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CONTRIBUTED PAPERS

Conserving alpha and beta diversity in wood-production landscapes

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Abstract

International demand for wood and other forest products continues to grow rapidly, and uncertainties remain about how animal communities will respond to intensifying resource extraction associated with woody bioenergy production. We examined changes in alpha and beta diversity of bats, bees, birds, and reptiles across wood production landscapes in the southeastern United States, a biodiversity hotspot that is one of the principal sources of woody biomass globally. We sampled across a spatial gradient of paired forest land-uses (representing pre and postharvest) that allowed us to evaluate biological community changes resulting from several types of biomass harvest. Short-rotation practices and residue removal following clearcuts were associated with reduced alpha diversity (−14.1 and −13.9 species, respectively) and lower beta diversity (i.e., Jaccard dissimilarity) between land-use pairs (0.46 and 0.50, respectively), whereas midrotation thinning increased alpha (+3.5 species) and beta diversity (0.59). Over the course of a stand rotation in a single location, biomass harvesting generally led to less biodiversity. Cross-taxa responses to resource extraction were poorly predicted by alpha diversity: correlations in responses between taxonomic groups were highly variable (−0.2 to 0.4) with large uncertainties. In contrast, beta diversity patterns were highly consistent and predictable across taxa, where correlations in responses between taxonomic groups were all positive (0.05–0.4) with more narrow uncertainties. Beta diversity may, therefore, be a more reliable and information-rich indicator than alpha diversity in understanding animal community response to landscape change. Patterns in beta diversity were primarily driven by turnover instead of species loss or gain, indicating that wood extraction generates habitats that support different biological communities.

KEYWORDS
alternative energy, biodiversity, bioenergy, biomass, community, multispecies, occupancy modeling, resource extraction

Conservación de la Diversidad Alfa y Beta en Paisajes de Producción Maderera

Resumen: La demanda internacional de madera y otros productos forestales sigue creciendo rápidamente mientras permanecen las incertidumbres sobre cómo responderán las comunidades animales a la intensificación de la extracción de recursos asociada con la producción de bioenergía leñosa. Examinamos los cambios en la diversidad alfa y beta de murciélagos, abejas, aves y reptiles en los paisajes de producción maderera en el sureste de los Estados Unidos, un punto caliente de biodiversidad y una de las fuentes principales de biomasa leñosa a nivel mundial. Muestreamos a lo largo de un gradiente

espacial de usos de suelo forestales emparejados (representando la pre- y postcosecha) que nos permitió evaluar los cambios en las comunidades biológicas resultantes de varios tipos de recolección de biomasa. Las prácticas de corta rotación y de eliminación de residuos después de la tala estuvieron asociadas con la reducción de la diversidad alfa (−14.1 y −13.9 especies, respectivamente) y una diversidad beta más baja (es decir, diferencia de Jaccard) entre los pares de uso de suelo (0.46 y 0.50, respectivamente), mientras que el raleo de rotación media incrementó la diversidad alfa (+3.5 especies) y beta (0.59). Durante la duración de una rotación permanente en una sola ubicación, la cosecha de biomasa generalmente derivó en menos biodiversidad. La respuesta de los taxones a la extracción de recursos estuvo muy mal pronosticada por la diversidad alfa: la correlación de las respuestas entre los grupos taxonómicos fue altamente variable (−0.2 a 0.4) con muchas incertidumbres. Como contraste, los patrones de diversidad beta fueron fuertemente coherentes y predecibles en todos los taxones, mientras que la correlación de las respuestas entre los grupos taxonómicos siempre fue positiva (0.05 a 0.4) con incertidumbres más limitadas. Por lo tanto, la diversidad beta puede ser un indicador más confiable y rico en información que la diversidad alfa para entender las respuestas de la comunidad animal a los cambios en el paisaje. Los patrones de la diversidad beta estuvieron impulsados principalmente por la rotación en lugar de la pérdida o ganancia de especies, lo que indica que la extracción de madera genera hábitats que mantienen a diferentes comunidades biológicas.

PALABRAS CLAVE
biodiversidad, bioenergía, biomasa, comunidad, energía alternativa, extracción de recursos, modelado de ocupación, multiespecie

保护木材生产景观的α多样性和β多样性

【摘要】国际上对木材和其它森林产品的需求在持续快速增长, 而动物群落如何应对与木质生物能源生产相关的日益加剧的资源开采, 仍然存在不确定性。美国东南部是生物多样性的热点地区, 也是全球木质生物质的主要来源之一, 本研究分析了该地区木材生产景观中蝙蝠、蜜蜂、鸟类和爬行动物 α 多样性和 β 多样性的变化。我们沿空间梯度对森林土地利用情况两两取样 (代表采伐前和采伐后), 以评估几种生物质采伐造成的生物群落变化。短期轮伐和皆伐后清除残留物都与成对的土地利用样方之间 α 多样性降低, (分别为 −14.1 个物种和 −13.9 个物种) 及 β 多样性 (即 Jaccard 异质性) 降低 (分别为 0.46 和0.50) 有关, 而中期轮伐间苗则可以增加 α 多样性 (+3.5 种) 和 β 多样性 (0.59) 。在单一地点的林分轮换过程中, 生物质采伐一般会导致较低的生物多样性。 α 多样性很难预测对资源开采的跨类群响应, 表现为类群之间响应的相关性高度可变 (−0.2 到 0.4), 有很大的不确定性。相比之下, 各类群之间的 β 多样性格局则具有高度的一致性和可预测性, 类群之间的响应都是正相关关系 (0.05 至 0.4), 不确定性较小。因此, 在理解动物群落对景观变化的响应方面, β 多样性可能是比 α 多样性更可靠、信息更丰富的指标。β多样性的格局主要是由周转而非物种丧失或增加所驱动的, 表明木材生产可以产生支持不同生物群落的生境。**【翻译: 胡怡思; 审校: 聂永刚】**

关键词: 关键词, 替代能源, 生物多样性, 生物能源, 生物质, 群落, 多物种, 占域模型, 资源开采

INTRODUCTION

Human land use has altered natural landscapes and biological communities globally (Foley et al., 2005; Radeloff et al., 2015). Land conversion, land-use intensification, and resource extraction can benefit humans through provisioning of ecosystem services (e.g., timber, fuel, and food production). However, these activities can result in biological system disruptions, such as biodiversity loss (Newbold et al., 2015), biotic homogenization (Gossner et al., 2016), and reduced functional diversity and redundancy (Flynn et al., 2009; Laliberté et al., 2010), which in turn can reduce ecosystem services (Díaz et al., 2006). Global increases in the extent of agricultural lands (Ramankutty et al., 2018; Song et al., 2018) are particularly concerning because intensive agricultural practices can diminish alpha diversity (species richness) and beta diversity (differences in community composition) (e.g., Edwards et al., 2010; Karp et al., 2012). How emerging human-driven land-use changes, such as renewable and alternative energy development, affect biodiversity is relatively unknown, in particular, whether alpha and beta diversity

are altered in similar ways across different taxa (Socolar et al., 2016).

Rapid intensification of woody biomass production across large land areas has hastened the need for robust appraisal of the potential effects of this form of renewable energy on biodiversity. Biomass makes up most of the global renewable energy supply (70%), and woody biomass (e.g., wood pellets and charcoal) comprises 85% of all biomass used for energy worldwide (WBA, 2019). Legislation in the United States (US), United Kingdom (UK), and European Union (EU), including the 2007 Energy Independence and Security Act (US) and the 2009 and 2018 Renewable Energy Directives (EU), has driven increased production and use of woody biomass for alternative energy (US DOE, 2016). Forest bioenergy supply chains in the United States expanded in response to increased international demand for wood-based biomass (Kittler et al., 2020), with pellet manufacturing capacity increasing from <0.3 million t prior to 2009 to approximately 9.0 million t (Aguilar et al., 2020). The large contribution of biomass to the bioenergy portfolio exists in part because large areas managed for wood production already exist to support the emerging industry. Currently, wood pellet mills source 80% of the fiber used to generate pellets from timber harvest residuals (i.e., treetops, limbs, bark, foliage, and other nonmerchantable materials) generated during roundwood timber harvests (Aguilar et al., 2020; Kittler et al., 2020).

A shift to bioenergy production may entail intensification that differs from traditional timber practices to supply wood fiber. These changes could include shortening stand rotation times, planting at higher densities, planting faster-growing tree species, and land conversion, each of which could result in negative impacts to native ecosystems (Aguilar et al., 2020) and biodiversity (Fletcher et al., 2011; Nuñez-Regueiro et al., 2021). Concerns about the sustainability and carbon neutrality of wood-based biomass production have resulted in the UK and EU mandating that such production meets sustainability standards along the supply chain (i.e., carbon neutrality, reforestation after wood harvest, protection of biodiversity, and compliance with best management practices to maintain environmental quality [e.g., water or soil quality]) (Dale et al., 2016; Hodges et al., 2019; Kittler et al., 2020). Wood fibers cannot be harvested from forest that is legally withdrawn from timber production (Aguilar et al., 2020); however, concerns about the sustainability of wood-based biomass production remain.

The U.S. coastal southeast (hereafter Southeast) contains 72% of the country's planted timberlands (Oswalt et al., 2014) and is one of the world's most important woody biomass production regions (Fletcher et al., 2011; Aguilar et al., 2020). In 2015, 80% of the global supply of woody bioenergy (in the form of wood pellets) was consumed in the EU; 98% of this supply was sourced from the U.S. Southeast (Duden et al., 2017). The Southeast also contains a biodiversity hotspot, the North American Coastal Plain (Noss et al., 2015). Although intensive forestry has been practiced throughout the Southeast for decades, recent emergence of a domestic U.S. bioenergy market and large exports of woody biomass to the EU (Duden et al., 2017) have resulted in rapid ecosystem-level changes (Aguilar et al., 2020). Historically, longleaf pine ecosystems were the dominant cover type in the Southeast, but their extent was greatly reduced due to extensive harvesting and fire suppression (Jose et al., 2006). Alongside expanding bioenergy production, efforts to restore longleaf pine ecosystems have grown substantially (Mcintyre et al., 2018).

We examined patterns of alpha and beta diversity of animal communities in wood production landscapes. We conducted biodiversity sampling across forest conditions, where wood resources were extracted in early, mid, or late rotation, representing different types of potential forest changes from three primary bioenergy harvests identified by the U.S. Department of Energy: residue removal following clearcutting, midrotation thinning, and reduced stand age from short-rotation practices, respectively (US DOE, 2016). We simultaneously surveyed bats, bees, birds, and reptiles, which may serve as environmental indicators of bioenergy sustainability (Efroymson et al., 2013), with a spatial sampling protocol that allowed direct estimation of management effects associated with bioenergy resource extraction. Our cohesive multitaxon sampling scheme allowed the examination of the degree to which different taxa exhibit consistent responses to bioenergy resource extraction and whether certain taxonomic groups might serve as clear indicators of the sustainability of different bioenergy practices based on cross-taxa predictability (Efroymson et al., 2013). Although such assessments traditionally emphasize alpha diversity in conservation, beta diversity could be more reliable in predicting consistent biodiversity changes that may arise from land-use change (Kessler et al., 2009). Despite this potential, this issue has rarely been addressed across taxonomic groups (but see, Kessler et al., 2009) and has not been tested in energy production landscapes.

We considered how different types of biomass resource extraction in wood production landscapes alter the species richness (alpha diversity) and compositional dissimilarity (beta diversity) of animal communities. We interpreted the potential conservation value of different land uses by examining dissimilarity with communities in longleaf pine ecosystems. We also considered the consistency of responses to resource extraction (i.e., predictability) across taxa.

METHODS

Study area and site selection

Our study area was the Southern Coastal Plains and Southeastern Plains of the North American Coastal Plain. We used a stratified sampling approach to select 68 sites (Figure 1a) across three geographic regions, where substantial contributions to current and future woody bioenergy supply are expected (Aguilar et al., 2020; Kittler et al., 2020). We contacted managers of large tracts of public lands and extension agents in each region to develop a list of potential sites for sampling. We then visited potential study sites to evaluate whether forest stands matched one of our six desired land-use types (see below). We filtered the pool of potential sites to ensure

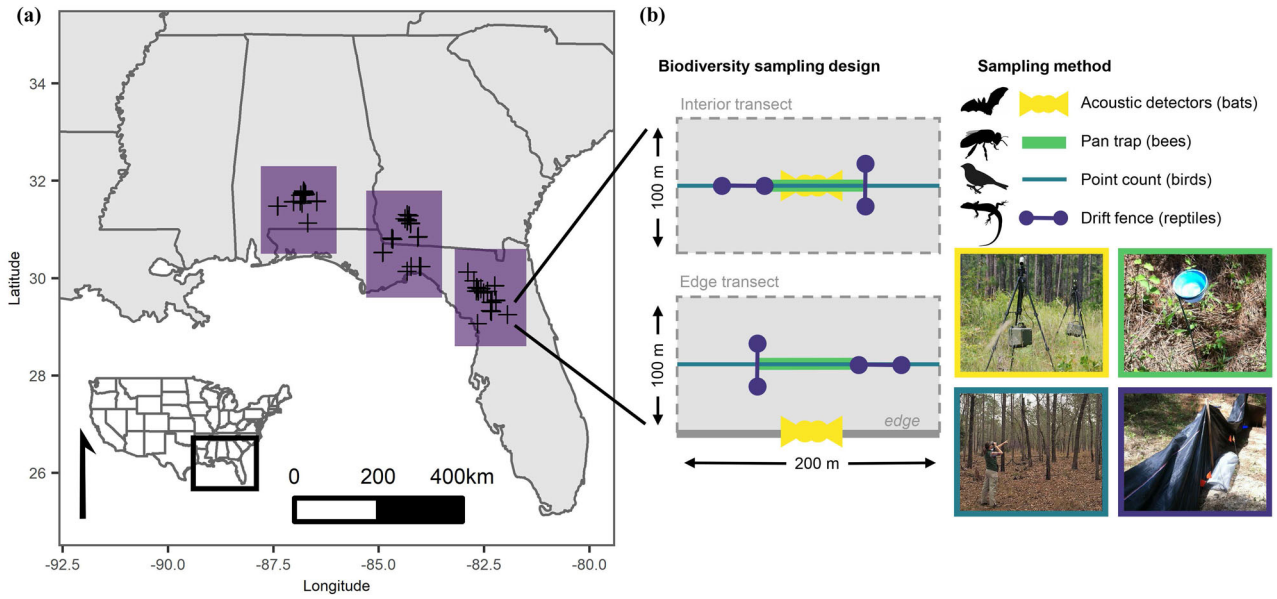

FIGURE 1 In a study of the effects of woody bioenergy harvest on biodiversity, (a) distribution of 68 study sites for biodiversity sampling across the southeastern United States (blue boxes, geographic regions) and (b) layout of transects for multitaxon sampling

balanced representation of different land uses across the three regions.

We chose sites across a wood-extraction gradient that would allow us to evaluate effects of woody biomass removal on biodiversity (Figure 2). The sites had either loblolly (*Pinus taeda*) or slash pine (*P. elliottii*), the two most common species for timber production in the Southeast (Smith et al., 1994). Study sites had six land-use types: clearcut (0–3 years postharvest) with logging residues removed ($n = 10$), clearcut of similar age (0–3 years) with residues remaining ($n = 11$), young plantation (8–10 years, $n = 11$), recently thinned midrotation stand (12–16 years, $n = 13$), unthinned midrotation stand (12–16 years, $n = 11$), or mature plantation (20–32 years, $n = 12$). Sampling across this management gradient allowed us to evaluate biodiversity effects of resource extraction at different points in the rotation. We developed three bioenergy contrasts (Figure 2): the residue contrast examined the potential effects of removing woody harvest residues for bioenergy use following clearcut management at the time of stand initiation (0–3 years postclearcut); the thinning contrast examined potential effects of midrotation (12–16 year) thinning for bioenergy; and the short-rotation contrast examined the potential biodiversity effects of shorter rotation times for exclusive bioenergy production (i.e., shift from older to younger forests). These alternatives are potential pathways for woody bioenergy production (US DOE, 2016).

Each study site was characterized by one of the six land-use types. The landscapes surrounding individual sites varied in forest cover extent; variability was higher among the three regions than within each region (Jones et al., 2020). Average size of sites ranged from 39 to 54 ha, depending on land-use type. Sampling of land-use types was balanced across years. Most forested land in the Southeast is privately owned. Therefore, we selected study sites in proportion to regional land ownership patterns: 74% of sites were privately owned (37% nonindustrial private landowners and 37% private industrial timber). The remaining 26% were local, state, or federally owned. The distribution of the six land-use types was not balanced across the three ownership types (nonindustrial private, industrial timber, and local, state, or federal) (Appendix S1). However, our primary objective was to balance representation of management types across regions (i.e., across years) rather than across ownership types.

Biodiversity sampling

We synchronously sampled bats, bees, birds, and reptiles at each study site (Figure 1b). Surveys were conducted in two, 100 × 200 m transects. One transect was at least 150 m from the stand edge (interior transect), and the other was at the stand edge where the contrast with adjacent habitat was greatest (edge transect). The two transects were placed at least 100 m apart. Each transect included acoustic detectors for sampling bats, pan traps for sampling bees, counts for sampling birds, and drift fences for sampling reptiles. Each site was surveyed two to four times during each field season (April–July); surveys were typically separated by 3–4 weeks. Surveys were conducted during spring and summer of 2013, 2014, and 2015; different sites were visited each year (i.e., the same site was not visited in multiple years to increase spatial coverage of sampling).

At each site, we placed four Anabat II echolocation detectors coupled with Zero Crossing Analysis Interface Modules (ZCAIMS, Titley Electronics, Ballina, NSW). The first unit was placed on the interior transect and directed toward the least vegetative obstruction. The second was positioned 5 m from the first and oriented 180° from it (Duchamp et al., 2006). The third and fourth units were positioned similarly, but on

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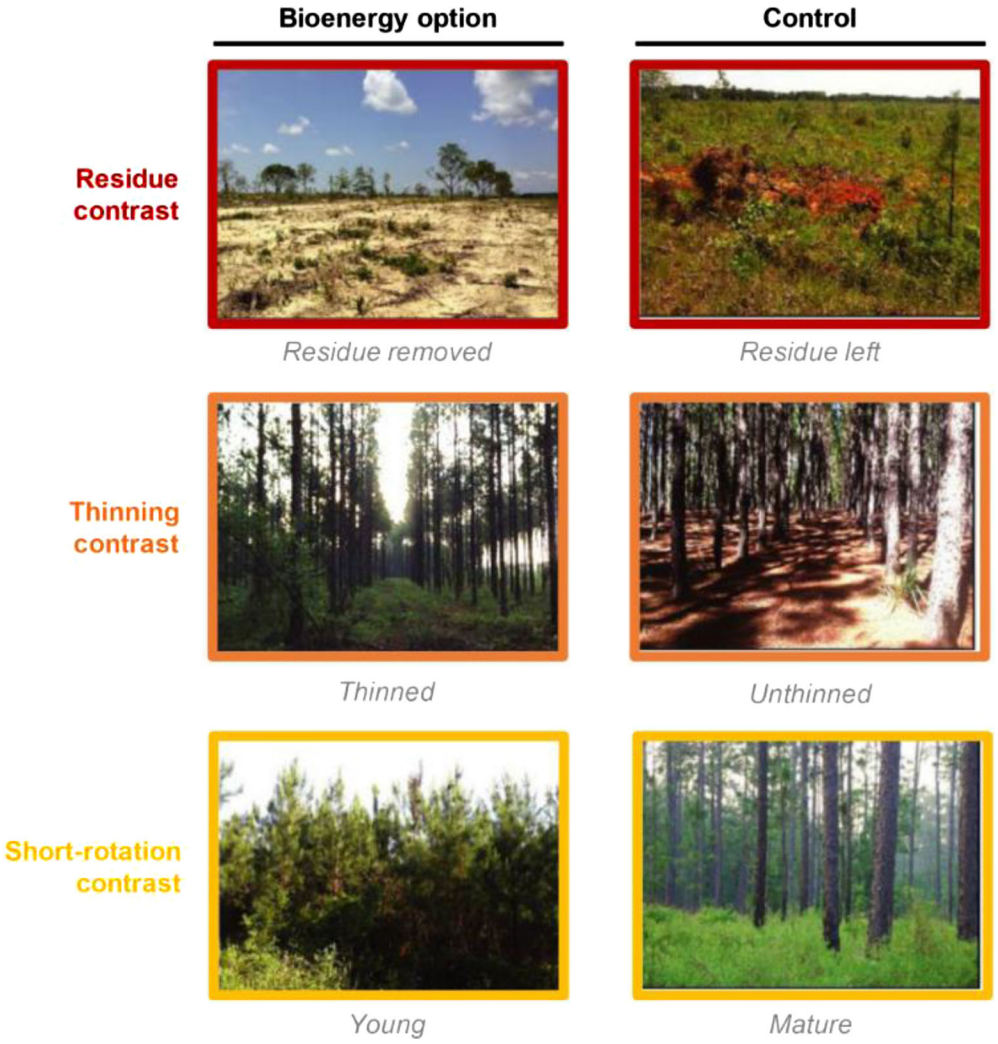

FIGURE 2 Three a priori bioenergy forestry contrasts (residue, thinning, and short rotation) in six land uses

the edge transect. The two detectors within each pair were treated as observers, such that detection histories reflected the double-observer approach for estimating detection probability (Duchamp et al., 2006). Microphones were positioned on tripods 1.5 m above the ground, housed in protective shrouds, and oriented 40° from horizontal to maximize sampling volume. Detectors recorded from 30 min before sunset to 30 min after sunrise and were calibrated two to four times each field season (Larson & Hayes, 2000). We used Kaleidoscope Pro 3.14B (Wildlife Acoustics, Maynard, MA) and the Bats of Florida Classifier to classify calls to species or species groups. We filtered out ambiguous and low-quality bat calls to ensure low rates of species identification errors by using the balanced sensitivity and accuracy setting in Kaleidoscope Pro (which gives parity to both sensitivity and accuracy); checking files with characteristics of multiple species and retaining only those in which >50% of the calls matched the species identification assigned by the software; and manually reviewing files with unexpected species classifications based on range maps. To aid in manual validation, we compared recordings with those in a reference library we compiled of echolocation calls from bats across the Southeast. Additional details are in Ober et al. (2020).

We used pan traps and aerial netting to collect bees (Westphal et al., 2008). Traps were plastic cups (96 mL, model P325, SOLO Cup Company) painted ultraviolet bright blue, white, or yellow filled with a dilute detergent and water solution (Kearns & Inouye, 1993; Westphal et al., 2008). At each site, we placed 15 pan traps ~40 cm above the ground on wire stakes so they would be visible above herbaceous vegetation. We positioned traps so that colors alternated along the center 100 m of the transect. Pan traps were set in the morning and collected after 24 h. We netted bees along the length of the transect for 30 min, excluding handling time. The pan trap and netting records were combined to form a detection history for each visit to account for imperfect detection. We accounted for potential differences in detectability between the two methods with a covariate for survey type (Appendix S2). Bee surveys were postponed on cloudy or rainy days, and each transect was sampled up to four times on separate days, amounting to up to eight sampling days per site. We preserved

collected bees in ethanol or pinned them. We identified each specimen to species or occasionally genus in the laboratory. We keyed all specimens to the genus level and 92% of taxa to the species level based on Discover Life online keys (https://www.discoverlife.org), Michener (2000), Michener et al. (1994), and Gibbs (2011). Our identifications were verified by Ismael Hinojosa (Universidad Autonoma de Mexico) and Sam Droege (USGS). Sam Droege identified many specimens (particularly *Lasioglossum*) to species and confirmed identification of 100% of our *Dialictus* specimens. Additional details are in Loy et al. (2020).

We surveyed birds along line transects (Emlen, 1971). Trained observers walked at a standard pace down the center line of each transect and recorded all birds observed by sight or sound within the boundaries of the transect. During each sampling occasion, each transect was surveyed twice between sunrise and 0930 to account for variation in detectability. Surveys were postponed if wind or rain compromised an observer's ability to detect birds. Additional details are in Gottlieb et al. (2017).

We sampled reptiles with drift fences and pitfall traps (Gibbons & Semlitsch, 1981). Drift fences were 5 × 0.5 m sections of siltation fence or aluminum flashing placed vertically in the soil. We placed one pitfall trap (19-L bucket) at each end of the drift fence. Two drift fences with pitfall traps were installed in the interior transect and two in the edge transect, totaling four drift fences and eight pitfall traps per site. Detections were pooled across drift fences at each site. In 2014 and 2015, funnel traps were placed midway along either side of each drift fence (2/fence) to increase captures of snakes capable of escaping pitfall traps (Heyer et al., 2014). We accounted for this difference in trapping method across years in our statistical analyses (see below). We monitored traps every 4 weeks over 16 weeks each year (four sample weeks/site/year). During each sampling occasion, we opened traps on day 1 and checked once a day for three consecutive days. We used this 3-day record to account for imperfect detection. When not in use, we placed lids on pitfall traps and placed funnel traps vertically to prevent captures. We shaded the pitfall and funnel traps and placed a wet sponge to minimize the risk of desiccation of animals. Additional details are in Jones et al. (2020).

Multispecies occupancy modeling

We used multispecies occupancy modeling to evaluate community richness and composition at each study site while accounting for imperfect detection (Dorazio & Royle, 2005). We fitted a different multispecies occupancy model for each taxon because detection differed among groups due to variation in survey methods and taxon-specific biology (Appendix S2). We assumed closure of occupancy models would be violated (Rota et al., 2009), at least for some species, because visits occurred over 16 weeks. Therefore, we designated populations closed within visits (based on multiple sampling efforts within visits) but open between visits (i.e., those that occurred every 3–4 weeks) by treating each visit as a separate detection history (i.e., each visit contained repeated samples as specified above) and specifying site as a random effect (Rota et al., 2009). In these models, the occupancy component for all taxa was structured as

$$z_{ik} \sim \text{Bernoulli}\,(\psi_{ik}) \text{ and logit}\,(\psi_{ik}) = \beta 1_k \,\text{land use}_i + \text{region}_{ik} + \text{site}_{ik}, \quad (1)$$

where z_{ik} is the true occurrence state for site $i = 1, 2, \ldots, N$ (where each site was a site-visit combination to relax the closure assumption) and species $k = 1, 2, \ldots, K$. The probability of occupancy, ψ_{ik}, was modeled as a function of fixed effects for land-use type (land use_i) with the means parameterization (Kery & Royle, 2016) and random effects for geographic subregion (region_{ik}) and study site (site_{ik}) to account for spatial clustering and repeated sampling. We pooled interior and edge transect surveys for analysis of bird, bee, and reptile data and retained only interior transect surveys for analysis of bat data because strong edge and ecotone associations among bats in our study area (Ober et al., 2020) obscured potential associations with the focal land-use type.

We fitted the multispecies occupancy models in JAGS version 4.3.0 (Plummer, 2003) in the R programing environment of package jagsUI version 1.5.1 (Kellner, 2016) to sample from posterior distributions with the Markov chain Monte Carlo (MCMC) algorithm. We used prior distributions for fixed-effects parameters that were uninformative when back-transformed to the logit scale: normal ($\mu = 0$, $\sigma = 1.4$) (Hobbs & Hooten, 2015; Northrup & Gerber, 2018). For each taxon, we ran three chains; each began with a burn-in of 5000 iterations. Then, we sampled from the posterior distribution for 20,000 iterations with a thin rate of 200 to select samples, resulting in a posterior sample of 300 across all chains for each parameter. Convergence was assessed using the Rubin–Gelman statistic (all $\hat{R}$ values < 1.1). We used posterior samples of the true occurrence state matrix ($\mathbf{z}$) to derive estimates of alpha and beta diversity corrected for imperfect detection. Sites in $\mathbf{z}$ produced from the occupancy model represented site-visit combinations. We collapsed $\mathbf{z}$ by site to reflect the highest estimated true occurrence state across visits for downstream analyses. For example, we used 1 if it was the estimated as the latent state in any of the four visits. We retained $\mathbf{z}$ from each MCMC iteration to compute alpha and beta diversity. Posterior estimates of alpha diversity in each land-use type are in Appendix S3.

Effects of bioenergy alternatives on biodiversity

We estimated potential effects of different bioenergy alternatives on each taxon with a priori contrasts between land-use types that represented expected changes in structure, age, or management practices associated with bioenergy resource extraction (Figure 2). For alpha diversity, bioenergy contrasts were computed by subtracting the posterior distribution of the control land-use effect from the bioenergy option land-use

effect (e.g., thinning effect $= \sum_{i=1}^{N} (z_{ik})_{\text{thinned}} - \sum_{i=1}^{N} (z_{ik})_{\text{unthinned}}$, repeated for each posterior sample) (Figure 2). Thus, the alpha-diversity bioenergy contrasts represented the expected change in species richness resulting from bioenergy resource extraction. For beta diversity, contrasts were computed using the average pairwise Jaccard dissimilarity of **z** between control and bioenergy option land uses, repeated for each posterior sample. Thus, the beta-diversity contrast represented the degree to which community composition would be expected to change because of bioenergy resource extraction (i.e., proportion of species not shared between the two land uses). Because we computed beta diversity with output from multispecies occupancy models, estimates of beta diversity were corrected for imperfect detection of species.

We made synthetic inferences about all taxa combined by pooling posterior distributions from all four taxonomic groups. For pooled estimates of alpha diversity, we summed the posterior distributions of the bioenergy contrast effects across the four taxa to obtain total species richness. For beta diversity, we averaged the posterior distributions of the bioenergy contrast effects across the four taxa to obtain an average beta diversity.

Often, beta diversity is compared within land uses to examine, for example, biotic homogenization associated with a given land use type (e.g., intensive agriculture [Karp et al., 2012]). We focused on beta diversity among land uses in paired contrasts (Figure 2) to examine expected community differences associated with land-use change. We also computed beta diversity among all pairwise land-use comparisons (including within land use). Moreover, we decomposed beta diversity effects into nestedness and turnover components (Baselga, 2010) to better understand the ecological mechanisms underlying beta diversity. Results from these analyses are in Appendices S4–S6.

Conservation value of land uses

To put into context the conservation value of biological communities in each land-use type, we evaluated beta diversity between each of the six land-use types (Figure 2) and communities sampled in an additional land-use type: longleaf pine forest. Thus, we treated biological communities in extant longleaf pine ecosystem as a reference community. We sampled animals in longleaf pine forest in the same manner described above for the other six land-use types. Like the bioenergy contrasts, we computed beta diversity as the average pairwise Jaccard dissimilarity of **z** between longleaf and each of the six other land-use types (on an individual basis), repeated for each posterior sample. Thus, the beta diversity contrast represented the degree to which community composition in each of the six land uses differed from longleaf pine communities, or the proportion of species not shared between the two land uses. Greater similarity with longleaf pine communities would highlight greater conservation value of that land use.

Diversity accumulation across management scenarios

Because forest management land uses change with succession and stand rotation, we developed a suite of five land-use scenarios to evaluate potential effects of different bioenergy pathways on how species richness accumulated through time (Table 1). Scenarios included combinations of the six land-use types (Figure 2) and should be conceptualized as a temporal sequence of land uses (i.e., moving through different land-uses as succession occurs during the stand rotation from initial conditions through early, mid, and late rotation). Therefore, we evaluated how species might accumulate in a stand through time under each scenario. Temporal diversity was evaluated by computing the unique species added to the species pool with each subsequent land use in the rotation with **z**. For example, beginning with the species present in clearcuts with residues removed (initial conditions), we added the complement (or set difference) of species in young forest to compute the accumulated diversity at early rotation. This process was repeated for mid and late rotation to produce cumulative species richness throughout the full rotation. We also computed the average richness during the stand rotation and the total richness at the end of the rotation for each scenario.

Predictability of alpha and beta diversity patterns

We evaluated the consistency and predictability of biodiversity patterns among taxa to assess the potential value of certain taxa as indicators of bioenergy sustainability, as well as how the choice of diversity component (alpha or beta diversity) might affect this inference (e.g., Kessler et al., 2009). To evaluate predictability of alpha diversity, we computed the Pearson correlation coefficient (r) of site-level species richness (alpha diversity) for all pairwise comparisons between taxa (e.g., birds vs. bees, etc.) for each sample from the posterior distribution. This measure can be interpreted as the degree to which the richness of one taxon is correlated with (or able to be predicted by) the richness of another taxon at the site level. We focused on site-level richness, not just contrasts between sites of different land uses. For beta diversity, we computed the Mantel correlation coefficient (r) of pairwise Jaccard dissimilarity for each sample from the posterior distribution (for all pairwise comparisons between taxa). This measure shows the degree to which community dissimilarity (or difference in community composition) between two sites for a given taxon can be predicted by another taxon. We focused on dissimilarity in species composition among all pairs of sites, not just contrasts between sites of different land uses. We, therefore, obtained posterior distributions of r for alpha and beta diversity, which allowed us to evaluate its direction and magnitude in relation to zero (i.e., no predictability between taxa) and precision. We also examined which biodiversity metric (alpha vs. beta) resulted in higher cross-taxa

TABLE 1 Landscape scenarios used to estimate how species richness accumulates in a forest stand through time

Landscape scenario	Land-use sequence	Description of sequence
1, no bioenergy	residue left, young, unthinned, mature	Stand is initiated with a clearcut with harvest residues left (0–3 years), advances to young stand (8–10 years), remains unthinned midrotation (12–15 years), and advances to mature stand (20–32 years).
2	residue removed, young, unthinned, mature	Stand is initiated with a clearcut with harvest residues removed (0–3 years), advances to young stand (8–10 years), remains unthinned midrotation (12–15 years), and advances to mature stand (20–32 years).
3	residue left, young, thinned, mature	Stand is initiated with a clearcut with harvest residues left (0–3 years), advances to young stand (8–10 years), receives thinning midrotation (12–15 years), and advances to mature stand (20–32 years).
4	residue removed, young, thinned, mature	Stand is initiated with a clearcut with harvest residues removed (0–3 years), advances to young stand (8–10 years), receives thinning midrotation (12–15 years), and advances to mature stand (20–32 years).
5	residue removed, young, residue removed, young	Stand is initiated with a clearcut with harvest residues removed (0–3 years), advances to young stand (8–10 years), and then is clearcut and advances to a young stand again in a dedicated bioenergy short-rotation system.

predictability and, therefore, may act as a better general indicator of biodiversity patterns.

RESULTS

Alpha diversity increased with thinning and decreased with residue removal and short rotation (Figure 3a). Alpha diversity increased as thinning increased by 3–4 species (3.5 species, 95% Bayesian credible interval [CRI] −4.9 to 13.8), and although the effect overlapped 0, there was an 88% likelihood the effect of thinning was positive. Alpha diversity was expected to decline on average by 14 species (−14.1 species, 95% CRI −25.7 to −4.6) from residue removal following clearcutting, an effect largely driven by bird responses. Similarly, short rotation was expected to result in declines in alpha diversity (−13.9 species, 95% CRI −23.1 to −4.6). These overall patterns of alpha diversity differences were seen in bats, bees, and birds, but reptiles showed a nearly opposite pattern (Figure 3a).

Patterns of beta diversity closely tracked patterns in alpha diversity (Figure 3b). Beta diversity was highest in thinned and unthinned forest (Jaccard dissimilarity 0.59, 95% CRI 0.52–0.62), indicating thinning for bioenergy would result in a nearly 60% difference in community composition. Beta diversity was lower for residue removal (Jaccard dissimilarity 0.46, 95% CRI 0.41–0.51) and short rotation contrasts (Jaccard dissimilarity 0.50, 95% CRI 0.44–0.54), indicating bioenergy management would result in relatively small but still considerable (46–50%) changes in community composition. These overall patterns of beta diversity from bioenergy contrasts were similar for all taxa except birds, which showed the largest changes in community composition in the residue removal contrast and similar changes from thinning and short rotation (Figure 3b).

For most taxa, beta diversity among land uses in the bioenergy contrasts was primarily driven by species turnover, as opposed to nestedness (Appendix S4), meaning that differences in species composition between control and treatment sites were primarily driven by the presence of distinct species groups as opposed to nested subsets of species. The only exception was bats, where nestedness explained more of the overall variation in beta diversity in thinning and short-rotation contrasts (Appendix S4). Full reporting of Jaccard dissimilarity, turnover, and nestedness for all among and within land-use comparisons is in Appendices S5 and S6.

Of the six land-use types, mature forest communities were the most similar to longleaf pine communities across all taxa (Figure 4). The posterior mode of Jaccard dissimilarity between longleaf and mature forest was 0.27 (bats) to 0.57 (bees). The exception to this was that bee communities in both clearcuts were more similar to longleaf pine communities (Jaccard dissimilarity 0.54, 95% CRI 0.48–0.60 and 0.53, 95% CRI 0.48–0.59 for residue removed and residue left, respectively) than were bee communities in mature forest. In contrast to bees, dissimilarity was highest for birds in clearcuts where residues were removed (Jaccard dissimilarity 0.67, 95% CRI [0.61, 0.73]). Dissimilarity was typically relatively high in midrotation unthinned forest for most taxa, but particularly so for bats (Jaccard dissimilarity 0.55, 95% CRI 0.44–0.63) and bees (0.71, 95% CRI 0.65–0.76).

Species richness increased and then converged among land-use scenarios (1–4) that allowed stands to reach the mature forest stage through the full rotation (Figure 5c). Scenario 5 (dedicated short rotation) resulted in lower richness (100 species across all taxa, 95% CRI 75–126) because no additional species accumulated after early rotation. Scenario 1, which involved no bioenergy land-use regimes (i.e., no residue removal, no thinning, and full rotation), resulted in the highest cumulative species richness (145 species across all taxa, 95% CRI 118–170).

The consistency of biodiversity patterns varied among taxa and metrics. High site-level alpha diversity for a given taxon was sometimes positively and sometimes negatively correlated with alpha diversity for other taxa (Figures 6a & 6b). The correlation coefficient (r) of alpha diversity ranged from 0.07 (95% CRI −0.36 to 0.49) for birds and reptiles to 0.40 (95% CRI 0.19–0.59) for bats and bees (Figure 6b). Credible intervals for all alpha diversity comparisons overlapped zero except for bats and

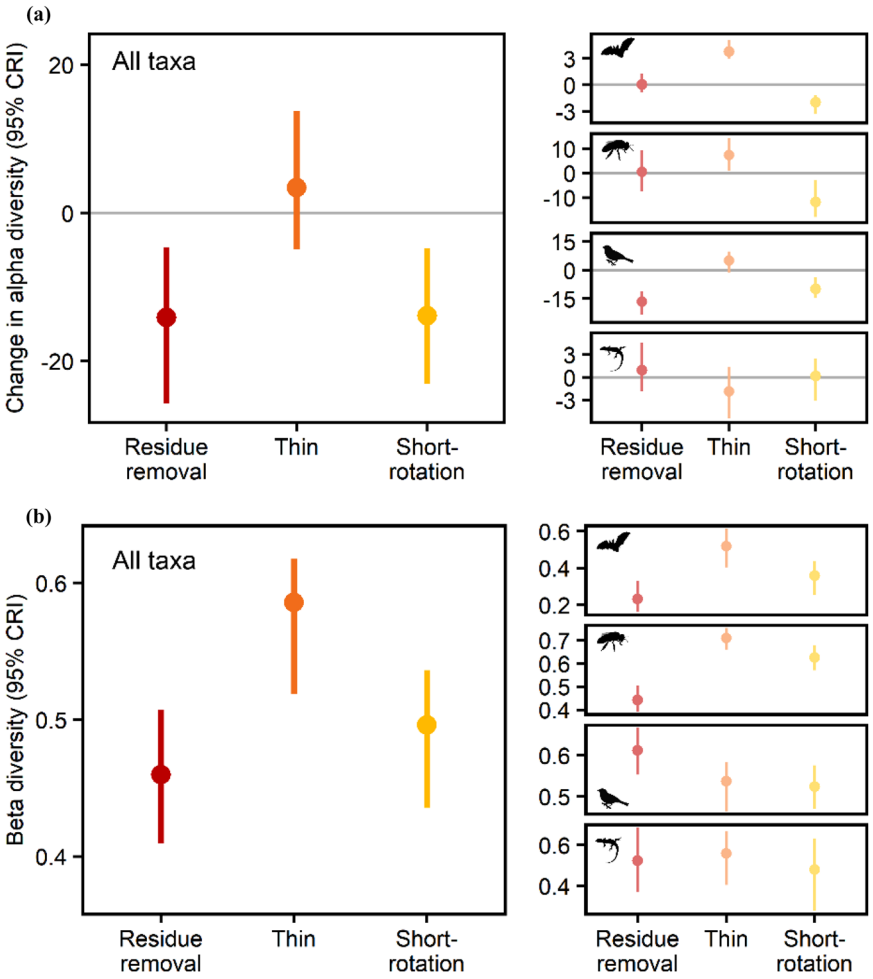

FIGURE 3 (a) Expected change in alpha diversity (species richness) and (b) beta diversity (community composition) resulting from bioenergy resource extraction across the three bioenergy forestry contrasts (points, posterior modes; lines, 95% Bayesian credible intervals [CRI]; color scheme as in Figure 2). Beta diversity is the Jaccard dissimilarity index and can be interpreted as the proportion difference between the two communities being contrasted

bees. In contrast, beta diversity was positively correlated across all taxa (Figures 7a & 7b). With only one exception (bats and reptiles), 95% credible intervals for posterior distributions of *r* did not overlap 0 (Figure 7b).

DISCUSSION

Understanding how alternative forest management strategies may affect biodiversity is of long-standing interest and is increasingly relevant with new demands on forest resources, such as the demand for woody biomass for bioenergy. Certain types of woody resource extraction relevant to bioenergy, such as woody residue removal following clearcutting and shorter rotation times, were associated with overall lower alpha and beta diversity of four taxonomic groups across a large portion of the southeastern United States. In contrast, midrotation thinning resulted in increased alpha and beta diversity. Biological communities in mature plantation forests tended to approximate most closely those of reference longleaf pine communities, suggesting their high conservation value. However, other land-use types (including clearcuts and thinned forests) offered similar high conservation value for some taxa. From the perspective of maximizing biodiversity, a landscape scenario involving no bioenergy-type harvests resulted in the highest cumulative species richness (145 species). Yet, no single scenario came close to supporting the full complement of species observed in the system (224 species), suggesting that a landscape composed of various management regimes might boost measures of biodiversity. Although alpha and beta diversity showed congruent patterns in terms of bioenergy contrasts (Figure 3), alpha diversity of one taxon could not predict the diversity of another, whereas beta diversity could (Figures 6 & 7). Thus, beta diversity was considerably more predictable than alpha diversity and may be a more versatile metric for biodiversity monitoring across landscapes.

How do our findings inform sustainable resource extraction in bioenergy landscapes? When considering the effects of resource extraction on biodiversity, one should consider a change in local biodiversity in terms of direction (i.e., negative or positive), relative magnitude, and approximation of a community to a reference community; all might inform complex decisions surrounding management trade-offs. One interpretation of our results from a biodiversity maximization perspective is that the lowest impact bioenergy forest management practice (midrotation thinning) is the only beneficial resource extraction practice for bioenergy because residue removal and shorter rotation times have clear negative consequences for

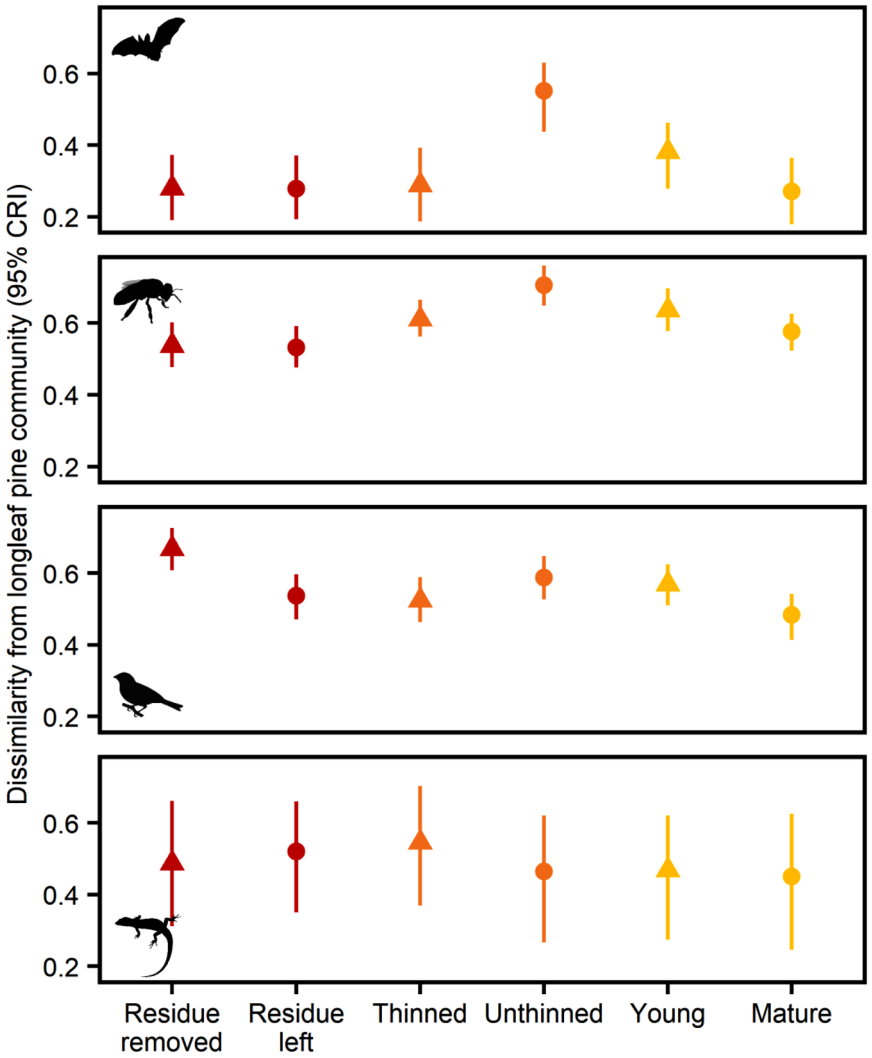

FIGURE 4 Beta diversity between each of the six land-use types and the reference longleaf pine community for each individual taxon (points, posterior modes; lines, 95% Bayesian credible intervals [CRI]; triangles, bioenergy option land uses; circles, control land uses [see Figure 2]; color scheme as in Figure 2). Beta diversity is the Jaccard dissimilarity index and can be interpreted as the proportion difference between the two communities in the contrast

alpha and beta diversity. This interpretation is reasonable when considering only the direction of the effect in bioenergy contrasts, where residue removal and shorter rotations reduced average alpha diversity by 14.1 and 13.9 species, respectively (Figure 3). This inference generally holds when considering our beta diversity analysis as well, but with some exceptions. When comparing thinned and unthinned land uses, communities in thinned forests were far more similar to those in reference longleaf pine ecosystems (except for reptiles) (Figure 4); that is, thinning appeared beneficial when a longleaf pine ecosystem was the conservation benchmark. Similarly, communities in young forests were more dissimilar to longleaf ecosystems than mature forests, suggesting that short-rotation systems would move communities away from the longleaf pine benchmark. Yet, our beta diversity analysis showed that, at least for bats and bees, clearcutting (residue removed and residue left) yielded communities quite similar to the reference longleaf ecosystems. This makes some sense, given that longleaf ecosystems are generally open in structure and both these taxa may benefit from such. These results suggest that alpha and beta diversity, when considered together, may do a better job of describing patterns of local biodiversity.

Biodiversity does not occur in isolated, static spatial units, but within larger, dynamic landscape mosaics. To understand how management regimes affect biodiversity, the broader spatial and temporal patterns of land use should be considered. In our temporal scenarios of bioenergy land use, scenario 1 represented a no bioenergy scenario, but scenario 3 could be thought of similarly given that generally, most stands are thinned in managed southeastern pine forests (Table 1). Both scenarios showed the highest cumulative diversity, suggesting that over the course of a stand rotation, biomass harvesting generally leads to less diversity (Figure 5). This is a novel result that we had not assessed previously (Gottlieb et al., 2017; Jones et al., 2020; Loy et al., 2020; Ober et al., 2020). Our landscape scenarios, focused on temporal accumulation of species richness, produced inferences about bioenergy effects to biodiversity that were not apparent in analyses of alpha and beta diversity. For example, although midrotation thinning increased alpha and beta diversity at the stand scale (Figure 3), the scenario with unthinned midrotation stands yielded the highest cumulative species richness (Figure 5). The reason for this counterintuitive result seems to be partly explained by unthinned stands having lower alpha diversity than thinned stands and unthinned stands containing

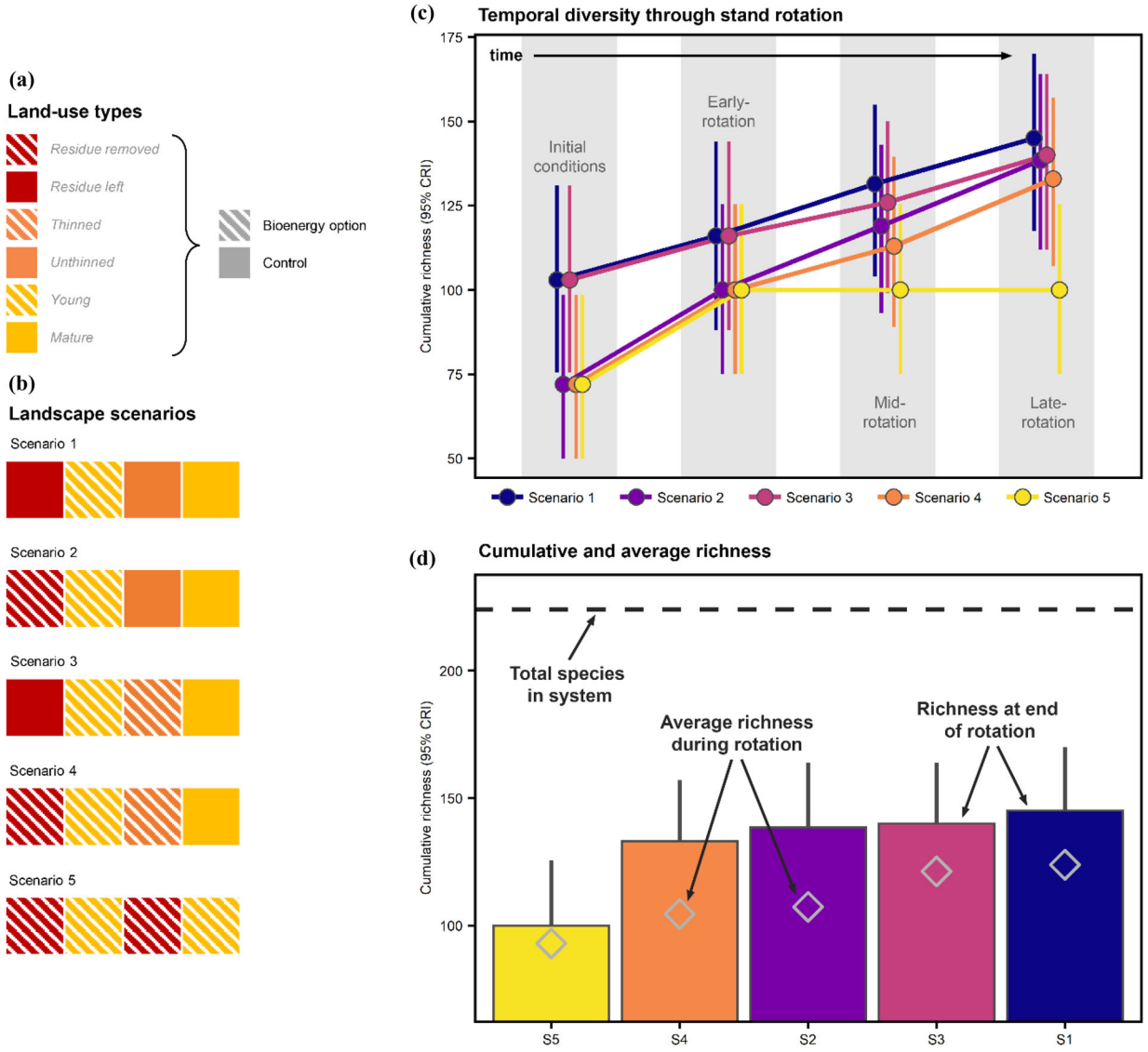

FIGURE 5 Diversity responses to temporal scenarios of bioenergy land use: (a) description of the six land-use types used to develop temporal scenarios (see Figure 2), (b) five landscape scenarios used to estimate the accumulation of species richness (see Table 1), (c) temporal accumulation of diversity through the lifetime of a stand under different management regimes, and (d) cumulative species richness under each landscape scenario, including the average richness during the rotation, final richness at the end of the rotation, and the maximum species observed in the system. Point estimates in (c) and (d) represent posterior median and lines represent 95% Bayesian credible intervals (CRI)

more unique species not shared by clearcuts and young forests (those land uses that precede midrotation in the management cycle). That is, although thinned stands may be more species rich, the species they contain may be more likely to also occur in clearcuts and young forests compared with unthinned stands.

Different types of woody resource extraction also have different spatial footprints that, in combination with landscape context, might inform biodiversity conservation in bioenergy landscapes. For example, short-rotation energy plantations are a highly intensive wood production system that maximize biomass produced for bioenergy but result in lower alpha and beta diversity (Figures 3 & 5). Although they are production intensive, a smaller spatial footprint (Heaton et al., 2008) is required to generate comparable amounts of biomass in short-rotation energy plantations relative to thinning and residue removal (Munsell & Fox, 2010; Gottlieb et al., 2017). This difference can be conceptualized in a land sparing and sharing framework (Fischer et al., 2008; Anderson-Teixeira et al., 2012), where resource extraction can be thought of as either extensive but low-impact or intensive but high-impact. Recently, Betts et al. (2021) framed modern wood production forestry in the context of the land sparing and sharing binary and a hybrid triad approach, in which both extensive and intensive management approaches are mixed with reserves within a landscape mosaic to minimize costs of resource extraction to biodiversity. Supporting biodiversity conservation in this intensifying bioenergy production landscape may include a mosaic of land

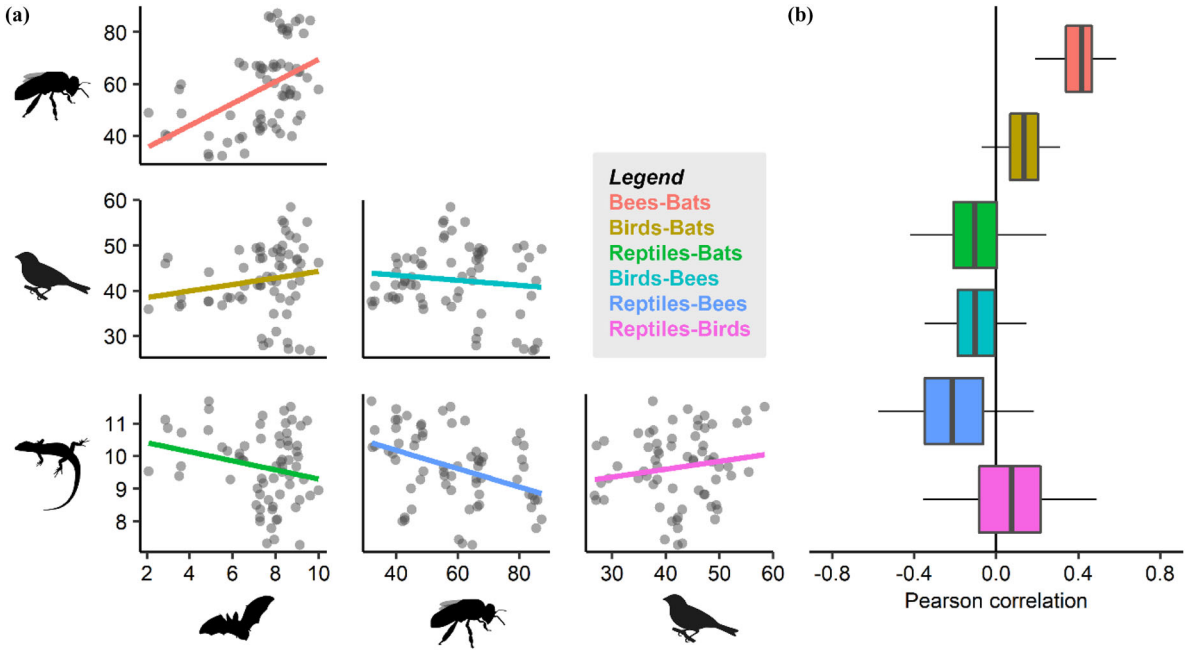

FIGURE 6 Alpha diversity consistency and predictability in bioenergy landscapes across taxa: (a) posterior means of alpha diversity (gray dots) between pairs of taxa on each axis (silhouettes) and (b) posterior distribution of Pearson correlation coefficient (*r*) (whiskers, 95% credible interval; boxes, interquartile range; central lines, mean)

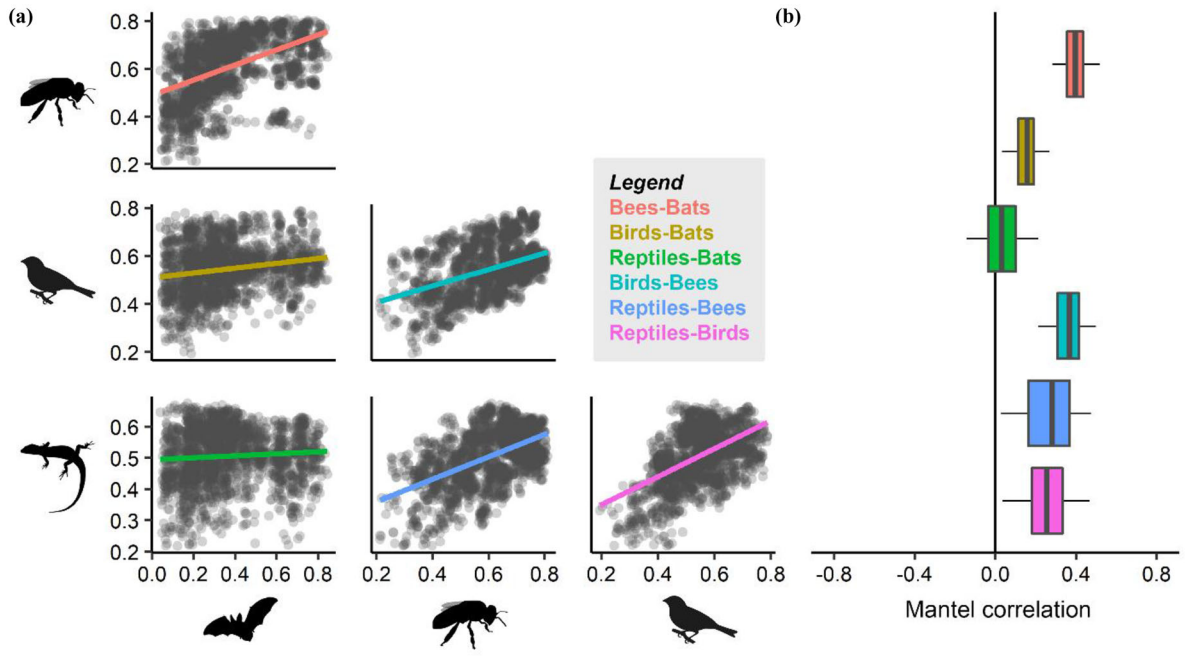

FIGURE 7 Beta diversity consistency and predictability in bioenergy landscapes across taxa: (a) posterior means of beta diversity (gray dots) between pairs of taxa on each axis (silhouettes) and (b) posterior distribution of Mantel correlation coefficient (*r*) (whiskers, 95% credible interval; boxes, interquartile range; central line, mean)

uses and management regimes. The forest industry is engaging in intensive management; however, private landowners in the Southeast are less willing to engage in intensive management approaches, owing to concerns about exotic feedstocks, low prices for wood-based biomass, and a culture of managing land for multiple benefits (including timber production, hunting, and aesthetic values) (Hodges et al., 2019; North & Pienaar, 2021). This heterogeneity in landowner motivations may contribute to a diverse mosaic of land uses across landscapes that promotes high regional biodiversity.

Biodiversity conservation and monitoring may be further guided by our finding that forest stands with a similar number of species (alpha diversity) can be composed of a very different set of species (beta diversity). This finding raises an important question: is high beta diversity good for biodiversity conservation (Socolar et al., 2016) within the context of bioenergy landscapes? The answer partly depends on what process is shaping beta diversity. Beta diversity can be driven by nestedness and turnover (Baselga, 2010). Nestedness represents the compositional difference among sites because of species loss; turnover represents differences driven by the occurrence of different species between sites. Therefore, if beta diversity is primarily driven by turnover, then higher beta diversity may reflect biological communities with unique (i.e., either high or low) conservation value. Beta diversity in our study was primarily driven by turnover (except for bats) (Appendices S4–S6), suggesting that high beta diversity between different land uses could mean disturbances from resource extraction might be generating diverse habitats that support different biological communities. However, even if primarily driven by turnover, higher beta diversity might not indicate conservation benefits in these wood production landscapes if turnover is primarily driven by non-native species, generalists, or species that depend on habitats that are not of conservation interest. Moreover, evaluating beta diversity between different land uses and a reference community (here longleaf pine) may provide one means to evaluate conservation value (Figure 4).

Beta diversity has emerged as a potentially useful concept for informing biodiversity conservation (Socolar et al., 2016), partly because unlike alpha diversity, it recognizes species identity. Our findings suggest that beta diversity may be a better ecological indicator of biodiversity response to resource extraction than alpha diversity. We found that patterns of beta diversity were relatively predictable across taxa, with higher prediction coefficients and narrower uncertainty (Figure 7). In contrast, patterns of alpha diversity were less transferrable across taxa. Therefore, predictability of patterns of biodiversity depends on the component of diversity considered (Kessler et al., 2009). One implication of this finding for biodiversity monitoring is that beta diversity may provide more general insights about community response to land-use change than alpha diversity—even if a limited number of taxa can be sampled. Beta diversity may help clarify otherwise messy relationships between land use, resource extraction, disturbance, or other landscape factors and biodiversity.

Effectively conserving biodiversity in large production and resource extraction landscapes requires understanding and predicting responses to environmental changes. Our pairwise land-use comparison design allowed us to explicitly capture the dynamic nature of managed forest landscapes across a spatial gradient and develop informed predictions regarding biodiversity responses to intensifying wood production. As demand for bioenergy in the UK and EU accelerates landscape changes in the Southeast (Aguilar et al., 2020), our results can inform management that facilitates natural resource extraction to support human needs while maximizing the ability of production landscapes to support biodiversity.

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