



RESEARCH ARTICLE

Accounting for connectivity alters the apparent roles of spatial and environmental processes on metacommunity assembly

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Abstract

Context Understanding the relative contributions of spatial and environmental processes on community assembly is a central question in ecology. Despite this long-standing interest, our understanding of how landscape structure may drive spatial processes of community assembly remains poorly understood in part because of the challenge of tracking community assembly across landscapes and quantifying key aspects of landscapes that may impact assembly processes.

Objectives We examined the roles of spatial and environmental processes on structuring assemblies of ants in 72 cleared patches embedded within a forested landscape.

Methods To examine the role of spatial processes, we contrasted the use of geographic distances between patches and effective distances estimated from connectivity modeling accounting for matrix vegetation structure hypothesized to be important for ant community assembly. To examine the role of environmental processes, we quantified patch age and

abundance of a key competitor and invasive species, the fire ant *Solenopsis invicta*.

Results We found evidence for the importance of both spatial and environmental processes in structuring ant communities. When spatial processes were quantified as geographic distance, environmental variables were the predominant factors accounting for variation in ant community dissimilarity among patches. However, accounting for matrix resistance with circuit-theoretic connectivity modeling resulted in higher accounting of variation in ant community dissimilarity than geographic distance and changed the predominant variables accounting for that variation from environmental to spatial processes.

Conclusions These findings show that accounting for connectivity through the matrix can be decisive in determining the primary drivers of community assembly.

Keywords Community ecology · Community assembly · Formicidae · Beta diversity · Matrix · Generalized dissimilarity modeling

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Introduction

Communities assemble through a combination of processes that occur at different scales (Leibold et al. 2004; Vellend 2010). Understanding the contributions

of these processes in shaping communities at different spatial scales is a central question in ecology (Leibold et al. 2004; Logue et al. 2011). In particular, determining the relative importance of spatial and environmental processes in community assembly is a matter of widespread interest and deliberation (Cottenie 2005). However, the apparent roles of spatial and environmental processes in community assembly may hinge on how variables are quantified. While spatial processes in community assembly are often quantified as geographic isolation (Cottenie 2005), the growing understanding of the role of the importance of the matrix in mediating connectivity (Fletcher et al. 2016) suggests that geographic isolation alone may often be insufficient for quantifying the role of this process. Moreover, whether or not the resistance of the matrix is accounted for may change the interpretation of the relative contribution of spatial and environmental processes in community assembly (Biswas and Wagner 2012).

Ecologists have long recognized the importance of spatial processes in community assembly—for example, the pattern that isolation of patches influences the diversity and distribution of species (MacArthur and Wilson 1967; Hanski 1994). The role of the matrix surrounding patches has been emphasized for its influence on connectivity among patches (Ricketts 2001), which in turn plays an important role in species occurrence and community structure (Wiens 1997; Prugh et al. 2008; Minor et al. 2009). Increased connectivity among patches allows for greater rates of colonization of patches and allows immigration to offset extinction events (Damschen et al. 2019). Accounting for connectivity by modeling the role of matrix landcover on potential flows across the landscape can be important for providing better estimates of isolation (and conversely of connectivity) than geographic isolation alone (McRae and Beier 2007; Watling et al. 2011). Thus, dispersal processes, potentially mediated by landscape connectivity, set the template for the species that can occur in a given patch.

Community assembly is further constrained by environmental processes that “filter” (select for or against) species in local communities (Poff 1997; Vellend 2010; Germain et al. 2018). These processes are often separated into environmental characteristics (or scenopoetic factors; e.g., vegetation structure) and biotic interactions (bionomic factors; e.g., competitive

exclusion; Connell 1961; Tilman 1977; Hutchinson 1978; Vellend 2016). However, as environmental processes can interact in complex ways, the contributions of environmental characteristics and biotic components in structuring local communities can be challenging to separate (Kraft et al. 2015; Cadotte and Tucker 2017).

We examined the spatial and environmental processes influencing species turnover in assemblies of ants from 72 cleared patches embedded within a forested landscape in South Carolina, USA (Fig. 1). This dynamic landscape, consisting of a patchwork of intermittently created cleared patches that subsequently undergo regeneration within a mostly forested matrix, provides a useful setting for examining community assembly. Ants are an ideal taxon for examining the drivers of community assembly in this system for two primary reasons. The first reason is that patch openness is a key driver of local variation in ant communities (Puntila et al. 1991; Underwood and Fisher 2006; Andersen 2019). Therefore, we predicted that age since the clearing of patches would be an important determinant of ant species composition given that patch openness is dynamic as forest cover regenerates through natural succession and growth of planted trees over time. We also predicted that accounting for openness in matrix connectivity would better account for species dissimilarity among patches than geographic distance alone. Although ants disperse by flying, sometimes at heights higher than a forest canopy (Markin et al. 1971; Helms 2018), the openness of the matrix may direct the flight and landing behavior of queens (Dhami and Booth 2008; King and Tschinkel 2016). Matrix openness is also relevant for the colonization of patches as open gaps and linear elements (e.g., power-line corridors) in the matrix provide suitable nest sites for ants that inhabit unforested areas. The second reason that ants are an ideal taxon for examining the drivers of community assembly in this system is that interspecific competition, particularly with dominant species, is considered key in structuring local ant communities (though the strength of this is context-dependent; Hölldobler and Wilson 1990; LeBrun et al. 2012; Cerdá et al. 2013; Parr and Gibb 2010; Gibb et al. 2019). Dominant invasive ants are often particularly strong drivers of ant community change (Williams 1994; Holway et al. 2002; Sanders et al. 2003). In the southeastern United States, the fire ant *Solenopsis invicta* is an invasive

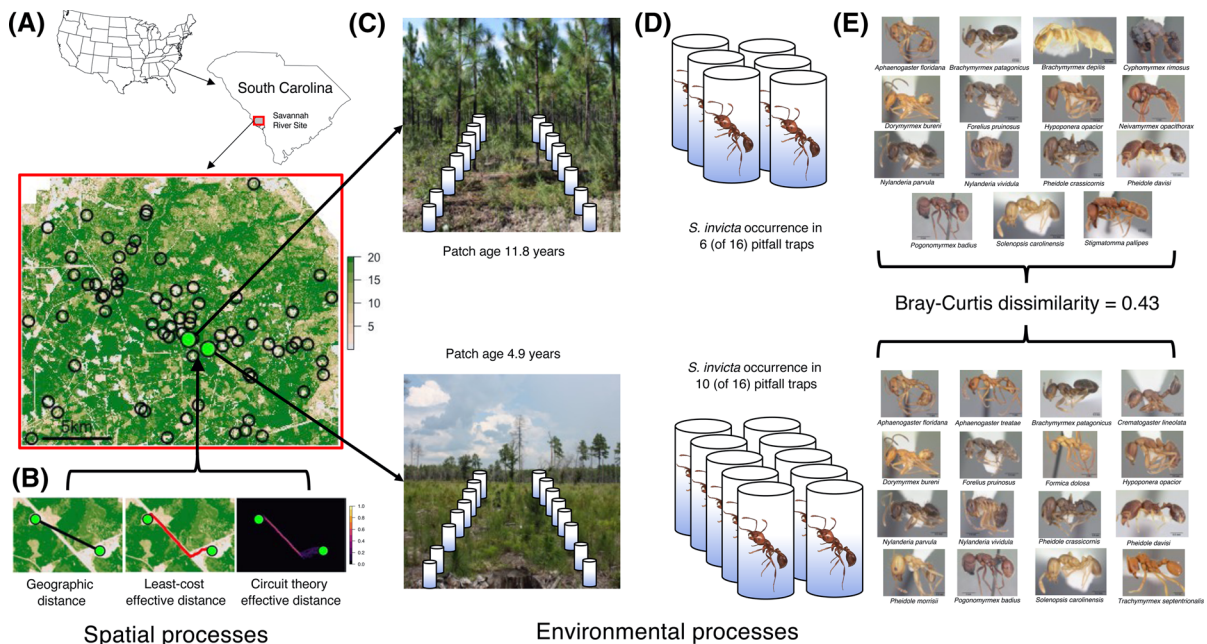


Fig. 1 Overview depiction of this study showing **a** the study's geographic location at the Savannah River Site, SC, USA including the spatial extent of the study area (box in red) and 72 sampling sites (circles). Color scale of the map represents vegetation height in meters from a LiDAR-derived raster. Facility and water surfaces are generally inhospitable and are assigned the maximum raster value of 20 m to represent high resistance. Two example sites are marked as green dots and are used to illustrate spatial and environmental processes. **b** Spatial processes quantifying isolation (or conversely connectivity) were geographic, least-cost, and circuit theory effective distances. Here an open power-line corridor appears to be

species that is dominant in open areas and is thought to be an important driver of changes in ant species composition (Porter and Savignano 1990; Gotelli and Arnett 2000; LeBrun et al. 2012; Resasco et al. 2014; but see King and Tschinkel 2006, 2008, 2013; Stuble et al. 2013). We, therefore, predicted that *S. invicta* abundance would be an important biotic determinant of local ant community structure.

To determine if accounting for connectivity alters the apparent roles of spatial and environmental processes on ant metacommunity assembly, we contrasted geographic distances between patches and effective distances estimated from connectivity modeling accounting for matrix vegetation structure hypothesized to be important for ant community assembly. To test the roles of spatial processes on shaping ant communities, we tested the relationship between species turnover (beta-diversity) between

providing connectivity between the sites through the forested matrix. **c–d** Environmental processes quantified are: **c** vegetation structure as patch age (time since timber clearing; photo credit, Julian Resasco) **d** fire ant (*Solenopsis invicta*) abundance, calculated as pitfall trap incidence, depicted by the number of pitfall traps corresponding to occupied pitfall traps out of 16 for each of the example sites. (E) Photographs of ant assemblages in the two example sites with species dissimilarity between them calculated with the Bray–Curtis index. Photographs of ants are from the California Academy of Science's AntWeb (www.antweb.org; photo credit, April Nobile; accessed March 2020)

each pair of the 72 sites and distance measures quantifying isolation. We had three hypotheses. First, we hypothesized that (hypothesis 1a) dispersal would be a constraining factor in community structure such that geographic distances between sites should be positively associated with pairwise community dissimilarity. Moreover, (hypothesis 1b) the openness of the matrix between patches would be important for structuring assemblages such that accounting for vegetation structure (using LiDAR-derived canopy height) with resistance-based connectivity should be more strongly associated with community dissimilarity than geographic distance. To test the roles of environmental processes on shaping ant communities, we tested the relationship between species turnover between sites and both measures of vegetation structure and *S. invicta* abundance (controlling for spatial dependence). Second, we hypothesized that vegetation

structure would be a constraining factor in ant community structure (hypothesis 2), such that differences in the time since clearing between pairs of patches should be positively associated with pairwise species dissimilarity. Our last hypothesis (hypothesis 3) was that biotic interactions would be a constraining factor in community structure, such that differences in *S. invicta* abundance between pairs of sites should be positively associated with pairwise species dissimilarity.

Material and methods

Study area

This study was conducted at the United States Department of Energy's Savannah River Site, a National Environmental Research Park. The Savannah River Site (33° 18' N, 81° 37' W) is approximately 80,000 ha in area and is located on the Upper Coastal Plain and Sandhills physiographic provinces of South Carolina (Fig. 1a). Most of the Savannah River Site is forested (93%) with pine plantation, mixed pine-hardwood forest, or hardwood forest (Kilgo and Blake 2005; Parresol et al. 2017). The United States Department of Agriculture (USDA) Forest Service manages the natural resources of the Savannah River Site (Kilgo and Blake 2005). Timber harvest operations of mature forest stands create a patchwork of open and regenerating patches in this otherwise forested matrix.

Ant collection and data

In the summer of 2009, we collected ants at 72 early successional patches that had recently been cleared for timber harvest across the northern and central portions of the Savannah River Site (Fig. 1a–b). Patches were selected using USDA Forest Service at Savannah River timber stand management maps. Patches varied in time since timber harvest ranging from a few months to over a decade in age (Fig. 1c). At each patch, 16 total pitfall traps were placed along two transects 20 m apart (8 pitfall traps per transect). To control for edge effects from varied patch shapes and sizes (Vasconcelos et al. 2006), we ran transects along a randomly selected edge abutting mature forest and aligned them toward the center of the patch. Pitfall

traps were set at 0, 10, 20, 40, 60, 80, 100, and 120 m along the transects. Pitfalls traps were 15-dram, 28.6-mm inner diameter plastic vials (Thornton plastics; <http://www.thorntonplastics.com/>), 1/3 filled with 50% propylene glycol and inserted into the ground flush with the soil surface. To reduce “digging-in effects,” we left pitfall traps capped in the ground for 48 h (Greenslade 1973). Once uncapped, pitfall traps were open for 48 h. We identified ants to species using keys developed for ants of the southeastern United States (MacGown 2003). We used species pitfall trap occurrence (Fig. 1d) as a measure of abundance because ants are social and counts of individuals from pitfall traps can result in skewed estimates of abundance, for example, if a pitfall trap happens to be placed near an ant nest (Gotelli et al. 2011). To assess the thoroughness of the sampling effort, we compared observed species richness to the Chao2 estimator, a widely used nonparametric method to estimate species richness for incidence data (Chao et al. 2009; Gotelli and Colwell 2011).

We calculated turnover of ant assemblages between each pairwise combination of sites using the Bray–Curtis dissimilarity index (Fig. 1e; Bray and Curtis 1957; Oksanen et al. 2010). Bray–Curtis dissimilarity varies between 0 and 1, with 0 indicating identical assemblages and 1 indicating completely different assemblages. We used the Bray–Curtis dissimilarity index, out of the many possible choices for quantifying beta diversity, because it excludes joint absences and is appropriate for comparisons using species occurrences and abundances (Anderson 2011; Legendre and Legendre 2012). We removed *S. invicta* from the species matrix before calculating dissimilarity because *S. invicta* abundance was used as a predictor variable.

Spatial processes: geographic distances and connectivity

We calculated the geographic distance between sites as the pairwise distances between patch centroids on the World Geodetic System (WGS) ellipsoid model (Fig. 1b). We calculated connectivity between patches accounting for matrix resistance using two commonly used approaches in landscape ecology, least-cost and circuit theory modeling (Fig. 1b; McRae et al. 2008; Etherington 2016; Fletcher and Fortin 2018; Dickson et al. 2019). Least-cost modeling identifies the path of

least resistance between locations and this “least-cost distance” can be used as an effective distance for interpreting isolation. In contrast, circuit theory can be derived from the concept of random walks and related metrics of commute time (or distance) and resistance distances can be calculated that take into account the potential likelihood of random walk movements between locations. Because ants respond strongly to patch openness (Puntila et al. 1991; Underwood and Fisher 2006; Andersen 2019), we inferred landscape resistance as the height of the vegetation canopy from a LiDAR-derived raster layer (higher vegetation height values indicate mature forest cover, lower values indicate open cover; Fig. 1a–b). These remotely sensed data were collected from aircraft flown over Savannah River Site in February and March 2009, the same year of this study (McGaughey and Reutebuch 2009). These data were collected using two Leica ALS50-II 150 kHz Multi-pulse enabled LiDAR Systems (a full report on the LiDAR data acquisition and processing is in McGaughey and Reutebuch 2009). Canopy height values were created using the FUSION CanopyModel program by subtracting the ground elevation from each LiDAR reading and the maximum return height for each 2×2 m pixel; this value was retained as the canopy height value for each pixel. In the raster, outlier filtering was used to omit any returns above 50 m (McGaughey and Reutebuch 2009). However, because some artifacts could be present (e.g. birds flying below 50 m) and because canopy height variation among mature trees may be less important for ant occurrences, we set all pixel values > 20 m equal to 20 m. Impermeable surfaces of facilities and large bodies of water are inhospitable to most ants, we set the values of those surfaces at the maximum value of vegetation height in the raster to represent high connectivity resistance. We aggregated the grain of the raster layer to 20×20 m pixels to increase the computation speed of analyses. Connectivity estimates for least-cost and circuit theory modeling at larger (40×40 m) and the smallest (2×2 m) grains were similar. We then created a transition layer as the inverse of canopy height to model conductance (conductance = $1 / \text{resistance}$) between pixels (McRae et al. 2008). From this transition layer, we calculated least-cost and circuit theory derived distances (expected random-walk commute time) between sites (Fig. 1b). As alternatives to modeling resistance as a linear function of

canopy height, we tried three non-linear transformations of canopy height values: $\log + 1$, exponential, and sigmoid. However, because we found that these transformations did not improve model fits, we used the untransformed canopy height for modeling connectivity.

Environmental processes: patch age

Patches decrease in openness over time through successional dynamics and tree growth. Such changes in vegetation structure affect abiotic conditions like light penetration and microclimate for ants. Consequently, we used time since patch clearing (“patch age”; Fig. 1c) as a variable to quantify environmental variation among sites. Patch age was determined from timber harvest data provided by the USDA Forest Service. We corroborated patch age data by plotting patch age values against mean canopy height values and by visually checking ground-level photographs of each sampling site.

Environmental processes: biotic interactions with fire ants

As with species abundance values of Bray–Curtis dissimilarity calculations, we used pitfall trap occurrence as a measure of *S. invicta* abundance (see above; Gotelli et al. 2011).

Generalized dissimilarity modeling

We used a generalized dissimilarity modeling approach (Ferrier et al. 2007) for interpreting patterns of beta-diversity to test our hypotheses. Generalized dissimilarity models are extensions of matrix regression that analyze variation in species dissimilarity among sites by fitting relationships as functions of spatial and environmental gradients (Ferrier et al. 2007; Fitzpatrick et al. 2020). This approach can accommodate the commonly encountered nonlinear relationships of environmental or spatial distances on species dissimilarity between sites using I-splines, or splines that are constrained to be monotonic (Ferrier et al. 2007). This approach can also accommodate matrix resistance weighted distances between sites (Ferrier et al. 2007). In this context, partial plots from generalized dissimilarity models are useful for interpreting the importance of predictor variables on

species turnover. In these plots, partial ecological distance (i.e. the relative partial prediction of dissimilarity on the link scale) is plotted to provide a means to visualize the relative importance of each predictor variable to dissimilarity. The summed coefficients for each predictor variable describe the dissimilarity explained by that variable and are reflected in the partial plots as the maximum height of the I-spline (Ferrier et al. 2007; Fitzpatrick et al. 2013). The I-spline slopes indicate the rate of species turnover along the gradient of the predictor. We fitted generalized dissimilarity models including the environmental variables of patch age and *S. invicta* abundance, and each of geographic distance, least-cost distance, and circuit theory-based commute distance using three knots for the I-splines. We calculated estimates of uncertainty for fitted I-splines using bootstrapping (1000 iterations). Ecological variables, like those used in the environmental processes examined, often show spatial dependence (Wagner and Fortin 2005; Fletcher and Fortin 2018). Consequently, we included geographic distance and, separately, resistance-based effective distances from least-cost and circuit theory modeling, between sites in the models. Finally, because environmental variables can be interrelated and this collinearity can confound interpretation of drivers of community assembly (Cadotte and Tucker 2017), we correlated these measures to assess this interrelatedness.

Software

All analyses were performed in R version 4.0.2 (R Core Team 2020). We used the *vegan* package version 2.5–6 for calculating species richness estimates and Bray–Curtis dissimilarity (Oksanen et al. 2010), the *gdm* package version 1.4.2 for generalized dissimilarity modeling (Fitzpatrick et al. 2020), the *raster* package version 3.3–13 for visualizations, manipulations, summaries, and analyses of raster layers (Hijmans 2020), the *gdistance* package version 1.3–6 for connectivity analyses (van Etten 2017), the *sp* package version 1.4–2 (Pebesma and Bivand 2005), the *reshape2* package version 1.4.4 (Wickham 2007), and the *rgdal* package version 1.5–16 (Bivand and Keitt 2019) for various data formatting tasks.

Results

We collected and identified 35,621 ants of 56 species. Observed species richness across sites was 91% of estimated species richness ([observed species richness/Chao2] \times 100). Species richness (excluding *S. invicta*) varied among sites ranging from 2 to 20 species and at the site level observed species richness was on average 67% of estimated richness. Bray–Curtis dissimilarity varied strongly among sites ranging from 0.20–1.00, with a mean dissimilarity of 0.57. Patch ages ranged from 0.2–12 years with a mean of 6.2 years. Occurrences of *S. invicta* in pitfall traps varied among sites from 0–16 (0%–100% of pitfall traps) and the average pitfall trap occurrence per site was 10 (63% of pitfall traps). Because the abundance of *S. invicta* was not strongly correlated with patch age (Pearson's $r = -0.28$), we did not consider collinearity to be problematic in our models (Dormann et al. 2013).

Of the fitted generalized dissimilarity models, including the environmental variables of patch age, *S. invicta* abundance, and each of geographic distance, least-cost distance, and circuit theory distance, the model including geographic distance resulted in 30.7% of the deviance explained. Similarly, the model including least-cost distance resulted in 30.3% of the deviance explained. The model including circuit theory resistance distance resulted in 33.1% of the deviance explained.

In relation to hypothesis 1a, species dissimilarity increased with pairwise geographic distance between patches. Yet the total magnitude of geographic distance change on species dissimilarity (summed coefficients = 0.19; represented by the maximum height of each spline in Fig. 2) was less than that of each of the environmental variables (patch age summed coefficients = 0.81, *S. invicta* summed coefficients = 0.42). Results from the least-cost distance model were similar to those of the geographic distance model (Fig. 2). However, accounting for landscape resistance using circuit theory modeling (hypothesis 1b) explained more variation in species turnover among sites (Fig. 2) compared to either geographic distance or least-cost path distance. Moreover, accounting for landscape resistance using circuit theory modeling resulted in greater accounting for species dissimilarity by the spatial process variable (summed coefficients = 0.76) than each of the environmental process variables (patch age summed

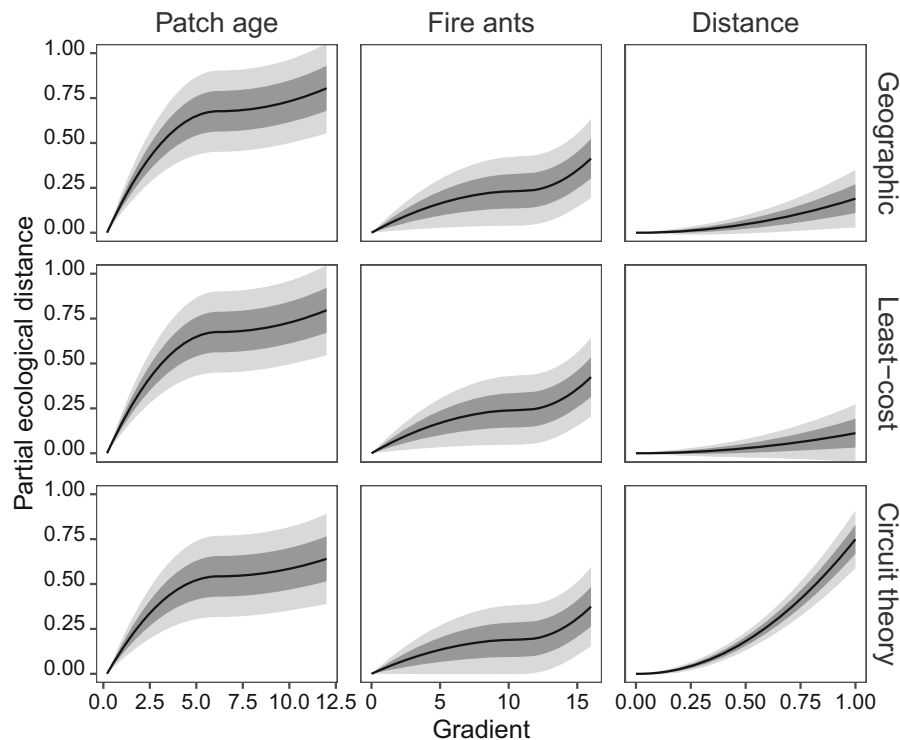


Fig. 2 Partial plots from three generalized dissimilarity models (rows) modeling ant dissimilarity across early-successional stands at the Savannah River Site, SC, USA using predictor variables to approximate spatial and environmental processes in community assembly. Spatial variables to quantify isolation used in each model were geographic distance, least-cost effective distance, and circuit-theory effective distance (scaled by dividing by the maximum value to facilitate comparisons among variables). Environmental variables used in all models were patch age (years since timber clearing) and fire ant

(*Solenopsis invicta*) abundance (pitfall trap occupancy out of 16 traps). Lines represent I-spline predictions of dissimilarity on the link scale (partial ecological distance) as a function of distance along spatial and environmental gradients. The maximum height of each spline represents the total magnitude of change along the gradient. Shaded areas show uncertainty as \pm one (dark gray) and two (light gray) standard deviations calculated from bootstrapping. Due to the monotonic forcing of the I-splines, the bootstrap uncertainty goes to zero at small values of each explanatory variable

coefficients = 0.64, *S. invicta* summed coefficients = 0.38; Fig. 2). Species dissimilarity increased with pairwise change in patch age (hypothesis 2; Fig. 2) and *S. invicta* abundance (differences in *S. invicta* pitfall trap occurrence; hypothesis 3; Fig. 2) between patches.

Discussion

Understanding how processes at various scales assemble communities is a key question in ecology. The results from this study show evidence for the shared importance of isolation, patch structure, and species interactions in metacommunity assembly. How isolation was measured was critical. Measuring isolation in

a way that accounted for structural connectivity of the matrix with circuit theory modeling performed better at explaining species turnover among sites than quantifying patch isolation through geographic distance or using least-cost modeling of connectivity. Moreover, accounting for connectivity with circuit theory modeling reversed the interpretation of spatial processes from a secondary role compared to environmental processes (when geographic distance was used) to a primary role. We discuss these results and their role in driving metacommunity assembly below.

As a general pattern across taxa, species assemblages become more different with geographic distance (Soininen et al. 2007). Therefore, our finding that ant assemblages are more dissimilar with increasing geographic distance was expected. Geographic

distance is often used to measure patch isolation in metacommunity studies (Cottenie 2005). Nonetheless, there is increasing evidence that geographic distance alone may be insufficient to interpret isolation across landscapes for populations and communities (e.g. Prugh et al. 2008; Watling et al. 2011). This study (and others, e.g. Minor et al. 2009) suggests that matrix connectivity is an important spatial component that would otherwise have been missed if accounting for dispersal was done using geographic distance alone. This may especially be true in cases where the matrix is heterogeneous (Brudvig et al. 2017). Connectivity mapping with circuit theory modeling improved accounting for species turnover compared to geographic distance and changed the interpretation of primary processes driving community assembly. Connectivity mapping with circuit theory modeling has been applied in a variety of applications in landscape ecology from mapping gene flow to flows of ecosystem services (Dickson et al. 2019), but circuit theory has received less attention in the context of metacommunity assembly (but see Brodie et al. 2016; Dong et al. 2016; Benito et al. 2018). This may be due to the challenges of mapping connectivity for species assemblages whose constituent members may have disparate or unknown dispersal abilities and matrix use. In the case of our study, patch openness was relevant to many species of ants in similar ways (Andersen 2019). The applicability of assemblage-wide connectivity modeling for quantifying spatial processes on community assembly may be limited to demarcated species assemblages with coherent responses to the matrix. Assemblages with species with more heterogeneous use of the matrix would likely require more nuanced species-specific or trait-based connectivity modeling (Hartfelder et al. 2020).

As predicted, patch age was an important predictor of community dissimilarity. This makes sense considering that patch openness is key in driving ant community composition. In a review of ant responses to disturbance, Andersen (2019) proposed principles for understanding the disturbance responses of ants which include: (1) that the most important effects of disturbance on ants are through effects on vegetation structure, microclimate, resources, and species interactions, (2) that openness is a key driver in ant community change, and (3) that ant species responses to disturbance are largely determined by responses to openness. There was a rapid increase in partial

ecological distance with small changes in stand age between 0 and 5 years. In contrast, the spatial effects, including those of circuit theory distance, appear to be more relevant at larger distances across the gradient.

The spread of *S. invicta* across the southeastern US has been implicated for the displacement of native ant species (Wojcik et al. 2001 and references therein). Studies, including some that have compared invaded to uninvaded sites, have generally concluded strong effects of *S. invicta* on co-occurring ants (Camilo and Phillips 1990; Porter and Savignano 1990; Morris and Steigman 1993; Jusino-Atresino and Phillips 1994; Wojcik 1994; Gotelli and Arnett 2000). While the effect of *S. invicta* in its introduced range on co-occurring ants has been extensively studied, it remains contentious (Lach and Hooper-Bùi 2010). Occurrence and abundance of *S. invicta* are often intertwined with disturbance and environmental variables whose contribution to community structure are difficult to tease apart (King and Tschinkel 2008; LeBrun et al. 2012; King and Tschinkel 2013; Roeder et al. in review; Tschinkel 2006; Tschinkel and King 2007; Stuble et al. 2013), as is often the case with invasive species (Didham et al. 2005; MacDougall and Turkington 2005). While this study does not settle the debate on the role of *S. invicta* on co-occurring ants, the weak correlation between *S. invicta* abundance and patch age along with compelling evidence from previous studies suggest that *S. invicta* plays an important role in driving local ant species composition.

Variance explained by our models was relatively low but within the range of variance explained by spatial and environmental processes in metacommunity studies (Cottenie 2005). The unexplained variance could come from spatial and environmental process variables that are unaccounted for (e.g. soil properties) and neutral (drift) processes. At the spatial and temporal scales of this study, the role of speciation can be safely ignored (Vellend 2016). It is important to note that environmental variables show spatial dependence such that the environment can potentially cause similar patterns as a dispersal-driven process (Wagner and Fortin 2005; Vellend 2016; Fletcher and Fortin 2018). We recognize there could be unmeasured variables that could show spatial dependence among sites and explain, at least in part, this observed spatial pattern of dissimilarity.

In conclusion, our results highlight that interpretation of the relative roles of spatial and environmental

processes is sensitive to how those processes are quantified. In particular, the role of the matrix on connectivity is an important issue to quantify as ignoring it could lead to underestimating the role of spatial isolation in community assembly. Therefore, connectivity mapping tools like circuit theory and related frameworks (Fletcher et al. 2019) are promising and important to add to the community ecologist's toolbox.

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