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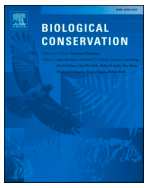

Protecting biodiversity via conservation networks: Taxonomic, functional, and phylogenetic considerations

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ABSTRACT

A key element of conservation action involves the incorporation of sites into networks of protected areas. Historically, most network-creation strategies have been based on considerations of species richness and site complementarity. Nonetheless, phylogenetic or functional biodiversity may be more critical to the maintenance of ecosystem resilience or functioning than is the number of species. Therefore, we explore the efficacy of three strategies (i.e., random, sequential, and simultaneous inclusion of sites into conservation networks of particular sizes) to maximize species richness in a network, and explore associated consequences to aspects of functional and phylogenetic biodiversity. We do so for passerines in Connecticut, bats in Paraguay, and trees in North Carolina, which differ in β, functional, and phylogenetic biodiversity. The efficacy of sequential and simultaneous strategies for conserving species richness are similar at all network sizes and represent improvements over random strategies for each of the three taxa, conserving all species in as few as 35 % of the sites required based on a random strategy. For aspects of functional and phylogenetic biodiversity, metrics converged on the value of the entire biota, even when networks contained as few as five sites, suggesting that richness-based approaches can be effective in guiding conservation action from multiple perspectives. Evaluation of networks intended to conserve biodiversity at spatial extents that include more complex environmental gradients than the examples presented here, or that comprise more heterogenous environments than those represented in our analyses, are needed to more fully explore the generality of our conclusions.

1. Introduction

Anthropogenic threats to biodiversity continue to increase at local, regional, and global scales, rendering the creation of conservation networks to protect biodiversity from these threats an urgent need and critical task. Indeed, networks of protected areas represent a cornerstone of conservation action for protecting regional biotas (Dobson et al., 1997; Scott et al., 2001). Increasing demands by humans continue to result in the conversion of natural habitats to human uses, increasingly fragmenting populations and communities (Vitousek et al., 1997; Monastersky, 2015). Moreover, the resulting mosaics of fragmented habitats increase the likelihood of local extinction in the remaining isolated patches (Vie et al., 2009; Newbold et al., 2014) that no longer experience rescue effects from source populations (Gotelli, 1991). In addition, the isolation of populations can alter species behavior (Hargis et al., 1999), have negative effects on interspecific interactions (e.g., predatory-prey, competition; Aizen and Feinsinger, 1994), and compromise ecosystem processes (Cardinale et al., 2006; Jones et al., 2009). Habitat conversion has resulted in over a third of currently protected areas being influenced by intense human activity associated with agricultural practices or human habitations (Jones et al., 2018). Indeed, the Anthropocene is defined by human-dominated and human-modified habitats, with the rate of human-induced effects continuing to increase and requiring decision makers to explicitly consider the conservation value of disturbed and secondary habitats in conservation efforts to promote biodiversity and preserve endangered or threatened

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species (Chazdon et al., 2009; Van de Perre et al., 2018). Within this context, effective conservation action via construction of networks of protected areas is critical for reducing the tempo and impact of the Earth's sixth mass extinction on the loss of ecosystem services, ecosystem function, or biodiversity (Ceballos et al., 2015).

Historically, the primary criterion guiding the design of reserve networks has been the total number of species in a network (γ-level richness). Consequently, a strategy to increase network richness via selection of sites (e.g., Margules and Pressey, 2000; Andelman and Willig, 2002, 2003) emphasizes site richness (α-level richness) and site complementarity (β-level richness). This focus generally parallels developments in community ecology and biogeography that have evaluated biodiversity dynamics based on species richness (Ricklefs, 1987; Gaston, 1998; Magurran and McGill, 2011) and more recently β diversity (Tuomisto, 2010; Jost et al., 2011). Nonetheless, biodiversity has multiple dimensions that extend beyond considerations of species richness, a measure that considers all interspecific differences to be equal, and emphasizes salient differences among species based on their abundances (Scheiner, 2012), ecological functions (Noss, 1990; Petchey and Gaston, 2006; de Vandewalle et al., 2010), or phylogenetic affinities (Losos, 1996; Webb et al., 2002; Pavoine and Bonsall, 2011; Pavoine et al., 2017). Functional biodiversity reflects variation among species in ecological attributes associated with how species respond to environmental variation as well as the effects of species on ecosystem processes and services (Petchey and Gaston, 2006). Consequently, functional biodiversity provides a mechanistic link to ecosystem resistance, resilience, and functioning (Petchey and Gaston, 2006), which are important considerations for sustainable biological conservation over the long term. Most arguments for conserving phylogenetic biodiversity rely on the idea that phylogeny is an effective surrogate of functional traits or niche conservatism (Losos, 2008). More recently, this idea has been summarized as the "phylogenetic gambit", as using evolutionary relationships may be an efficient approach for capturing variation in form and function without having to quantify traits, behaviors, or responses by the myriad of species that contribute to ecosystem services and function (Mazel et al., 2018; Tucker et al., 2019). Reasons for the conservation of phylogenetic biodiversity, beyond the idea that doing so may conserve functional biodiversity, include enhanced benefits to ecosystem processes, improved human experiences in nature associated with preferences for variety and novelty, a decrease in extinction rates, and greater evolutionary potential (Tucker et al., 2019). Nonetheless, species richness often remains the primary or only metric used to evaluate sites as candidates for incorporation into conservation networks, and it is frequently the basis for strategies to attain conservation goals.

Conservation networks designed to maximize species richness may insufficiently capture or conserve these other dimensions of biodiversity (Rodrigues and Gaston, 2002; Devictor et al., 2010; Bennett et al., 2014; Presley et al., 2018; Véron et al., 2019). Accurate estimates of the abundances of species at multiple sites are time- and resource-intensive endeavors (Kikuchi et al., 2019). In contrast, for many taxa throughout the world, species-level phylogenies (e.g., Jones et al., 2005; Jetz et al., 2012; Burgio et al., 2019) are reasonably well known, making considerations of phylogenetic biodiversity feasible if community composition is well documented. In contrast, functional information about most species remains poorly understood or unavailable regardless of taxon or region, especially with regard to "effect traits" and "response traits" (Etard et al., 2020; Tobias et al., 2020). Even reasonably well-populated databases, such as the TRY database for flowering plants (Kattge et al., 2020), are characterized by substantial numbers of missing values. To the extent that niche conservatism of functional traits characterizes the speciation process, measures of phylogenetic biodiversity may be used as proxies for functional biodiversity (e.g., Cisneros et al., 2014), but the strength of that correlation is disputed, and may be taxon or region specific (e.g., Mazel et al., 2017, 2018). Such logistical impediments and information deficits have limited the effective incorporation of dimensions of biodiversity beyond species identity into the design of conservation networks.

As a consequence of these circumstances, and considering the data available for most taxa, we explored consequences of site selection strategies based on species incidence information, which is the most likely to be known, on phylogenetic and functional biodiversity information, which are less likely to be known. Using different approaches, others (e.g., Rodrigues and Gaston, 2002; Rodrigues et al., 2011; Pollock et al., 2015; Rosauer et al., 2017; Mazel et al., 2018) have used attributes of functional or phylogenetic biodiversity to inform site selection and network design. They have generally concluded that decisions based on phylogenetic information are effective in conserving functional biodiversity as well as taxonomic biodiversity (Rodrigues et al., 2011; Ng et al., 2022). However, no study has explicitly evaluated if strategies to maximize species richness in a network, which remains the typical focus of real-world conservation site selection, perform well with respect to other dimensions of biodiversity.

Because species incidence is the most common information available and the easiest to obtain, and because conservation networks are generally assembled randomly as parcels of land become available, the primary goals of this study were: (1) to evaluate the efficacy of conservation networks constructed based on species richness to conserve aspects of phylogenetic or functional biodiversity, and (2) to compare the random selection of sites to strategies that optimized the number of species protected in resulting networks. We did this by considering three different strategies for choosing sites (random, sequential, and simultaneous [described below]) and calculating metrics of taxonomic, functional, and phylogenetic biodiversity of emerging networks after the addition of each site. These strategies were compared using three exemplar biotas from different biogeographical domains: passerines in Connecticut (Klingbeil and Willig, 2015, 2016a, 2016b), bats in Paraguay (López-González, 1998, 2005; Willig et al., 2000), and trees in North Carolina (Burrill et al., 2018). These exemplar networks represent a range of well-sampled sites (from 20 to 30 sites) and metacommunities that differ in β (i.e., γ biodiversity/α biodiversity sensu Jost, 2007), functional, and phylogenetic biodiversities. In addition, these three data sets share a number of attributes that make them useful test cases for exploring how effectively randomly assembled networks using a species-richness based approach conserve biodiversity compared to optimized network strategies, as well as how effectively phylogenetic and functional biodiversity of the regional biota are conserved. First, each domain comprises at least 20 sites for which excellent species inventories are available. Second, phylogenetic and functional trait information for each biota is well known. Third, considerable variation among sites exists with respect to species richness and composition. Fourth, variation in richness and composition results in distinctive patterns of α (i.e., mean biodiversity of sites within each network) and β diversity in each network (Table 1), enhancing the general applicability of this set of example data to a wider range of empirical contexts. In addition, these taxa differ in their relative phylogenetic and functional biodiversities. Connecticut passerines have relatively low phylogenetic, functional, and β biodiversity; Paraguayan bats have moderate phylogenetic biodiversity, high functional biodiversity, and intermediate β diversity; and North Carolinian trees have high phylogenetic diversity, moderate functional diversity, and high β diversity. Importantly, the

Table 1
Summary diversity characteristics for the three datasets: passerines in Connecticut, bats in Paraguay, and trees in North Carolina. The percentage of the matrix that is filled is the inverse of β-diversity.

	Passerines	Bats	Trees
Number of sites	20	26	30
Number of species	36	48	70
Mean site richness	16.70	13.23	6.87
Mean number of sites at which a species occurs	9.28	7.17	2.94
Percentage of the site-species matrix that is filled	46.40	26.30	0.10
Phylogentic time depth (in millions of years)	61.29	72.70	325.05

goal in this work is not to evaluate the ability of these particular groups of sites to conserves their respective biotas, although some insights about this potentiality will be gleaned as a byproduct. Rather, the goal is to use these high-quality data to explore the effects of different mechanisms for constructing conservation networks on functional and phylogenetic biodiversity, as well as to determine the extent of benefits if ideal conservation strategies could be applied (i.e., the ability to optimize site selection to maximize biodiversity rather than to conserve sites based on availability).

2. Materials and methods

We use three example data sets to explore effects of different quantitative approaches to network design on biodiversity, rather than to understand the best approach for conserving the biodiversity of a region. Consequently, we present only brief summaries of the environment, taxa, and data collection for each of the three example networks. Nonetheless, detailed information about the species, regions, and sampling protocols are available in the references that are associated with each of the following sections.

2.1. Passerines of Connecticut

Connecticut is a small state (14,360 km^2) that is dominated by oak-hickory, northern hardwood, and coniferous forests (Butler, 2013). Extensive anthropogenic activities have altered habitats throughout the state (Drummond and Loveland, 2010), creating a fragmented landscape comprising patches of forest that are interwoven with human-dominated land cover types (e.g., urban and suburb developments, agricultural fields, roads).

Passerine (Passeriformes or perching birds) species composition was determined at each of 20 forested sites (Table S1, Fig. 1A) via intensive sampling based on a combination of point counts and acoustic surveys (Klingbeil and Willig, 2015, 2016a, 2016b). Sampling was conducted during the breeding season. In total, 36 species, 23 genera, and 11 families of Passeriformes were recorded during the study (Table S2). Species richness of sites ranged from 11 to 24 species.

2.1.1. Functional characteristics

Functional aspects of biodiversity for passerines were characterized based on 8 categorical and 6 continuous traits compiled from the literature (Poole, 2005; Pyle, 1997; Lislevand et al., 2007). Functional traits were associated with diet, foraging method, residency status, body size, and body shape, and reproduction (Table S2 and Supporting Information). Categorical traits characterized food consumption (insectivore, omnivore), foraging guild membership (aerial, gleaning, ground, bark), and migratory behavior (resident, migrant). Continuous traits characterized body size, body shape (bill length, body mass, wing length, tail length), and reproductive characteristics (clutch size, egg mass).

Jaccard dissimilarity was used to compute the functional distance between each pair of species (Jost et al., 2011; Scheiner et al., 2017a) for each group of categorical traits and the mean character difference was calculated for each group of continuous traits. The multivariate distance (d_{ij}) between pairs of species was determined by an equal-weight average of functional group-specific distances.

2.1.2. Phylogenetic characteristics

Phylogenetic aspects of biodiversity were based on a time-calibrated phylogeny of bird species of the World (Jetz et al., 2012, Fig. S1). This tree represents a synthesis of phylogenetic information that allows for species-level inference that reflects uncertainty in phylogenetic relationships. To incorporate this uncertainty, we selected 1000 trees at random from the posterior distribution of 10,000 available trees based on the "Hackett" backbone topology (available at http://birdtree.org; Jetz et al., 2012). We calculated a consensus tree from the set of 1000 randomly selected trees using the majority rule option, and used branch lengths from the consensus tree to calculate aspects of phylogenetic biodiversity.

2.2. Bats of Paraguay

Paraguay is a small, landlocked country that occurs at the convergence of southern subtropical and temperate zones. Despite its small size (406,752 km^2), Paraguay experiences appreciable gradients in mean annual temperature (21 °C to 26 °C) and in mean annual precipitation (400 mm to 1800 mm), with habitats in the northwest of the country being warm and dry, and conditions becoming progressively cooler and wetter toward the south and east (Fariña Sánchez, 1973). In Paraguay, geographical variation in edaphic features combine with climatological gradients to define seven phytogeographic biomes: Matogrosense, Alto Chaco, and Bajo Chaco to the west of the Río Paraguay, and Campos Cerrados, Central Paraguay, Alto Parana, and Ñeembucú to the East of the Río Paraguay (Hayes, 1995). Eastern Paraguay was deforested extensively during the late 20th century (Ríos and Zardini, 1989; Keel et al., 1993), resulting in less than 20 % of the original forest remaining (Huang et al., 2007) and landscapes that are dominated by agricultural activities (Universidad Nacional de Asuncion, 1994). Subsequently, the Gran Chaco, including western Paraguay, was rapidly and extensively deforested by cattle ranching companies (Baumann et al., 2017; Kuemmerle, 2017). However, data used here were collected prior to most of the deforestation of the Paraguayan Chaco.

Bat communities were characterized at 26 sites (Table S3) throughout the country (Fig. 1B) that span environmental gradients of precipitation, temperature, and edaphic characteristics. To achieve the most complete and accurate representation of bat species composition for each site, data from the intensive faunal surveys (Willig et al., 2000) was supplemented by an exhaustive search of museum records (López-González, 1998, 2005). Nomenclature followed the taxonomic treatment of Simmons (2005). These sites and bat community data are those used in previous work (e.g., López-González, 1998, 2005; Stevens et al., 2007; Presley et al., 2009).

In total, intensive surveys recorded 5012 bats, representing 6 families, 26 genera, and 48 species (Table S4; Willig et al., 2000). Richness of sites after supplementation by museum records ranged from 6 to 26 species (López-González, 1998, 2005). Paraguayan bats are members of 7 trophic guilds, including frugivores (9 species), nectarivores (1), gleaning animalivores (6), aerial insectivores (14), high flying insectivores (15), sanguinivores (2), and piscivores (1).

2.2.1. Functional characteristics

Functional aspects of biodiversity for bats were characterized based on 15 categorical traits and 10 continuous traits, all compiled from the literature (López-González, 1998, 2005; Cisneros et al., 2014). These functional traits are associated with six aspects of function: diet, foraging location, foraging strategy, body size, masticatory mode, and flight ability (Table S4 and Supporting Information). Categorical traits characterized diet (blood, fruit, invertebrates, nectar, vertebrates), foraging location (above canopy, canopy, open areas, over water, subcanopy, understory), or foraging strategy (aerial, gleaning, hovering, other) and were binary (i.e., a species did or did not exhibit a trait). Continuous traits were used to characterize body size (forearm length, mass), flight ability (wing aspect ratio, wing loading), and masticatory mode (breadth across upper molars, breadth of braincase, condylobasal length, greatest length of skull, maxillary tooth row length, post-orbital constriction), which reflect physiological constraints, foraging behavior, and diet, respectively. Functional distances were calculated using the approach described for passerines.

2.2.2. Phylogenetic characteristics

Phylogenetic aspects of bat biodiversity were based on a species-level supertree (Jones et al., 2005, Fig. S2). Three (i.e., *Lasiurus blossevillii*, *Molossus currentium*, and *Eumops patagonicus*) of the 48 species of

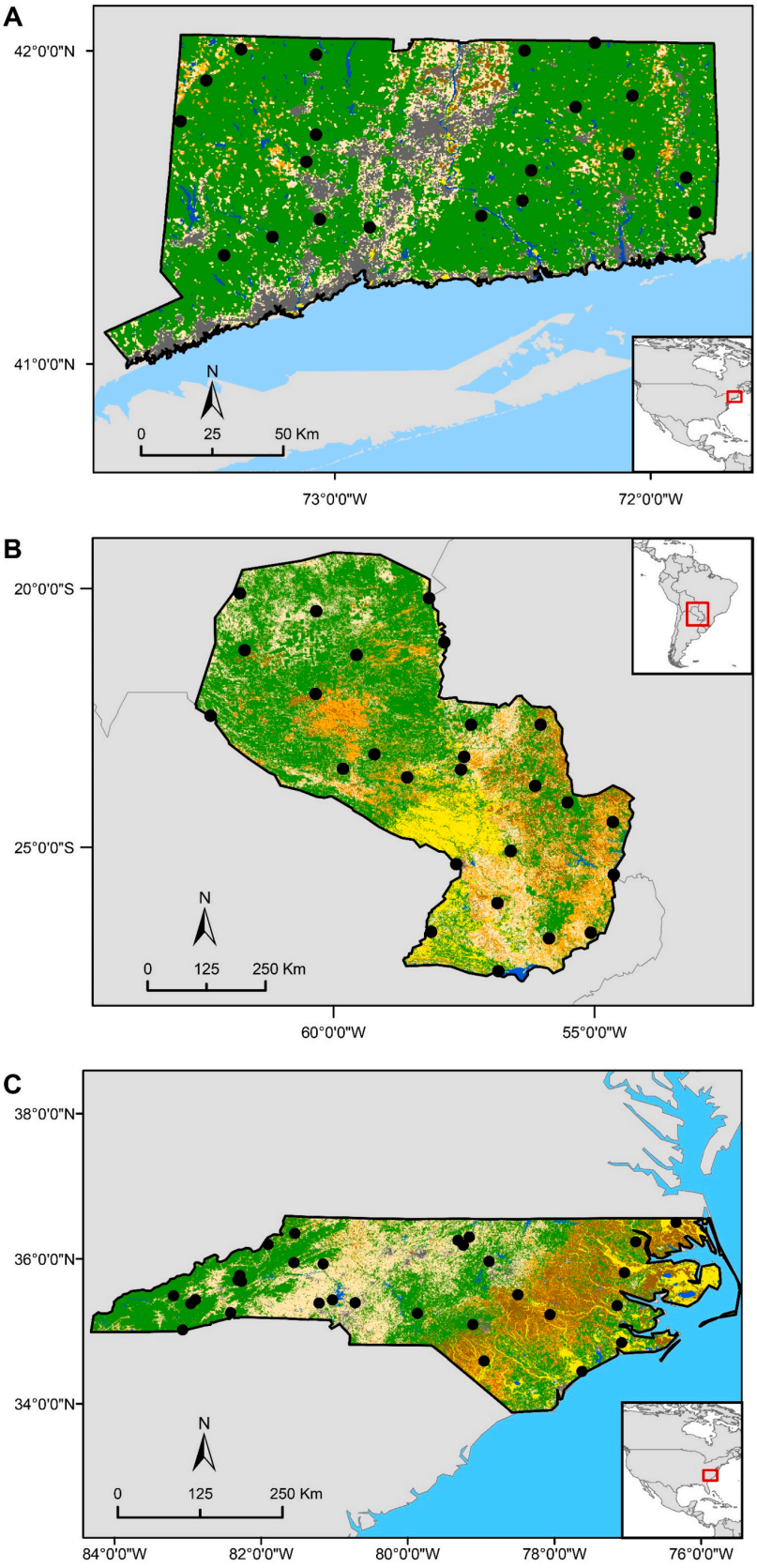

Fig. 1. Geographic distribution of (A) 20 sites in Connecticut, (B) 26 sites in Paraguay, and (C) 30 sites in North Carolina. Sites are indicated by black circles. Location of study areas depicted by red square in map of North America or South America. Land cover in Connecticut (2012), Paraguay (1996), and North Carolina (2012) were provided courtesy of European Space Agency Climate Change Initiative-Land Cover Database, 300 m resolution (ESA CCI Land Cover and EC C3S Land cover Version 2.07cds) summarized by seven categories present in each location: forest (green), grass/shrubland (beige), developed (gray), herbaceous cover (brown), cropland (orange), wetland (yellow) and water (blue). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

bat from Paraguay are not present in this supertree. For each missing species, we substituted a closely related congener in the supertree. Closely related congeners were determined by alternative phylogenetic or taxonomic sources (e.g., Morales and Bichkam, 1995; López-González and Presley, 2001; Gregorin, 2009). The effects of this type of substitution on aspects of phylogenetic biodiversity are small because terminal branches for congeners are generally the same or of similar lengths.

2.3. Trees of North Carolina

North Carolina is a mid-sized state (139,391 km^2) that spans a range of habitats from coastal floodplains to mid- and upper-elevational forests dominated by a mix of hardwoods and conifers, the latter mostly pines. Nearly all of these forests represent secondary growth: land that is maintained continuously as forest but harvested for timber, or land that was dedicated to agricultural production but was subsequently abandoned and allowed to revert to forest. Tree species composition was characterized at each of 30 sites (Table S5) distributed throughout the state (Fig. 1C) that span environmental gradients representing precipitation, temperature, and edaphic characteristics. These stands were selected from the Forest Inventory and Analysis (FIA) plots (USDA Forest Service, 2021).

Trees were represented by 70 species, 23 genera, and 11 families (Table S6). Species richness of sites ranged from 11 to 24. The original species lists for each site were trimmed to those having sufficient trait information (i.e., missing data for no more than a single trait). A total of 16 species were removed as a result. In all cases the removed species were rare, each being found in only one site, and with no sites containing more than one of them. Because our analysis is a test of a procedure rather than an attempt to be an accurate description of empirical patterns of tree diversity, the consequences of trimming the data are not relevant to the analyses that we illustrate.

2.3.1. Functional characteristics

Functional aspects of tree biodiversity were characterized using 6 continuous traits (wood density, specific leaf area, leaf N per dry mass, leaf P per dry mass, plant height, and seed dry mass). Functional trait information was extracted from the TRY database (Kattge et al., 2020). In the ten instances for which trait information was not available for a single functional trait of a species, values were imputed from the nearest relative based on a dated phylogeny for seed plants (see section 2.3.2): four for wood density and six for specific leaf area (bold values in Table S6). Functional distances were calculated using the same approach as described for passerines.

2.3.2. Phylogenetic characteristics

Phylogenetic aspects of biodiversity were based on branch lengths from a dated phylogeny for seed plants, ALLOTB (Smith and Brown, 2018), which was constructed for GenBank and Open Tree of Life taxa with a backbone from the Open Tree of Life project (https://tree.opentreeoflife.org/about/synthesis-release/v9.1). We used the functions node.depth and cophenetic.phylo in the "ape" R package (Paradis and Schliep, 2018) to prepare the metrics used for phylogenetic diversity calculations.

2.4. Quantifying taxonomic, functional, and phylogenetic biodiversity

2.4.1. Characterization of taxonomic biodiversity

Unlike functional or phylogenetic characteristics, metrics of taxonomic biodiversity consider all species to be equally different from each other. Species richness (S) is simply the number of unique species in an area, and historically has been used as the basis of conservation action and determination of conservation success. The extent to which species are present in multiple sites in a network is another useful attribute that can be incorporated into conservation goals (Andelman and Willig, 2002, 2003), as this is critical for mitigating the effects of local extirpation of species. We use a simple metric, species redundancy (R) to capture this network characteristic, and define it as the number of species that are present in at least two sites within a network.

2.4.2. Characterization of functional trait biodiversity

Metrics of functional trait biodiversity incorporate collective differences between species in trait values associated with niche dimensions, including where an organism lives, when it is active, what it consumes, where it obtains resources, and how it obtains resources. For each group of species, we used morphological, behavioral, or biochemical traits as appropriate. These traits include (1) the 14 traits for passerines that characterized diet, foraging method, residency status, body size, and body shape, and reproduction; (2) the 25 traits for bats that characterized diet, foraging location, foraging strategy, body size, masticatory mode, and flight ability; and (3) the 6 traits for trees that characterized aspects of plant height, density, and tissue composition. We used mean trait dispersion ($M[T_{T/P}]$) and Hill functional evenness ($^qE[T_P]$) to capture two aspects of functional biodiversity, the magnitude of functional trait differences among species and variability in those differences. Mean trait dispersion reflects pairwise trait differences, whereas Hill functional evenness reflects the homogeneity in pairwise distances among species (Scheiner et al., 2017a).

2.4.3. Characterization of phylogenetic biodiversity

Metrics of phylogenetic biodiversity incorporate differences among species based on considerations of evolutionary relatedness. We used mean proportional divergence ($M[P_T]$) and Hill phylogenetic evenness ($^qE[P_T]$) to characterize aspects of phylogenetic biodiversity. Mean proportional divergence reflects species divergence that is standardized for time depth, whereas Hill phylogenetic evenness reflects the symmetry of branch lengths in a phylogeny (Scheiner et al., 2017b).

Metrics of dispersion reflect relationships among species for a particular functional or phylogenetic space. In contrast, distance-based metrics of functional or phylogenetic evenness reflect the equability of species distributions in relevant spaces (i.e., functional trait or phylogenetic spaces), and is equal to the effective number of equally distinct species in a community from a functional trait or phylogenetic perspective (i.e., a Hill number; Hill, 1973). Dispersion and evenness (diversity) are different independent aspects of functional variability, both share the same interval of values [0,1]. Importantly, for any particular value of functional evenness, the corresponding dispersion value could range from 0 to 1. The metrics used in our analyses were chosen because they are independent of species richness, unlike many commonly used metrics of functional or phylogenetic diversity, such as Faith's phylogenetic diversity (Faith, 1992). Depending on the particular aspects of each dimension of biodiversity that are of critical concern, conservationists may choose whichever functional or phylogenetic metrics are most appropriate for their goals in constituting a network of protected areas.

The various measures of functional trait biodiversity and phylogenetic biodiversity should not be directly compared with each other. First, $M[T_{T/P}]$ and $M[P_T]$ represent means, whereas $^qE[T_P]$ and $^qE[P_T]$ measure variability. Second, functional biodiversity is based on differences between pairs of species, whereas phylogenetic biodiversity is based on the phylogenetic branch length of each species from its root. Consequently, our conclusions are based on patterns of change with regard to each metric.

For each of our example data sets, we used a consensus phylogenetic tree for simplicity in the presentation of results. However, for rigorous considerations of phylogenetic biodiversity of particular biotas, researchers may want to use a set of possible trees that capture the inherent uncertainty of phylogenetic reconstructions. Although this uncertainty in phylogenetic relationships may be important within the context of understanding evolutionary histories, it remains unclear how this uncertainty, especially with respect to more recent evolutionary events, affects values of phylogenetic biodiversity metrics that attempt

to capture complex relationships with a single value.

2.5. Quantitative analyses

To evaluate the efficacy of conservation decision-making based on maximizing species richness within a network, we explored three distinct strategies for site selection for each of the three regional biotas. Thereafter, we evaluated the consequences of the resultant network configurations on taxonomic, functional, and phylogenetic biodiversity.

2.5.1. Strategies for network design

Sites were assembled into networks based on three approaches: (1) random network configuration (hereafter, random strategy); (2) sequential maximum species richness network configuration (hereafter sequential strategy); and (3) simultaneous maximum species richness network configuration (hereafter simultaneous strategy). In the random strategy, sites were selected at random from the candidate pool (all sites under consideration for incorporation into a network), without regard to their species richness or to the composition of the network at the time of site addition. For each network size, all possible combinations of sites were sampled. This is a "naïve" strategy against which other approaches can be evaluated, but is consistent to some extent with how conservation networks have been and continue to be constructed. Generally, sites are added as they become available without full consideration of the consequences to particular biotas or resultant networks (Meir et al., 2004). In the sequential strategy, sites were selected consecutively in a manner that maximized the richness of the network at each step, predicated on the composition and richness of the previously selected sites. In our analyses, for computational simplicity, only a single sequence was sampled even if there might have been more than one maximal solution at a given network size. However, as indicated by our results, averaging over all possible sequences would likely not change the general conclusions. In the simultaneous strategy, sites were simultaneously selected for each network size (i.e., the set of sites that maximized S was selected for each network size rather than adding sites one at a time to a network, as characterizes the sequential strategy) so as to maximize the richness at that network size. All possible combinations of equally rich sets were sampled at each network size.

We implemented both the sequential and simultaneous strategies to account for the possibility that a site selected early during the sequential strategy may not be part of the best solution for networks of a larger size. For example, a prospective network site with the most species would always be selected first using a sequential strategy; however, it is possible that the site with the most species would not be one of the sites that would maximum species richness of a network with two or more sites. Each strategy was implemented using code written in Fortran 90 and available from the authors.

2.5.2. Evaluation of network strategies

For each strategy, we characterized networks of each size based on six attributes: species richness (S) and species redundancy (R) to represent taxonomic biodiversity, mean trait dispersion ($M[T_{T/P}]$) and Hill functional evenness ($^{q}E[T_P]$) to represent functional biodiversity, and mean proportional divergence ($M[P_T]$) and Hill phylogenetic evenness ($^{q}E[P_T]$) to represent phylogenetic biodiversity. Higher values for S and R represented better configurations for a particular number of sites in a network. For functional diversity, higher values indicate that species with more extreme trait differences are included. It is not obvious if maximizing functional diversity, and thereby potentially excluding more "typical" species from the network should be considered a good conservation strategy. Similarly, maximizing phylogenetic diversity favors the inclusion of highly divergent species (Véron et al., 2019).

3. Results

For passerines in Connecticut (Fig. 2A), bats in Paraguay (Fig. 3A), and trees in North Carolina (Fig. 4A), the efficacy of sequential and simultaneous strategies for conserving species richness was quite similar at all network sizes. Not surprisingly, each was more effective than the naïve approach (random strategy) until at least 75 % of available sites were incorporated into a network.

In general, redundancy increased in parallel to changes in species richness with increasing network size, regardless of strategy, until all species were protected by the network (i.e., seven sites for passerines, nine sites for bats, and 25 sites for trees; Figs. 2B, 3B, and 4B, respectively). Thereafter, as network size increased, redundancy increased but at diminishing rates until reaching a maximum of 30, 41, and 35 species for passerines, bats, and trees, respectively. Once all species were in a network, additional sites cannot increase species richness and therefore the order in which such sites were added was effectively random. Consequently, the increase in redundancy after maximum S was dictated by the particular form of the distribution of redundant species in the remaining sites.

Mean trait dispersion converged on the value for the entire biota for networks as small as five sites and exhibited similar values for all larger networks, regardless of strategy and for each biota (Figs. 2C, 3C, 4C). The same convergences occurred for Hill functional evenness (Figs. 2D, 3D, 4D). For trees, this convergence happened with a network containing just over half of the species. Thus, the identity of sites included in a network would only affect functional biodiversity when network size is small, especially when a relatively small number of sites can conserve all of the distinct functions (i.e., areas of trait space) performed by a biota. This can occur for small networks when using richness maximization strategies that result in early inclusion of sites with complementary species composition. However, for passerines, variation in both functional biodiversity metrics was quite large for the random strategy for networks of small or moderate size. Consequently, even though the mean expectation from the random strategy is quite close to that of the sequential and simultaneous strategies, a naïve approach may not adequately protect those aspects of biodiversity in small conservation networks.

As with functional biodiversity, phylogenetic measures of biodiversity generally converged regardless of strategy or domain, once at least five sites were in a network (Figs. 2E, F,3E, F, 4E, F). The trend for mean proportional divergence in passerines (Fig. 3E) was distinctive in that the sequential and simultaneous strategies conserved greater biodiversity than did the random strategy, even for networks that comprised 75 % of sites. Moreover, mean proportional divergence for passerines was highly variable based on the random strategy until most sites were in the network. Conversely, the random strategy for trees (Fig. 4E) conserved greater phylogenetic biodiversity than did the other strategies for networks comprising up to a third of the sites, likely due to the deep phylogenetic division between coniferous and eudicot species.

4. Discussion

4.1. The efficacy of species richness in constructing conservation networks

A common goal in conservation is to capture as many aspects of each dimension of biodiversity as possible. Nonetheless, the availability of reliable data on the identity, abundance, functions, and evolutionary relationships of species can inhibit the identification of valuable conservation sites or their incorporation into an effective network design. Most sites, especially those with high species richness in tropical areas, have not been surveyed comprehensively for any taxon, and likely are not currently incorporated into protected areas. Practically, sites cannot be considered to be candidates for guiding conservation action until the completion of accurate surveys for the taxa of interest. Importantly, incomplete data constrain the design of optimal reserve configurations

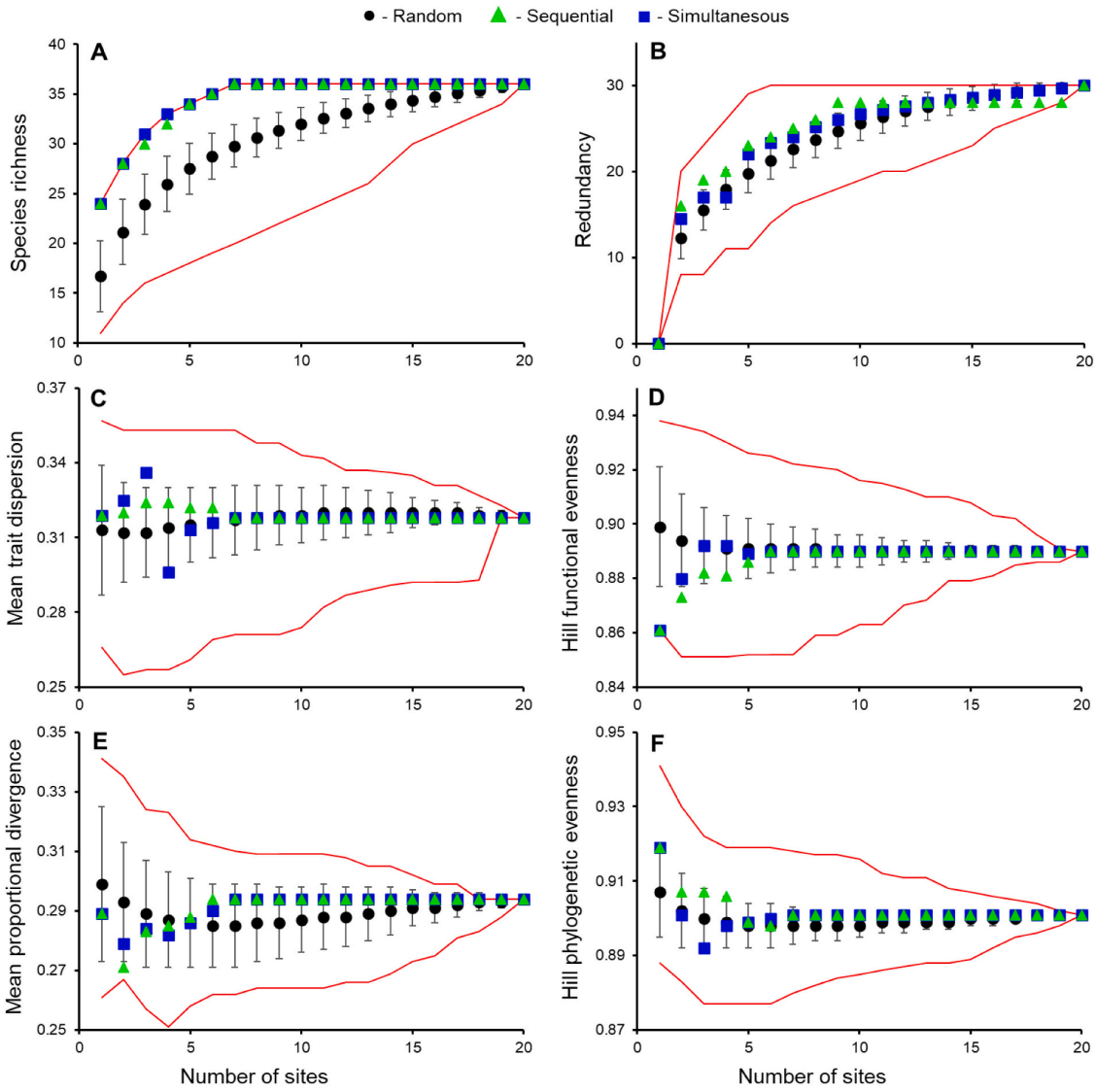

Fig. 2. Trends in aspects of taxonomic (A, species richness; B, redundancy), functional (C, mean trait dispersion; D, Hill functional evenness), and phylogenetic (E, mean proportional divergence; F, Hill phylogenetic evenness) biodiversity of passerines in Connecticut as a function of network size based on each of three strategies for configuring a network (i.e., random, indicated by black circles; sequential, indicated by green triangles; and simultaneous, indicated by blue squares). Error bars associated with the random strategy are standard deviations based on all possible combinations of sites that correspond to a network size). Regardless of strategy, red lines indicate the maximum and minimum possible values for each metric at each network size. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

in conservation networks regardless of design strategy or conservation goal. It is these constraints that often result in the reliance on species richness to make conservation decisions.

Our analysis of different taxa in different regions shows that it is possible to capture aspects of functional and phylogenetic biodiversity by basing network configuration decisions on species richness. Indeed, metrics of functional and phylogenetic biodiversity rapidly converged on the biodiversity of the entire network of sites, and did so much faster than species richness itself converged on its maximum (Figs. 2-4). Although there have been many calls for conservation efforts to focus on dimensions other than taxonomic biodiversity (e.g., Pereira et al., 2012; Brum et al., 2017; Girardello et al., 2019; Xu et al., 2019), we contend that those dimensions may be conserved adequately when richness is maximized. Even a naïve approach (random strategy), which performed poorly for maximizing species richness, effectively captured aspects of other dimensions of biodiversity in conservation networks of modest size. An important caveat to these conclusions is that they may only be true when conservation efforts are directed at the creation of a network of protected sites. Conservation efforts with different goals (e.g., the protection of endangered species), may require an approach to optimize other dimensions of biodiversity, such as conserving phylogenetically or functionally distinct species (Rosauer et al., 2017; Kosman et al., 2019).

We considered two maximization strategies for conservation networks based on species richness: sequential and simultaneous. The difference between these strategies is whether the entire network is created in a single instance (simultaneous) or built over time (sequential). Due to computational complexity, the specific sequential sequence that we generated may have resulted in the early omission of sites that could have better maximized functional or phylogenetic biodiversity while still maintaining maximum species richness. This arises because we did

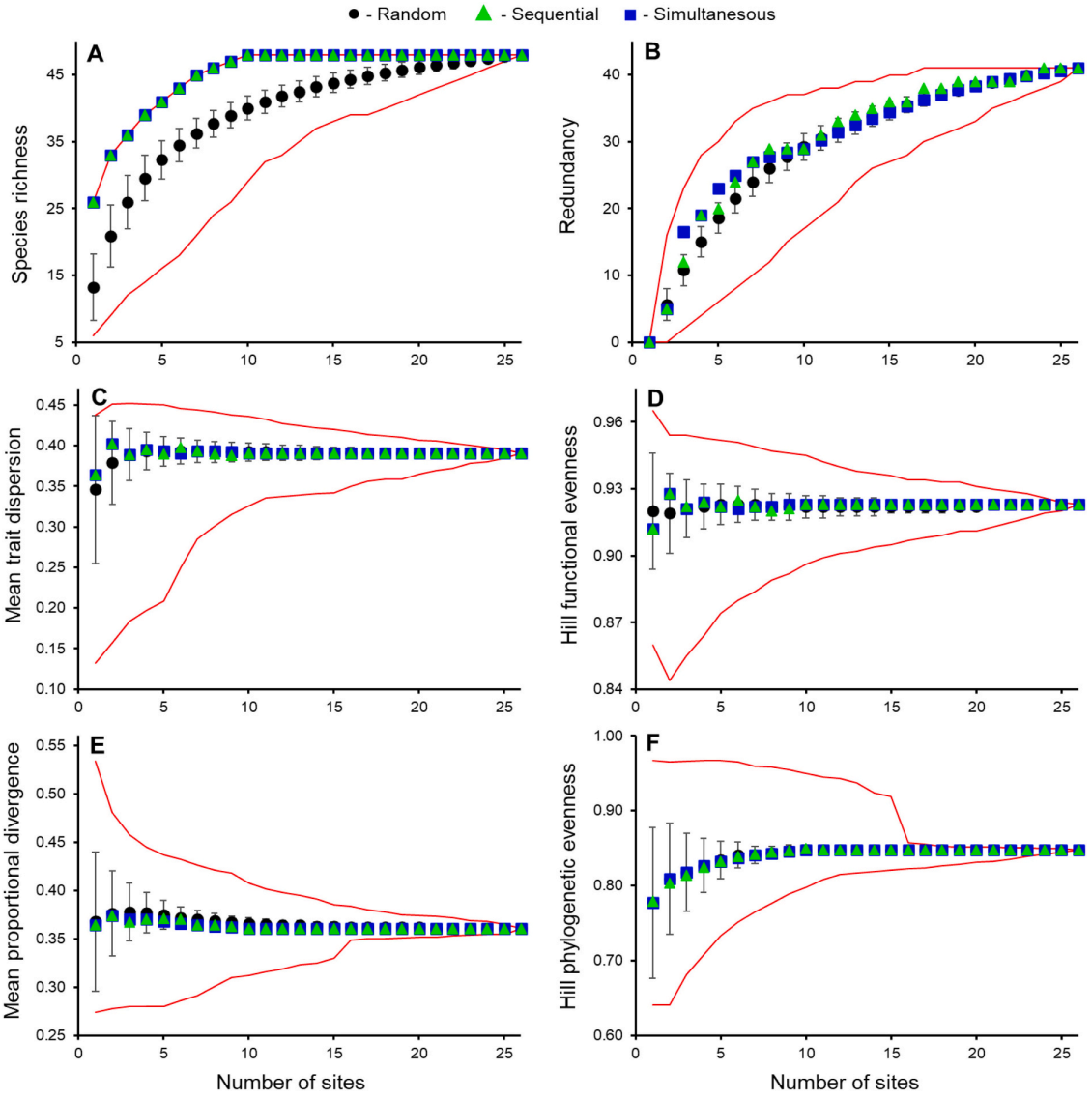

Fig. 3. Trends in aspects of taxonomic (A, species richness; B, redundancy), functional (C, mean trait dispersion; D, Hill functional evenness), and phylogenetic (E, mean proportional divergence; F, Hill phylogenetic evenness) biodiversity of bats in Paraguay as a function of network size based on each of three strategies for configuring a network (i.e., random, indicated by black circles; sequential, indicated by green triangles; and simultaneous, indicated by blue squares). Error bars associated with the random strategy are standard deviations based on all possible combinations of sites that correspond to a network size. Regardless of strategy, red lines indicate the maximum and minimum possible values for each metric at each network size. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

not calculate all possible sequential pathways after each addition of a site to a network. However, it is likely that our specific realization would not have differed substantially from the other possible pathways with respect to functional or phylogenetic biodiversity, especially given how stable those values were after achieving relatively small network sizes (Figs. 2-4). Importantly, the number of combinations of sites that maximize species richness is a very small percentage of the possible choices. For example, only four of the possible 65,780 combinations of sites maximized richness of networks of size five for Paraguayan bats, a network size at which functional and phylogenetic biodiversity had already converged toward their respective values for the suite of all sites in the domain.

Our analyses ignored species abundances. When prioritizing sites in a network, one might want to choose sites that contain large populations of each species so as to decrease the likelihood of stochastic species extinction, thereby increasing the probability of long-term maintenance of biodiversity. Whereas such considerations are unlikely to alter our conclusions about how a focus on species richness affects phylogenetic or functional biodiversity in a network, it may affect the ordering of site priorities. Moreover, incorporating abundance information will more heavily weight the importance of abundant species, which generally are less of a conservation concern than are rare species. In addition, the number of individuals harbored by a site is associated with species richness (Srivastava and Lawton, 1998), likely rendering the omission of abundances a relatively minor concern when constructing conservation networks. Moreover, when data on relative abundance are available and incorporated into metrics of biodiversity, the addition of rare species, regardless of their interspecific differences in function or evolutionary

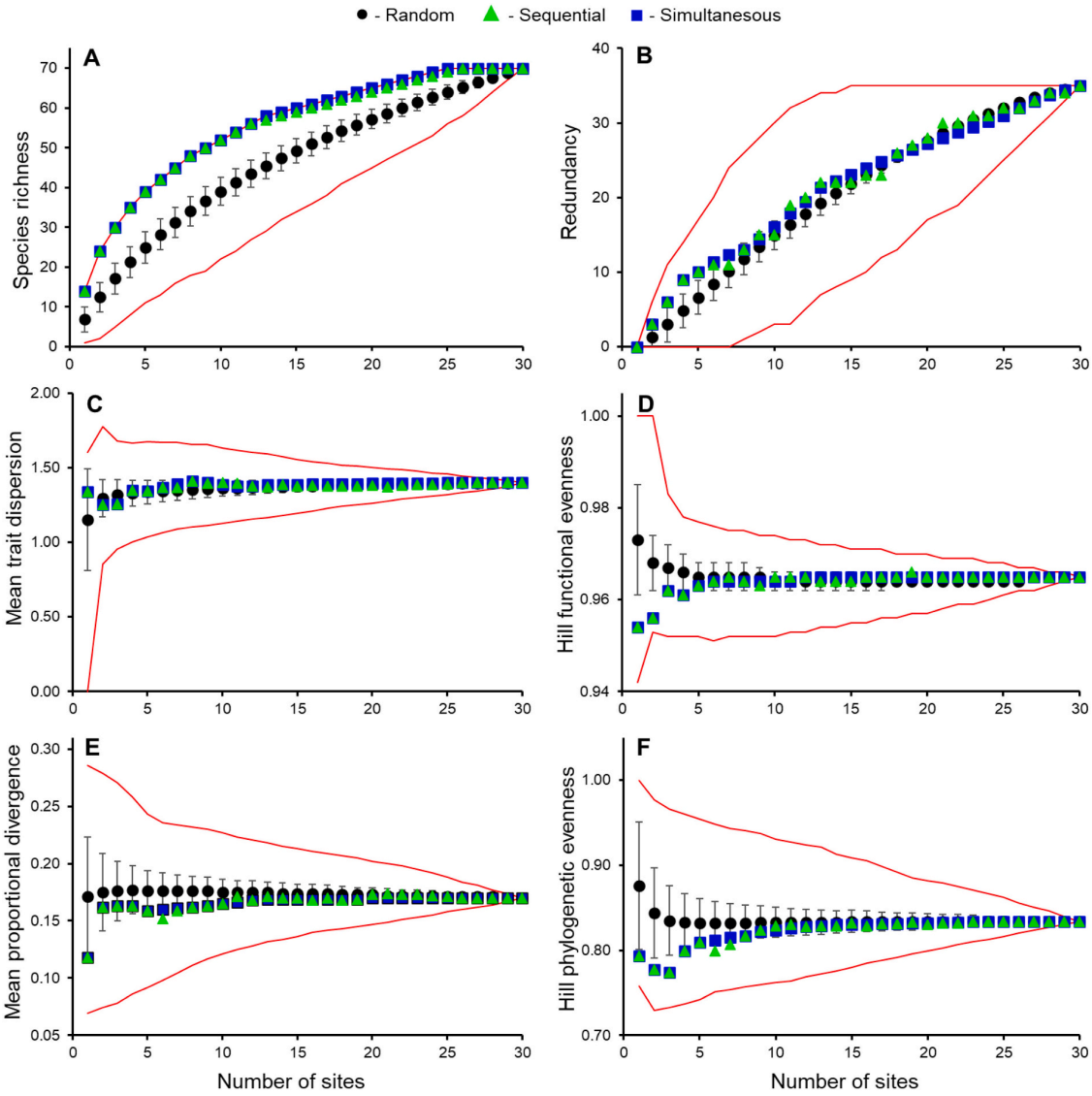

Fig. 4. Trends in aspects of taxonomic (A, species richness; B, redundancy), functional (C, mean trait dispersion; D, Hill functional evenness), and phylogenetic (E, mean proportional divergence; F, Hill phylogenetic evenness) biodiversity of trees in North Carolina as a function of network size based on each of three strategies for configuring a network (i.e., random, indicated by black circles; sequential, indicated by green triangles; and simultaneous, indicated by blue squares). Error bars associated with the random strategy are standard deviations based on all possible combinations of sites that correspond to a network size). Regardless of strategy, red lines indicate the maximum and minimum possible values for each metric at each network size. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

history, has a small effect on the resultant magnitude of biodiversity.

Because metrics of functional and phylogenetic biodiversity measure the magnitude or evenness of dispersion or divergence, and are not counting metrics like species richness, it is unsurprising that functional and phylogenetic biodiversity converged to the values of the complete domain at a much smaller number of sites than did species richness. This pattern is consistent with the notion that the full array of functional roles accumulates early during network assembly when network-wide species richness is prioritized. Constructing networks to maximize network richness results in the early inclusion of complementary sets of species that typically occur in distinct habitat types. Consequently, habitat diversity is maximized via a species richness focus, resulting in a representation of all functional roles. If functional traits are phylogenetically conserved, then all clades also are represented, even in relatively small networks. Subsequent additions to the network that result in smaller increases in species richness are likely to be adding species that are functionally and evolutionarily redundant with species already present in the network. This pattern occurred for the functional and phylogenetic metrics used here as well as for bat assemblages along an elevational gradient in Peru (Scheiner et al., 2017a, 2017b).

4.2. Random network designs and variation in functional and phylogenetic biodiversity

Although the random strategy on average performed as well as non-random strategies with regard to phylogenetic and functional biodiversity in each domain, a large amount of variation about the mean characterized the data, especially for small to moderately-sized

networks, indicating that about half of the time a random strategy might result in greater phylogenetic or functional biodiversity than would the simultaneous or sequential strategies (Fig. 2-4). Of course, this also means that about half of the time a random strategy would result in less phylogenetic or functional biodiversity than would the simultaneous or sequential strategies. The variation associated with the random strategy shows the potential for alternative strategies of network construction, specifically those with the goals of maximizing phylogenetic or functional biodiversity, resulting in a much different selection of sites than does the maximization of species richness. However, we caution that the maximization of dispersion or equability metrics for functional or phylogenetic biodiversity likely are inappropriate goals for conservation networks. These kinds of metrics decrease in magnitude when functionally or phylogenetically redundant species are added to a community or network. Consequently, the maximum values of functional or phylogenetic biodiversity were appreciably greater for networks of small to intermediate size compared to larger networks that included all species (Fig. 2-4). In contrast to the behavior of these kinds of biodiversity metrics, functional (and, probably, phylogenetic) redundancy are ecologically valuable, as they can increase ecosystem stability and resilience (Fonseca and Ganade, 2001; Biggs et al., 2020), making optimization strategies based on metrics that devalue redundancy a poor choice for conservation networks. Rather, the values of functional and phylogenetic biodiversity based on the entire biota likely represent desirable outcomes as they reflect the greater redundancy supported by each regional environment and likely a natural level of functional biodiversity that can stabilize ecosystem services and functions compared to alternative network options that maximize functional or phylogenetic biodiversity. Because of phylogenetic uncertainty, the use of phylogenetic biodiversity as a basis of network configuration may be inadvisable. The uncertainty of phylogenetic biodiversity would imbue equivalent uncertainty in network design recommendations. An evaluation of the effects of phylogenetic uncertainty on Faith's PD, which is highly correlated with species richness and estimates of evolutionary distinctiveness showed that Faith's PD values can differ by up to 38 % and that the rankings of species based on evolutionary distinctiveness can change greatly due to typical levels of phylogenetic uncertainty (Ritchie et al., 2020). The variation in estimates of phylogenetic biodiversity caused by phylogenetic uncertainty can render the conservation value of particular sites ambiguous, leaving conservation managers unable to defend conservation site choices based on phylogenetic biodiversity approaches (Mimouni et al., 2016). In general, large uncertainties in the estimation of divergence times (Diniz-Filho et al., 2013), even in comprehensive phylogenies, continue to make using phylogenic biodiversity as the primary basis for conservation action extremely risky.

4.3. *Caveats and future research*

Our analyses included datasets that differed in site-specific characteristics of biodiversity, suggesting that our results are robust with respect to these aspects of networks (Table 1). Importantly, all three example networks represent only regional extents and involve conservation of just a single taxonomic group. For larger domains, especially those that traverse steep environmental gradients with considerable habitat heterogeneity, results may differ. If the goal is to conserve a range of types of species (e.g., plants and birds and insects), it is not clear what might be the best strategy, even when focusing only on species richness. For example, should networks maximize richness of just one taxonomic group (e.g., the one with the greatest β diversity) or simultaneously maximize richness of all taxa? Are there instances when optimizing functional or phylogenetic biodiversity is the preferable approach? Future research should explore such issues to evaluate the generality of our observations and recommendations.

CRediT authorship contribution statement

Michael R. Willig: Conceptualization, Writing – original draft, Methodology, Supervision, Funding acquisition. **Steven J. Presley:** Formal analysis, Writing – original draft, Data curation, Visualization, Methodology, Investigation. **Brian T. Klingbeil:** Writing – review & editing, Data curation, Visualization, Investigation. **Evsey Kosman:** Writing – review & editing, Methodology. **Tao Zhang:** Writing – review & editing, Data curation, Investigation. **Samuel M. Scheiner:** Conceptualization, Formal analysis, Software, Writing – review & editing, Methodology.

Declaration of competing interest

Steven J. Presley reports financial support was provided by National Science Foundation. Michael R. Willig reports financial support was provided by National Science Foundation. Tao Zhang reports financial support was provided by National Science Foundation. Michael. R. Willig reports financial support was provided by Audubon Connecticut. Steven J. Presley reports financial support was provided by Audubon Connecticut. Brian T. Klingbeil reports financial support was provided by Audubon Connecticut.

Data availability

The data used in this research are all from the literature and have already been made publicly available by those authors.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2022.109876.

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