

Different responses of predator and prey functional diversity to fragmentation

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Abstract. The study of functional diversity, or the range of species' ecological roles in a community, is a rapidly expanding area in ecology. Given the extent that ecosystems are being altered, effort should shift toward assessing variation in functional diversity across landscapes with the goal of improving land use management decisions. We construct a workflow that creates three-dimensional surfaces and maps of functional diversity to examine changes in beetle functional diversity across an Indiana, USA landscape. We sampled 105 prey wood-borer and predator beetle species along a gradient of forest fragmentation across Indiana and used a number of functional traits from literature sources to capture their functional roles. We developed newly measured functional traits to estimate several traits relevant to beetles' ecological function that was unknown and not easily measured. Functional diversity indices (FRic, FDis, FDiv, and FEve) were calculated from species abundance and functional traits and used to assess changes in functional diversity along the fragmentation gradient. We predicted that habitat fragmentation would have a greater negative impact on predator beetle functional diversity than prey wood-borer functional diversity. Landscape metrics most important to the functional diversity of both wood-borer and predator beetle communities were landscape division index (LDI, an assessment of landscape subdivision) and mean shape index (MSI, a measure of patch shape complexity). Overall, three-dimensional surfaces of functional diversity and functional diversity maps across the Indiana landscape revealed that beetle functional diversity was greatest with minimal landscape subdivision. Opposite to what we predicted, we found that the prey wood-borer functional diversity was more negatively impacted by LDI than the predator beetle functional diversity. Furthermore, predator beetle functional diversity was greater with increasing MSI. The map predicted predator FRic to be highest in forested areas with intact habitat and also less sensitive to habitat fragmentation adjacent to more continuous forest. We propose that land management may be guided by revealing landscapes that are most appropriate for maximizing functional diversity of multiple communities or shifting the relative abundance within prey and beneficial predator beetle functional groups with the use of three-dimensional plots or maps.

Key words: avian vision; Cerambycidae; functional diversity indices; functional traits; landscape response; mapping; multitrophic; perceptual modeling; predation; three-dimensional plots; wood-boring beetles.

INTRODUCTION

Functional diversity encompasses information on the range of species' ecological roles in a community (Tilman 2001). It is therefore considered a more direct measure than species richness of impacts on ecosystem services (Tilman et al. 1997, Díaz and Cabido 2001, Heemsbergen et al. 2004, Dang et al. 2005) and change following disturbance or fragmentation (Díaz and Cabido 2001, Ernst et al. 2006). Much attention in ecological research has therefore shifted toward using functional diversity over species diversity to estimate change to ecosystems. Results from previous functional diversity studies indicate that for many ecosystems function is reduced with habitat disturbance (Didham et al. 1996, Flynn et al. 2009). Given the rapid rate that ecosystems are being altered (and also the extent of managed ecosystems), it is therefore important to understand not only how habitat change impacts ecosystem services but also which landscapes maintain or are more suitable for ecosystem service provision

by the species they contain. A logical next step in functional diversity research is assessing functional diversity variation across landscapes to improve land use management decisions for promoting ecosystem service provision.

Forests provide many ecosystem services including timber production, nutrient cycling, and soil formation (Gamfeldt et al. 2013). However, habitat fragmentation and loss have been shown to impact many species that are important to forest ecosystem processes that contribute to ecosystem services. Two groups of forest beetles, wood-boring beetles and their beetle predators, are functionally diverse insects that perform many important roles in forests. Wood-borers (Coleoptera: Cerambycidae) contain species whose larvae develop in living wood and deadwood (Linsley 1961, Hanks 1999). The species whose larvae feed on healthy, living wood are considered pests of forests (Hanks 1999) because of the damage they inflict on trees destined for timber harvest (Duffy 1953:3–4.). However, those species whose larvae feed on moribund trees and deadwood help to improve forest health by hastening nutrient cycling through removing stressed trees or accelerating wood decomposition (Gutowksi 1987, Edmonds and Eglitis 1989). The adults of wood-borers are free living and many are pollinators of

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flowering plants (Linsley 1961, Kevan and Baker 1983). The predatory beetles also utilize wood of a particular condition and depredate prey at different life stages as larvae and adults (e.g., Böving and Champlain 1920).

Wood-boring beetles, including those in a separate family, the Curculionidae, and their beetle predators have been shown to respond differently to forest fragmentation. Previous studies suggest that certain wood-borer species are less sensitive to forest fragmentation and loss than their beetle predators. Many of these studies focus on the relationship of an economically important curculionid wood-borer, *Ips pini*, and its beetle predators. It has been observed that *Thanasimus dubius*, a clerid predator, has a greater dispersal ability than its *I. pini* prey, but, unlike its prey, is restricted to pine forests (Costa et al. 2013). Furthermore, Ryall and Fahrig (2005) found that isolated habitats contained a greater proportion of *I. pini* wood borers than their beetle predators (Ryall and Fahrig 2005). Cerambycid wood-borer response to habitat loss and fragmentation, however, is variable. Abundance may be higher in herbaceous fringes rather than

forests (Wermelinger et al. 2007). Other studies have found that the response of cerambycid wood-borer species to habitat loss (either positive or negative) is variable (Saint-Germain and Drapeau 2011) and may also depend more on tree quality than habitat amount (Vergara et al. 2016).

Here, our main objective was to take a functional diversity approach to examine how functional diversity of wood-boring beetles and their beetle predators respond to a gradient of forest fragmentation in Indiana, USA. These results will then be used to construct a map across a forested landscape that identifies where predator beetle functional diversity is high and wood-borer functional diversity is low (e.g., where the ecosystem service of predation is highest). We assess the relationship of beetle functional diversity with forest fragmentation using several different multidimensional indices (described in Fig. 1) that have previously been used as dependent variables to assess change in functional diversity of other taxa to disturbance (i.e., Laliberté et al. 2010, Villéger et al. 2010). These indices, each of which is an independent measure of functional trait space and how species

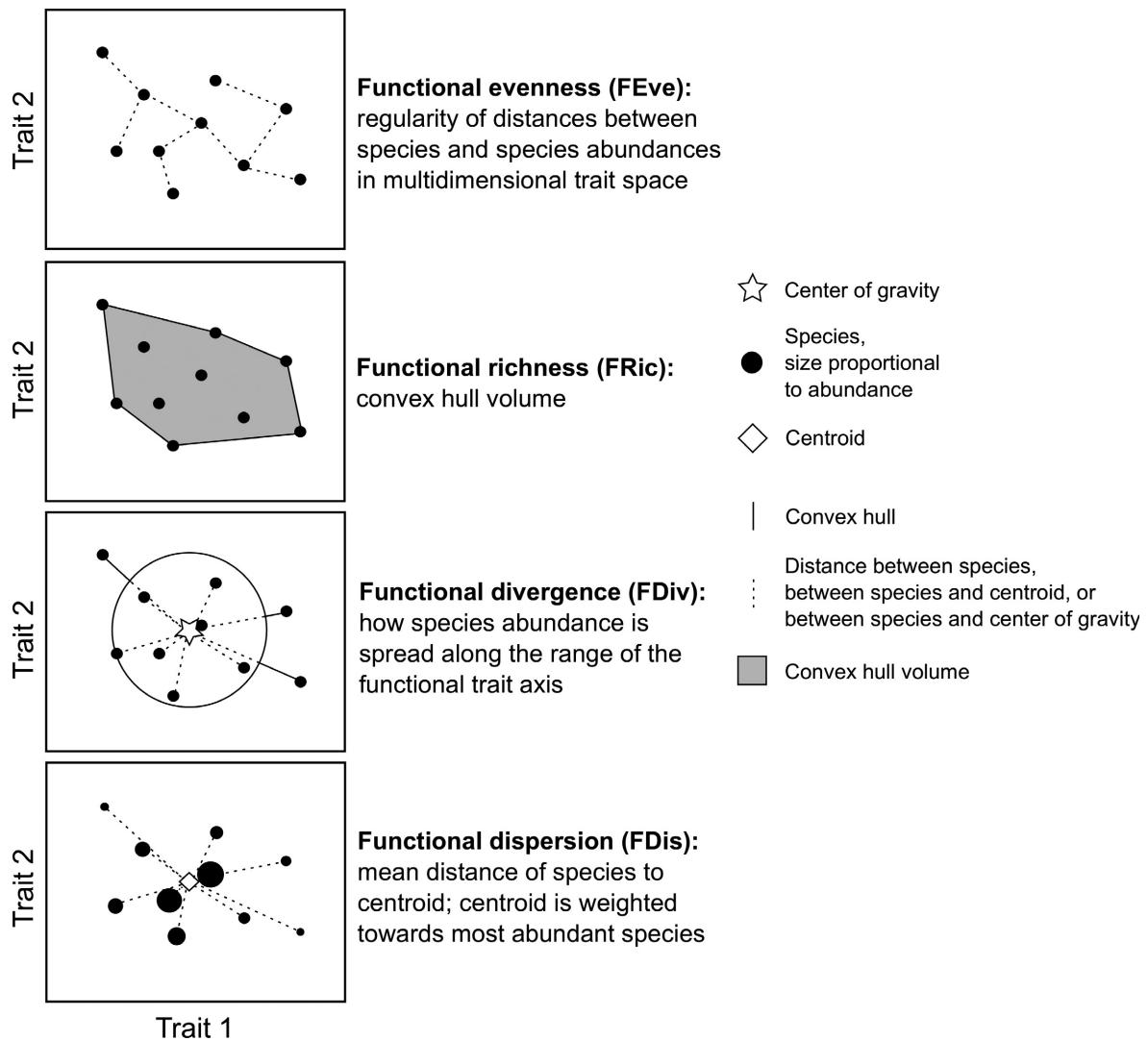


FIG. 1. Two-dimensional representations of functional diversity indices. Functional evenness (FEve), functional richness (FRic), and functional divergence (FDiv) were adapted from Villéger et al. (2008). Functional dispersion (FDis) was adapted from Laliberté and Legendre (2010).

are dispersed within it, include functional evenness (FEve), functional divergence (FDiv), functional dispersion (FDIs), and functional richness (FRic; Villéger et al. 2008, Laliberté and Legendre 2010). The calculations of FEve, FDiv, and FDIs incorporate species' abundances along with species' functional traits. FEve is constrained between 0 (low) and 1 (high) and takes into account the evenness of the spacing of species in the community with respect to their functional traits and the distribution of the species' abundances (Villéger et al. 2008). FDiv represents how species abundance is distributed within the functional trait space of a community (Villéger et al. 2008). It is low when the most abundant species have trait values that are close to the center of the community's functional trait range and is high when the most abundant species have diverse trait profiles (Villéger et al. 2008). FDIs is a calculation of the mean distance of individual species in the community to the centroid of the community's trait space (Laliberté and Legendre 2010). FRic, however, is simply the volume of functional trait space occupied by a given community. This convex hull volume is defined by species with the most diverse trait profiles, and any species with less extreme trait profiles are within the convex hull volume (Villéger et al. 2008).

Because the computation of these indices incorporates species' ecological traits, thorough knowledge on species' ecological function is therefore critical for accurately estimating how habitat disturbance impacts ecosystem function. But, even though important traits for many taxa are rapidly expanding and becoming available (i.e., the TRY Plant Database for plants [Kattge et al. 2011]), information on functional traits for many species is limited at the present time, or important traits related to function are difficult or impossible measure. Therefore, measures that estimate dimensions of ecological function that would otherwise be captured by these missing traits should be made to avoid misguided results on how habitat disturbance impacts ecosystem function.

There are several prior studies of forest beetle functional diversity. Some earlier studies have examined functional diversity of a number of beetle families (i.e., Didham et al. 1996, Lassau et al. 2005) and of saproxylic insects (i.e., Gibb et al. 2006, Johansson et al. 2007) by delineating functional groups with three or fewer functional roles. More recent studies have focused on dung beetles (Barragán et al. 2011) and ground beetles (Woodcock et al. 2010, Gerisch et al. 2012). These have collectively used a greater number of functional traits that further encompass beetle functional roles, including the ability to locate prey, dispersal and movement, body size, food relocation (specific to dung beetles), diurnal activity, and diet. Dung beetles and ground beetles are functionally different than the beetles in our study; thus, a different suite of traits should be obtained here. Many such traits include host tree preference and foraging preferences as larvae and adults. These traits are well known for wood borers and their beetle predators due to the economic importance of these beetles to forest ecosystems, both as beneficial species and as pests. However, there are other traits that are not easily measured or are not generally well known of the forest beetles included in our study. Such traits include dispersal, female fecundity, development rate, and antennal responses to volatiles. We estimate many of these dimensions of beetle functional trait space with one newly measured trait,

landscape response trend. Landscape response is a trend produced from the relationship between species abundance and landscape pattern measured at different analytical foci ("window sizes"). Different species respond to different phenomena within differently sized ecological neighborhoods. The scale at which species respond to landscape pattern reflects dispersal, population dynamics, foraging behavior, and other processes (Addicott et al. 1987, Dunning et al. 1992) including reproductive potential (Kallio 2014). Analytical focus (hereafter, focus) refers to the area at which the surrounding landscape correlates to species abundance (sensu Holland and Yang 2016). Our landscape response trend variable is a nominal class variable that groups species together according to the similarity in their overall response-foci profile.

We measure another trait that estimates details of inter-trophic interactions of beetles with important avian predators. Although previous studies have shown how disturbance affects the functional diversity of multitrophic systems (Lavorel et al. 2013, Moretti et al. 2013, Deraison et al. 2015, Lefcheck and Duffy 2015), they have not taken into account the ecological roles of species with respect to inter-trophic interactions between predators and prey. Beetles are known to use aposematic or camouflage patterning to minimize detection (and consequently mortality) by insectivorous birds (Jones 1934). Yet birds use multiple (direct and indirect) cues to visually detect insects (Sipura 1999) including beetles (Flower et al. 2014) against various backgrounds with different success rates (Mand et al. 2007). The interplay between detectability of beetles by avian predators and the potential consequences for the mortality of wood borers and predatory beetles has not been taken into account in the literature despite its major ecological implications (Stevens 2007). We addressed this gap by measuring another trait, avian visual sensory perception of beetles, which estimates the degree to which the avian sensory system can discriminate a beetle from the visual background (i.e., visual contrast), ultimately being a proxy of prey detectability. This sensory perspective provides a linkage between trophic levels in functional trait space as it can identify areas of overlap and segregation in prey cues directed to avoid detection by predators and enhance reproduction (Stevens 2007). As adults, the wood borers and predator beetles are free living. Many adult wood borers visit flowers and feed on bark, twigs, and leaves, and they disperse from their larval host trees in search of other oviposition sites (Linsley 1961). Many adult predator beetles, particularly in the Cleridae, hunt on tree trunks and branches (Böving and Champlain 1920). Furthermore, adult predator beetles living in galleries and under bark must disperse to find mates and also to seek to new habitat considering deadwood is an ephemeral resource (Sverdrup-Thygeson et al. 2014). During this time, they would be susceptible to a diverse array of avian insectivores present in Indiana forests.

We add these newly measured functional traits to encompass important dimensions of functional trait space of wood borers and their beetle predators for first estimating functional diversity indices that are later used for determining how changes in landscape features including habitat amount and fragmentation impact beetle functional diversity. Species at higher trophic levels are predicted to be less likely to persist in disturbed habitats than lower trophic levels because of the greater instability of their population dynamics (Pimm and

Lawton 1977). Models of predator-prey interactions predict that habitat loss has a greater negative impact on specialist predators than their prey (reviewed by Ryall and Fahrig 2006). This has also been demonstrated in empirical studies of wood borers and their predators (Ryall and Fahrig 2005, Costa et al. 2013) and other insects (i.e., Thies and Tscharnke 1999). Many of the predator beetles in our study specialize on wood-boring insects and thus are limited by the abundance of prey populations. Furthermore, many of the predator beetle species considered here are saproxylic and thus, like their prey, are restricted to deadwood of a particular stage of decay. Functional diversity is measured by the range of ecological functions species perform in an ecosystem (Tilman 2001). Therefore, we predict that, if predator species are more sensitive to habitat fragmentation than their prey, habitat fragmentation will have a greater negative impact on the functional diversity of predator beetles than on the functional diversity of their wood-borer prey. We also used this community to illustrate how consideration of landscape parameters influencing wood-borer (including pestiferous species) and beetle predator functional groups can be mapped and used to guide local management or select optimal sites for different production enterprises or conservation sites. We used these methods to produce a map of forest beetle functional diversity across a landscape. The aim of the mapping exercise was to bridge the gap between studying change in functional diversity with habitat disturbance and applied ecology.

MATERIALS AND METHODS

Beetle collection

Abundance of wood-boring beetles and beetle predators was needed for computing the functional diversity indices for assessing functional diversity along the forest

fragmentation gradient (Fig. 2(1)). Wood-boring beetles and their beetle predators were sampled at 25 sites along a forest fragmentation gradient in Indiana, USA (Fig. 3). The forest habitat was mature secondary growth forest fragmented by agriculture and urban areas. The land cover gradient spanned forest covers of 5–100% within 2 km of sampling sites. The range of distance between sites was approximately 8–250 km. At each site, beetles were trapped using one Lindgren multiple funnel trap (12 funnel size; Phero Tech, British Columbia, Canada), one Intercept panel trap for bark beetles (Integrated Pest Management Tech, Portland, Oregon, USA), and one multipane window trap, all baited with 100% ethanol (Holland 2006). Multiple traps were used to best sample the entire community of these beetles because different traps attract different beetle assemblages (Holland 2006; Appendix S1: Table S1). Abundances of species were summed within sites making each site the analytical replicate. Trapping lasted 70–90 d over the summers of 2006 and 2007. Wood borers were identified to species using Yanega (1996), Linsley (1962a,b, 1963, 1964), Linsley and Chemsak (1972, 1976), Arnett et al. (2002a,b), and Downie and Arnett (1996a,b). We re-examined trap residues in 2013 to obtain the predatory beetle data. We identified all specimens in the families, Cleridae, Cucujidae, Histeridae, and Passandridae, using keys in Arnett et al. (2002a,b) and Downie and Arnett (1996a,b). All specimens of wood borers were deposited into the Landscape Ecology and Biodiversity laboratory at Purdue University, and voucher specimens of the predatory beetle species were deposited in the Purdue Entomological Research Collection.

Beetle functional traits

Beetle functional traits (Fig. 2(1), Fig. 3(1–3), Appendix S2) were also important for computing the functional diversity

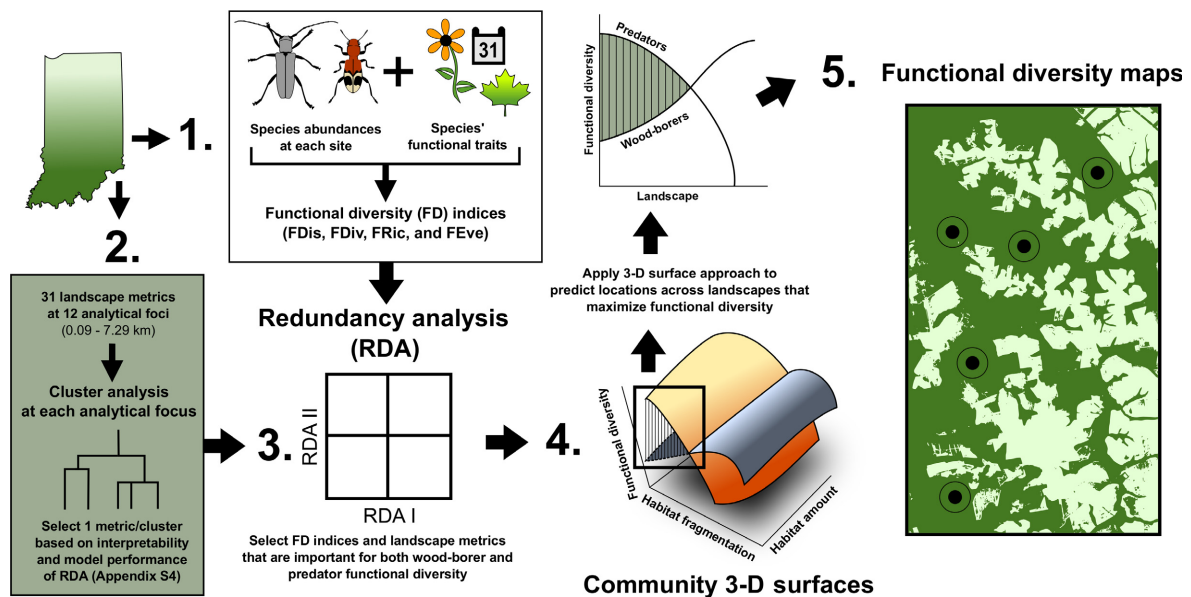


FIG. 2. Assessing changes in functional diversity along the fragmentation gradient and development of workflow to create landscape maps of functional diversity to aid land use management. FDis, functional dispersion; FDiv, functional divergence; FRic, functional richness; FEve, functional evenness; LDI, landscape division index; MSI, mean shape index. The approach for assessing community level functional diversity was applied to individual functional groups where Random Forest was used to identify best relationships.

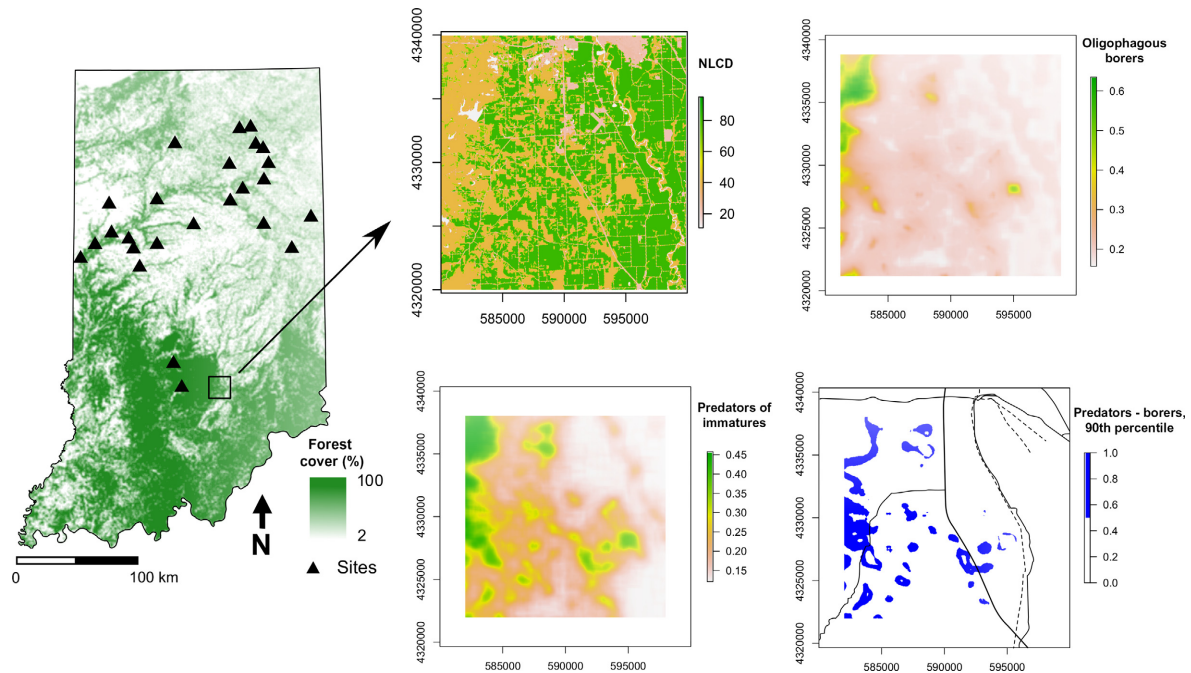


FIG. 3. Maps showing location of 25 field sites selected along a gradient of forest fragmentation in the state of Indiana, USA, and predictions of functional richness (FRic) across a selected Indiana landscape. Axes units are meters. Functional groups considered for the prediction maps were oligophagous borers and predators of immatures. NLCD, national land cover database; Oligophagous borers, predicted FRic of the oligophagous borer functional group; Predators of immatures, predicted FRic of the predators of immatures functional group; Predators – borers, 90th percentile, the selected areas in the 90th percentile of FRic of the beneficial predators of immatures functional group minus FRic of the oligophagous borer functional group. These areas represent locations with the greatest ratio of predators of immatures to oligophagous borer FRic.

indices (no. 1 in Fig. 2). For each beetle species, we compiled from the literature traits that describe their life history, habitat, and hosts (Fig. 4(1), Appendix S2). Variables included adult size, part of the tree and wood layer that larvae develop within (e.g., branch, stem; bark, cambium, and xylem), host wood condition (e.g., under stress, sound deadwood, and decayed), family of host tree (one to dozens of families), and number of tree families used as a measure of specialization. We included the beetle’s taxonomic subfamily (and additionally tribe for wood borers) because we assumed this would account for some biological traits that are shared due to the degree of phylogenetic relatedness that may be present within these taxonomic levels although these traits may not be known. Furthermore, considering that the bodies of wood-borers and predator beetles follow ecological function, inclusion of these lower taxonomic groupings was to efficiently include numerous physical traits of beetles. These lower taxonomic groups within the wood-borers and the predator beetles share numerous, very specific physical characteristics that are present in adult beetles and wood-borer larvae. Just a fraction of these characteristics includes dimensions of the antennae (related to response to pheromones and plant volatiles), the ratio of elytra to pronotal length (related to dispersal), and head shape (related to feeding behavior).

We included a newly measured trait that classifies how a species’ response to landscape changes with focus (Yang 2010) as an important dimension of their ecological role (Fig. 4(2)). The landscape data measured above were subjected to principal component analysis, and the site scores along the first principal component ($\lambda = 0.6$) at each focus were correlated

with a Spearman’s rank test to the species abundance at the sites. The trend of absolute values of the Spearman’s ρ across focus foci (radii) was examined. A forward stepwise ANOVA was used to determine whether higher order polynomials were justified to describe the relationship of $|\rho|$ vs. scale. The nature of the response trend (e.g., linear and second order) was used as one functional trait for each species.

To assess how wood borers and predatory beetles are perceived by avian predators (Fig. 4(3), Appendix S3), we used a perceptual modeling approach (Endler 1990, Vorobyev and Osorio 1998, Endler and Mielke 2005), which is widely accepted in the behavioral and sensory ecology literature (e.g., Kemp et al. 2015). Avian visual perception differs from that of humans because of the presence of an extra ultraviolet- or violet-sensitive cone photoreceptor type, oil droplet filters, and different absorbance properties of the ocular media (Cuthill 2006). Perceptual models estimate the chromatic and achromatic conspicuousness of an object against the background under a given set of ambient light conditions and from the perspective of a given visual system (Endler 1990, Vorobyev and Osorio 1998). We calculated the chromatic and achromatic contrasts of beetle dorsa against various backgrounds that occur where avian predators may find them, such as tree bark and leaves. We also conducted similar visual contrast calculations comparing the beetles to a “background” of several species of aposematic wasps that are common in the study area to incorporate the effect of mimicking wasps on predation by birds. We used all visual contrasts calculated through this approach. Details on the perceptual model calculations and how they were

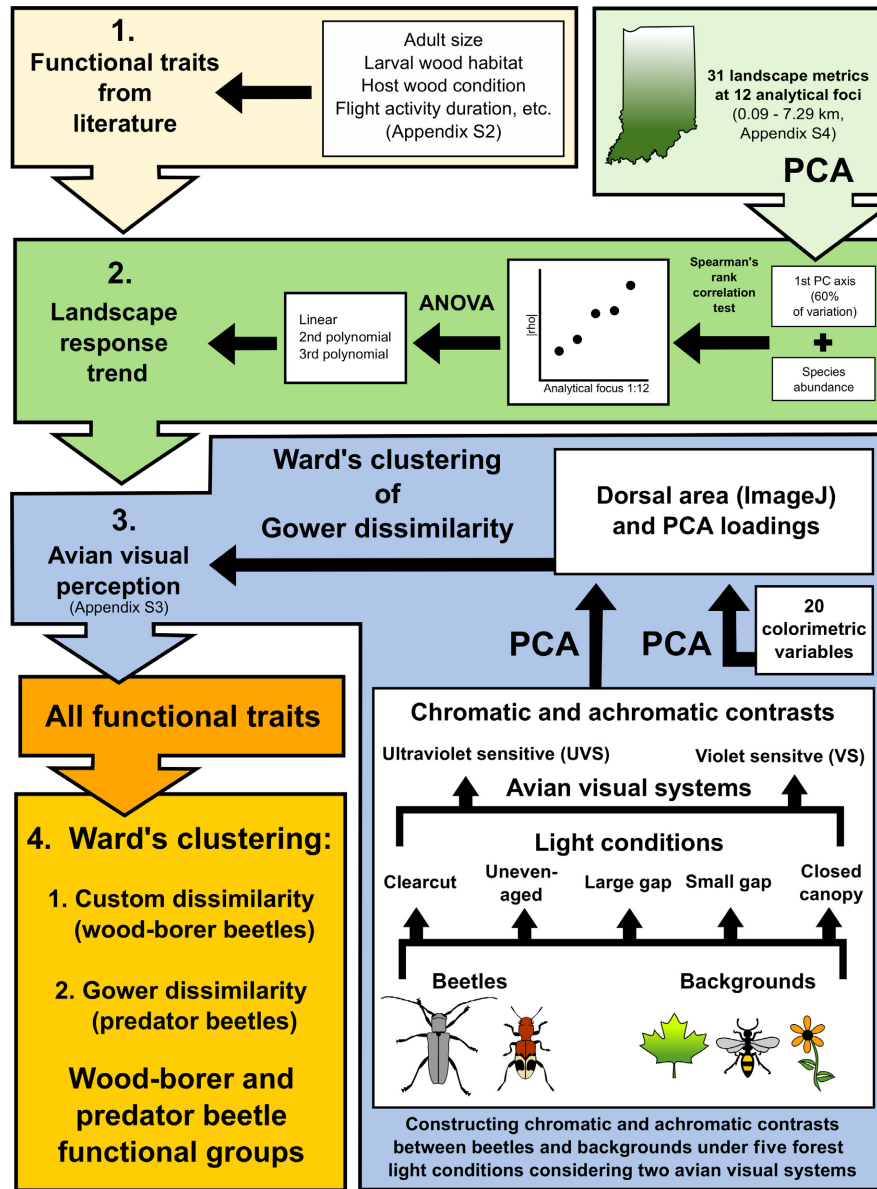


FIG. 4. Methods used to group beetles by ecological function. Methods include the collection and workflows to obtain all functional traits used to categorize wood-borer and predator beetles into functional groups. PCA, principal component analysis.

incorporated into our functional trait analysis are given in Appendix S3.

Functional groupings

We used a total of 17 traits of wood-borers and 14 traits of predator beetles (Appendix S2) to classify species into functional groups (Fig. 4(4)). All wood-borer traits except for one, larval host condition, were weighted so that all conditions within each trait summed to one. We considered a priori that larval host condition should have double the weighting of the other individual traits because these beetles spend most of their lives as larvae (Linsley 1961) and much of their roles in forest ecosystems revolve around the condition of the larval host tree (Hanks 1999). All noncontinuous variables were treated asymmetrically. However, we

encountered a problem when calculating dissimilarity of one wood-borer trait with 42 conditions (host family). We wished to compare species so that double zeros were not counted as matches for this trait, but considering the number of conditions, its summed matches would not approach the desired total weight of 1. To circumvent this problem, we created our own dissimilarity. We first calculated Gower dissimilarity of all wood-borer traits except host family using the FD package in R (Laliberté and Legendre 2010, Laliberté and Shipley 2011) and then used the vegan package in R (Oksanen et al. 2013) to calculate Jaccard's dissimilarity of the trait tree "host family." The two dissimilarity matrices were multiplied by the fraction of traits they contained (16/17 or 1/17), and these products were summed to obtain the final dissimilarity matrix for the wood borers. Gower dissimilarity was calculated for all predator beetle functional traits. The Gower

dissimilarity was preferred because we had several variable types (continuous, ordinal, and categorical) and missing values (Gower 1971, Legendre and Legendre 1998:258–260). Ward's minimum variance clustering method was computed upon the resulting dissimilarity matrix (Pla et al. 2011). To determine pruning height for the wood-borer dendrogram and thus delineate functional groups, we used k -means clustering to plot within groups sum of squares by number of clusters k . A scree plot determined pruning height for the predator beetle dendrogram.

Functional diversity indices.—After delineating beetle functional groups, functional diversity (FD) indices that describe how species abundances are dispersed in multidimensional trait space were calculated using the FD package in R (Laliberté and Legendre 2010, Laliberté and Shipley 2011) at the community level (i.e., across functional groups) for wood-borer and predator beetles. We included indices of functional dispersion (FDis), functional divergence (FDiv), functional richness (FRic), and functional evenness (FEve; Villéger et al. 2008, Laliberté and Legendre 2010) described in Fig. 1. We used the Cailliez correction method since our species–species distance matrix could not be represented in Euclidean space (Cailliez 1983, Laliberté and Legendre 2010, Laliberté and Shipley 2011). These functional diversity indices served as our final response variables for testing our prediction that predator functional diversity is more sensitive to habitat fragmentation than wood-borer functional diversity (Fig. 2(1)).

Gradient analysis

Landscape metric selection.—Habitat fragmentation may affect populations in different ways. For example, decreased patch area and increased patch isolation may reduce species persistence in the landscape (Fahrig 2003). Also, edge effects may negatively impact populations by (1) increasing the time species spend in nonpatch habitat (Fahrig 2002), (2) causing negative species interactions (Chalfoun et al. 2002), or (3) because species have varying sensitivities to edge (Costa et al. 2013) and habitat loss (Saint-Germain and Drapeau 2011). Furthermore, it is known that species, including those in our data set, respond to the landscape at different foci (radii; Addicott et al. 1987, Yang 2010). The use of more than one measure of fragmentation and assessing species response at different spatial foci are important for capturing relevant relationships (Trzcinski et al. 1999, Donovan and Flather 2002, Holland and Yang 2016). To our knowledge, this is the first study to investigate how forest fragmentation impacts wood-borer and predator beetle community functional diversity measured with functional diversity indices FDis, FDiv, FEve, and FRic. Therefore, it was unknown which measure of habitat fragmentation (i.e., habitat area, edge, and patch isolation) or which analytical focus (window size) is most important. To address this concern, we used methods (outlined in Fig. 2(2), detailed in Appendix S4) to first measure at several spatial foci relevant to beetles in our data set and then select landscape metrics that did not covary and were most important for predicting beetle functional diversity (Trzcinski et al. 1999, Donovan and Flather 2002). These landscape metrics are standard

measures similar to those found in FRAGSTATS that quantify forest area, edge, shape, core area, aggregation, subdivision, and isolation (program *available online*).⁵

Redundancy analysis.—We conducted redundancy analysis (hereafter, RDA) at each focus to examine whether habitat fragmentation (assessed with the landscape metrics previously selected) has a greater negative impact on predator beetle community functional diversity compared to wood-borer community functional diversity with the vegan package in R (Oksanen et al. 2017). We performed our analysis at multiple foci (Appendix S4: Table S4.1) to capture the relationship between beetle functional diversity and changes in landscape pattern. There was no overlap of spatial foci <5.67 km among sites. We used permutation tests to test the strength of the relationship between the functional diversity indices (FRic, FEve, FDiv, and FDis) and the landscape metrics (Fig. 2(3)). Wood-borer FDis was not considered because it was correlated with FEve. Permutation tests are powerful alternatives to parametric tests when the data do not meet the assumptions of such analysis. Permutation tests calculate exact P values, while tests that rely on a normal error distribution only calculate estimates of P values.

Three-dimensional surface of functional richness.—The redundancy analysis enabled us to summarize response of wood-borer and predator beetle functional diversity to changes in forest landscape pattern across several foci. Next, we aimed to visualize the most significant relationships identified by the redundancy analysis. We selected two different landscape metrics, landscape division index (LDI, a measure of habitat subdivision) and mean shape index (MSI, a measure of patch shape complexity), and one functional diversity index, FRic, from the resulting redundancy analysis triplot. These landscape metrics were chosen because they appeared to be correlated with both wood-borer and predator beetle community FRic at the same focus, 0.81 km. There were no other shared relationships between wood-borer and predator beetle community FD indices and the landscape metrics assessed at the other foci. LDI is the probability that two locations selected in the landscape are not located in the same patch. Therefore, the higher the LDI value, the greater the subdivision of habitat patches across a given landscape. MSI is a ratio of mean patch shape to compactness with values ranging from 1 (compact shape, i.e., a perfect square patch) to infinity where the larger the index, the more irregular the shape. We created three-dimensional (hereafter, 3D) plots to facilitate comparisons given that we had two landscape metrics (LDI and MSI) and one response for both community wood-borers and predator beetle FRic. LDI and MSI were used in polynomial regression with both wood-borer and predator community FRic. Wood-borer FRic was Box-Cox transformed with the MASS package in R (Venables and Ripley 2002) to meet normality assumptions. The difference between standardized predicted values within wood-borer community FRic and predator beetle community FRic in the polynomial regressions was plotted against LDI and MSI to obtain a 3D surface to visualize

⁵ <http://www.umass.edu/landeco/research/fragstats/fragstats.html>

how overall community functional diversity changed with these measures of landscape fragmentation.

Locations of high predator FRic vs. wood-borer FRic.—We had previously calculated functional diversity indices at the community level of wood borers and predator beetles. These indices served as our response variables to examine change in community-level functional diversity of these two groups using redundancy analysis. We then visually examined significant relationships with 3D curves and linear regression. However, we also aimed to locate sites across a landscape where the ecosystem service provision of predation (performed by predator beetles) is greatest compared to functions performed by wood-borer beetles. To do so, we elected to consider the response of separate beetle functional groups because each functional group is defined by distinct ecological function.

We previously identified that functional richness (FRic) was an important response out of the four functional diversity indices (FRic, FEve, FDiv, and FDis) at the beetle community level. Therefore, we calculated FRic for two of the three wood-borer functional groups and each predator beetle functional group (Fig. 5). The wood-borer functional group “specialist borers” was not considered because fewer than four species were present at many of the sites; thus, FRic (the trait space volume) could not be calculated. Redundancy analysis was not as successful as a method for identifying the response of individual functional group FRic. Therefore, we used Random Forest with the randomForest package in R (Liaw and Wiener 2002) to guide

the selection of best relationships between FRic and easily interpretable standardized landscape metrics within each cluster at each focus to use in subsequent multiple regression. The relationships between FRic of each beetle functional group and these selected metrics were examined with multiple regression. The significance of models and model coefficients was tested with permutation tests. Final comparisons were selected based on FRic of each functional group having a significant relationship with the same landscape metric, and final relationships were determined with polynomial regression.

Landscape metrics selected for the final polynomial regression models were applied to an Indiana landscape using the R package raster (Hijmans 2016) using a moving window with a radius corresponding to the focus examined in the polynomial regression models on a binary forest map. Raster maps of these computed landscape metrics across the Indiana landscape were multiplied by the coefficients of polynomial regression of the landscape metrics with functional group FRic to yield a predicting surface of predator beetle and wood-borer functional group FRic (Abdel Moniem and Holland 2013). We prepared the final map of beetle diversity by taking the difference between the predicted FRic of predator functional groups and predicted FRic of wood-borer functional groups and selected the areas in the 90th percentile of beneficial predator minus wood-borer beetle FRic. These areas represent locations with the greatest ratio of predator beetle-to-wood-borer FRic. All statistical analyses were performed using R (R Core Team 2017).

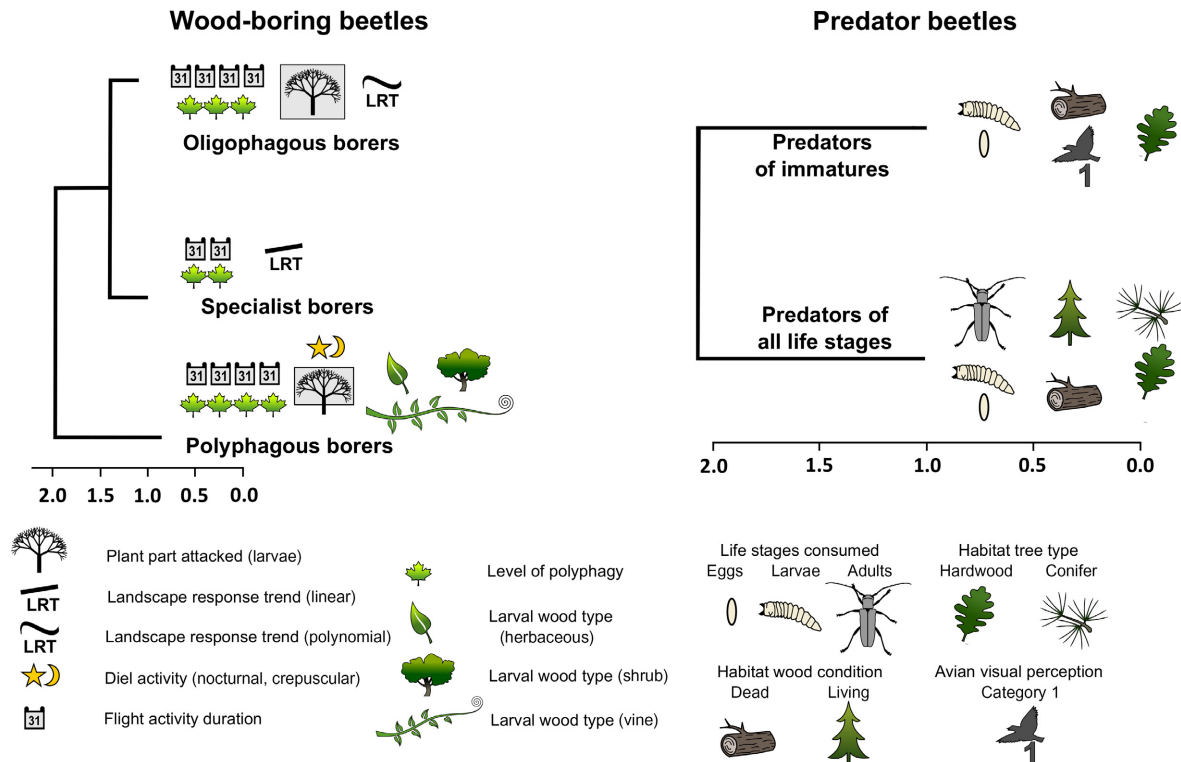


FIG. 5. Dendrogram depicting three wood-borer functional groups and two predator functional groups. Icons represent discriminating traits that were present in >50% of the species within the functional group. Functional group names are given out of convenience, and many traits are needed to delimit groups, but the functional group name may not be specifically appropriate for individual species. For example, a majority of species in the “specialist borers” functional group had a short flight season, had fewer number of larval host plant families compared to the other functional groups, and had a linear landscape response trend.

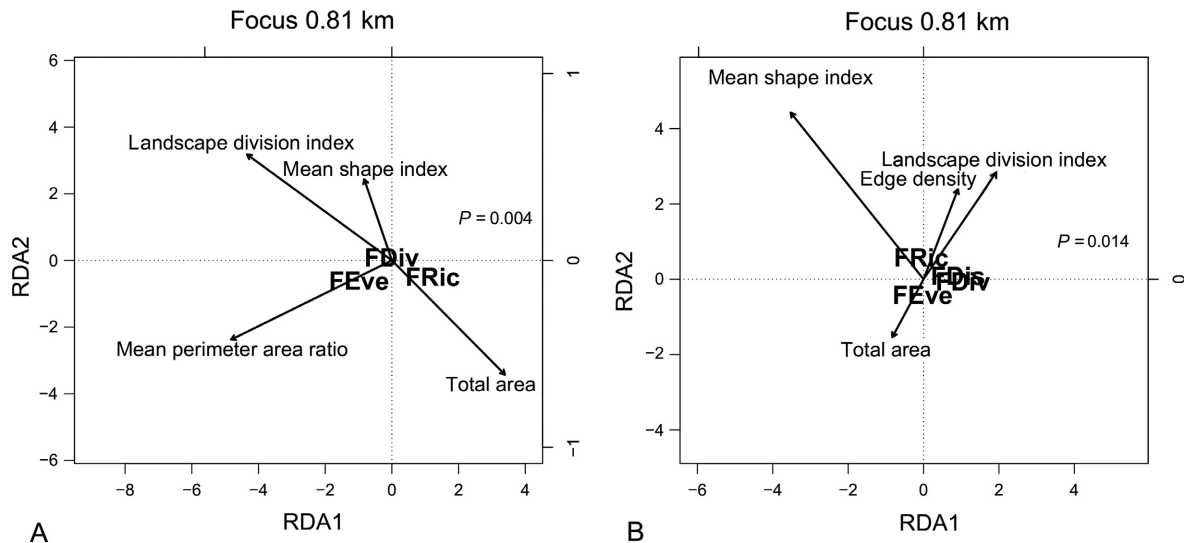


FIG. 6. Representative redundancy analysis triplots at analytical focus 0.81 km. (A) Wood-borer community functional diversity. (B) Predator beetle community functional diversity. Response variables are functional diversity indices that measure functional trait space and how species abundance is within it. FDis, functional dispersion; FDiv, functional divergence; FRic, functional richness; FEve, functional evenness.

RESULTS

Functional groupings

A total of 81 species of wood borers and 24 species from the four predatory beetle families were collected from the use of the three different flight intercept traps set within each of the 25 field sites. Species abundance data are uploaded as supplementary material (D1). Predator beetle species captured in each trap type are given in Appendix S1: Table S1. Cluster analysis on ecological traits revealed three wood-borer functional groups and two predator beetle functional groups (Fig. 5, Appendix S5). We used distinct traits present in >50% of members to characterize functional groups (Fig. 5). One newly measured trait, landscape response trend, was a discriminating trait of “specialist borers” and “oligophagous borers.” Many members of the predators of immatures functional group fell in the same avian predator visual perception category, one of the ten possible groupings resulting from our analysis. Note that the “avian predator visual perception” variable necessarily summarized variation in perception in a high dimensional space into a categorical variable for convenience (Fig. 4(3)).

Community (RDA analyses)

Wood borers and predator beetles responded to the fragmentation gradient differently, but contrary to our prediction, wood-borer functional diversity rather than predator beetle functional diversity was more sensitive to the fragmentation gradient (Fig. 6). We show here the RDA results corresponding to the focus (0.81 km) that was most important to both wood-borer and predator beetle functional diversity at the community level (Fig. 6). Functional diversity indices for the wood-borer and predator beetle communities are given in Appendix S6: Tables S1, S2. Among the functional diversity indices, functional richness (FRic) of both communities had the strongest correlation with LDI

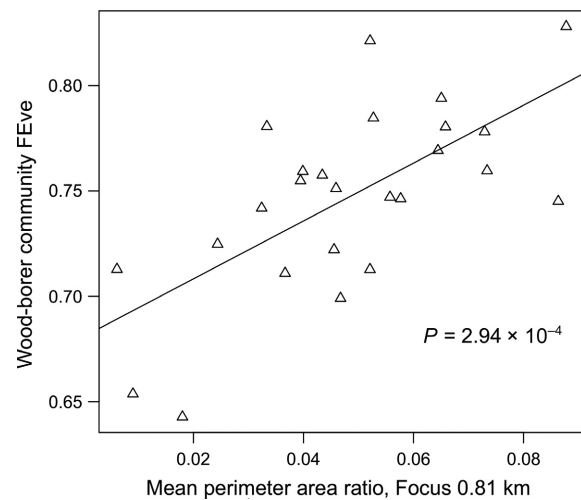


FIG. 7. Linear relationship between wood-borer functional evenness (FEve) and mean perimeter area ratio at analytical focus 0.81 km.

(landscape division index) and MSI (mean shape index). However, wood-borer community FRic was decreased (Fig. 6A) while predator beetle community FRic was increased (Fig. 6B) with LDI and MSI. There were no other common relationships between wood-borer and predator beetle community FD indices and landscape metrics aside from FRic with LDI and MSI. However, wood-borer community FEve was positively correlated with mean perimeter area ratio indicating that the evenness of functional traits increased with patch shape complexity (Fig. 7, $F_{1,23} = 18.16$, $P = 2.94 \times 10^{-4}$, $R^2 = 0.44$). The mean perimeter area ratio is an indicator for patch shape complexity where a higher value of mean perimeter ratio indicates a greater patch shape complexity. Predator beetle FEve was negatively correlated with edge density, but the relationship was not significant ($F_{1,23} = 0.32$, $P = 0.58$, $R^2 = 0.01$).

3D surface of functional richness and 3D map of functional richness

Overall, community functional richness (FRic) was greatest in intact forest landscapes. The 3D surfaces clearly show that wood-borer and predator beetle community FRic had different responses to landscape subdivision assessed with landscape division index (LDI) and patch shape complexity measured by mean shape index (MSI; Fig. 8). The curve of wood-borer community FRic ($F_{6,18} = 2.68$, $P = 0.049$, $R^2 = 0.47$, Fig. 8A) better predicted FRic with LDI and MSI than the curve of predator beetle community FRic ($F_{6,18} = 0.64$, $P = 0.70$, $R^2 = 0.18$, Fig. 8B). The final curve representing FRic across the entire beetle community (Fig. 8C) was most similar in shape to the curve of wood-borer community FRic. Wood-borer species that likely contributed most to this shape were rare or singleton species mostly within the “specialist” and “oligophagous” functional groups that were present in more intact (less subdivided) landscapes (i.e., those sites with lower LDI values).

Our map shows locations of high functional richness (FRic) along a gradient of forest fragmentation in an Indiana landscape (Fig. 3). Our map includes FRic of the oligophagous borers and FRic of predators of immatures. There were no significant relationships between FRic of the remaining functional groups and landscape metrics. FRic of the oligophagous borers and FRic of predators of immatures demonstrated a similar pattern across the landscape as FRic calculated for the wood-borer and predator community. In this map, forest fragmentation (high to low) runs east to west. There were differences between predicted areas of high oligophagous borer FRic and high predators of immatures FRic. The area of high oligophagous borer FRic was restricted to the northwestern portion of the map where the forest habitat patch was largest. Intermediate and low levels of oligophagous borer FRic were predicted to be dispersed evenly across the landscape, and levels were lowest in regions with high forest patch interspersions. FRic of predators of immatures was predicted to be highest in forested areas with intact habitat and decreased eastward with the fragmentation gradient. Unlike oligophagous borer FRic, it was less sensitive to habitat fragmentation adjacent to more

continuous forest. The final map showing the 90th percentile of predators of immatures FRic minus oligophagous borer FRic was in more fragmented forests.

DISCUSSION

Our assessment of functional diversity along a fragmentation gradient included considerable ecological information about the beetle species. We developed two newly measured functional traits that further incorporated such dimensions as multiscale interactions of species with the environment (landscape response trend) and the intertrophic interactions between beetles and avian predators (avian sensory perception). We then calculated functional diversity indices with these and other functional traits and the abundance of beetles at sites along the gradient. These functional diversity indices were used to examine changes in functional diversity of two trophic levels (wood borers and their beetle predators) with habitat fragmentation using redundancy analysis. These relationships were visually examined with 3D curves of each wood borer, predator, and overall community FRic with mean shape index (MSI) and landscape division index (LDI). Finally, we used FRic of individual beetle functional groups to map areas across a landscape where FRic of the wood-borer functional group oligophagous borers is low and FRic of the predator beetle group predators of immatures is high. We present this map and discuss implications for land use management with this and other ecological systems.

We predicted that predator beetle functional diversity would demonstrate a greater sensitivity to changes along the forest fragmentation gradient than would the wood-borer functional diversity. There are no previous studies to our knowledge that assessed change in beetle functional diversity with these functional diversity measures. But, predatory beetles can be more sensitive to edge (Costa et al. 2013) and fragmentation (Ryall and Fahrig 2005) than their prey. Functional groups with a greater number of species are more likely to share more diverse functional traits (Tilman et al. 1996), and dominant species may have more diverse trait profiles (Walker et al. 1999). Therefore, we predicted that fewer, less abundant predator species in fragmented forests would result in decreased functional diversity.

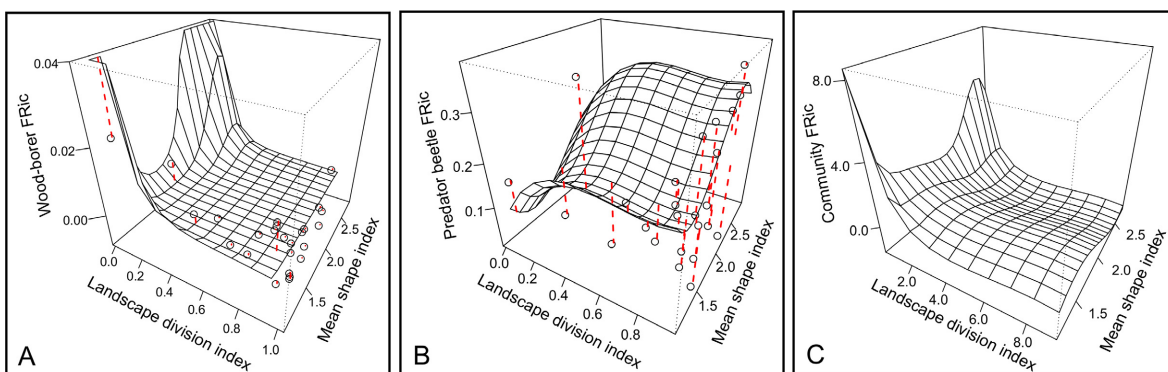


FIG. 8. Three-dimensional surface of beetle functional richness (FRic) across an Indiana landscape to guide land use management. FRic values are standardized by the “global” FRic that includes all species making FRic values constrained between 0 and 1 (Laliberté and Legendre 2010, Laliberté and Shipley 2011). (A) Wood-borer community functional richness; (B) predator beetle community functional richness; (C) overall community functional richness. Wood-borer functional richness was restricted to a representative range of FRic values.

At the community level, predator beetle functional richness increased with mean shape index (MSI) and landscape division index (LDI). However, wood-borer functional richness decreased with LDI and was greatest at low and higher MSI values. We did not assess community change at the species level since previous studies have already made such comparisons in other systems (e.g., Villéger et al. 2010, Baraloto et al. 2012). We based our prediction of greater negative response to fragmentation by the predator beetles by assuming that the abundance response of a common species would be similar to that of other predators, leading to a similar “scaled up” response in the larger functional groups. However, functionally redundant communities may harbor high species diversity but low functional diversity if functional redundancy is high. Functional richness (FRic), as measured in our study, is independent of species abundance. Therefore, FRic may be high even if few species are present, as long as those species have diverse trait profiles. Our findings thus suggest that studies measuring functional outcomes should consider both species abundance and functional richness, or functional diversity measures that indicate how species abundance is distributed within the functional trait space of a community.

Results from our study at the community level were echoed in our map of FRic of two functional groups, oligophagous borer and predators of immatures and overall FRic of these two functional groups. One interesting feature of our map is that higher FRic of predators of immatures had a broader distribution than that of oligophagous borer functional diversity. FRic of predators of immatures, like FRic of oligophagous borers, was greatest in more intact forested landscapes but was less restricted to them. Upon examining the 3D surfaces, we predict that this is due to FRic of the predators of immatures functional group not being as sensitive to forest edge and forest patch interspersions.

Management implications

We propose that the methods we present to produce prediction maps of functional diversity across landscapes can be incorporated into a strategy to select landscape configurations that maximize chosen ecological functions among single or multiple communities. A logical management application for our study would be the identification of locations across landscapes for production sites (e.g., hardwood plantation and orchard) where losses to beetles are minimized. Here, we have avoided grouping species according to human perception of their role based upon our focus of whether they conflict with human production interests. Such groups, much like “plant vs. weed,” are biologically hollow and run counter to the idea of functional diversity in a modern sense. The high trait dimensionality we used for delineating functional groups thus resulted in groupings that theoretically better approached beetle ecological functional roles in forests than if beetles were classified based on whether a “pest” or a “predator.” However, functional groups such as the oligophagous borer group still contain a number of species that are known to attack living, weakened, or dying trees (*Gaurotes cyanipennis*, *Gracilia minuta*, *Neandra brunnea*, *Neoclytus m. mucronatus*, *Parelapthidion*

incertum, *Prionus laticollis*). Therefore, our prediction map can serve as a proxy of areas where the ecosystem services provided by predator beetle species is highest.

The approach we develop is not limited to the forest beetles we consider here and may be applied to other ecological systems. For instance, agroecosystems represent a managed system where pollination is a critical ecosystem service. Our functional diversity map approach could be utilized by grouping native pollinating species by the range of their known ecological functions and examining the response of their functional diversity to habitat loss and fragmentation. Locations identified with high native pollinator functional diversity, particularly if assessed considering how species abundance is dispersed in functional trait space, could then be protected through conservation efforts.

Our workflow of constructing maps showing areas of high functional diversity is very transferrable and thus could be extended to other systems and across larger landscapes. Together with expanding availability of spatial data sets and databases on species functional traits (i.e., TRY Plant Database [Kattge et al. 2011]), locations of high functional diversity could be identified throughout the globe. This approach may further identify areas in need of conservation that would be potentially overlooked if considering biodiversity alone. This approach would have a broader impact, particularly in the arena of aiding policy decisions, because of the high anthropogenic pressure on ecosystems and the importance of functional diversity to provide ecosystem stability.

The construction of the 3D curves and maps should involve both the standardization of functional diversity indices of the different communities and the assessment of functional diversity response across species-relevant foci. Plots may then incorporate both communities and the resulting plot used to reveal landscapes most appropriate for maximizing functional diversity of multiple communities, or even those that favor certain ecosystem service providers over others. Ecological trends from the 3D curves of multiple trophic groups along landscape gradients could be distilled into maps that categorize the landscape based on how appropriate they are for various production systems or management goals.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.1780/full>

DATA ACCESSIBILITY

Additional data available from the Purdue University Research Repository: <https://doi.org/10.4231/r7cf9nb9>.