
Mean diameter at breast height	1	0.237	0.016	0.810	0.718
Residual	37	10.827	0.716		
Total	44	15.131	1		

Note: Significant results are bolded.

CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad at https://doi.org/10.5061/dryad.9ghx3ffn9.

ETHICS STATEMENT

There was no approval or permitting necessary to conduct this work.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Study sites for each land use type treatment.

Table S2. Results of Pearson's correlation analysis (Pearson's r), using the variables air temperature, humidity, soil temperature, soil compaction, tree count, plant species richness and mean tree diameter at breast height (DBH). Significant correlations are marked with asterisks*.

Table S3. Variance inflation factor (VIF) results of linear models. Significant results are bolded.

Table S4. Frequency of species presence in combined sampling locations per habitat type (i.e., a species present in 6/15 parks sampled would have a value of 0.4). Top five highest values are bolded.

Table S5. Tukey's post hoc tests comparing species richness by location type. Significant results are bolded.

Table S6. Permutation post hoc tests comparing species abundance of each of our three habitat types.

Figure S1. Map of the locations of all study sites, primarily within Worcester County, Massachusetts. Forest fragments are marked in grey triangles, urban parks are marked in black diamonds and agricultural sites are marked in white circles.