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Open Research statement:	All code required for data retrieval, data handling, network inference, and analysis of ecological network topologies is available at https://github.com/ErikKusch/Ecological-Network-Inference-Across-Scales. Data from the YFDP is available at the Smithsonian ForestGEO data portal, https://forestgeo.si.edu/. We are ready to submit code and data to Dryad upon acceptance of the manuscript.
Key words	Cooccurrence, Ecological Networks, Ecological Network Inference, Macroecology, Method Comparison, Network Betadiversity, Spatial Scale, Species Associations

ABSTRACT

Several methods of ecological network inference have been proposed, but their consistency and applicability for use across ecologically relevant scales require further investigation. Here, we infer ecological networks using two data sets (YFDP, FIA) describing distributional and attribute information at local, regional, and continental scales for woody species across North America. We accomplish this inference using four different methodologies (COOCCUR, NETASSOC, HMSC, NDD-RIM), incorporating biological data along an occurrence-performance spectrum while accounting (or not) for various confounding parameters. We contrast 1-1 associations at each evaluated scale to quantify consistency amongst inference approaches. We also assess consistency across scales within each inference approach. Ultimately, we find that inferred networks are inconsistent across scales and methodologies, particularly at continental scales. We highlight how such inconsistencies between network inference methods may be linked to using occurrence or performance information and incorporating or not confounding factors. Finally, we argue that identifying the "best" inference method is non-trivial. Thus, to facilitate the choice of inference methods for a given purpose, we suggest aligning specific research questions and the scale applicability of the method when interpreting the inferred links, network topology, and ecological processes governing network assembly.

INTRODUCTION

Climate change, habitat loss, and biological invasions are reorganising Earth's biosphere (Blowes et al. 2019), altering species interactions (Estes et al. 2011) and, consequently, ecosystem functioning (Woodward et al. 2010), resulting in a call for ecological research to consider species interactions when predicting the emergence of novel communities and changes in ecosystem behaviour and functioning (Gilman et al. 2010). This goal can be achieved by assessing how ecological networks, which encode species identities as nodes and

pairwise species interactions as links (Morales-Castilla et al. 2015), would be altered due to changes in the underlying composition of ecosystems and biological communities.

Traditionally, ecological network research efforts have focused on characterising species-species networks at local scales (Bimler et al. 2022). Recent works have taken a broader perspective by characterising networks at regional scales (Hackett et al. 2019) and integrating multiple local networks into global meta-networks (Fricke et al. 2022). Various models to quantify links between species in the absence of prior information on their likely interactions have also been proposed. These models exist on a continuum defined by two axes: (1) the used biological input data and (2) the capability to integrate additional data sources (Figure 1).

Biological inputs, which describe the first axis, can be classified along an occurrence-performance spectrum. Here, some network inference methodologies focus on occurrence (Veech 2013) or performance data either implicitly through abundance (Ulrich and Gotelli 2010) or explicitly through biomass or fitness measurements (Bimler et al. 2022). This occurrence-performance axis arguably represents one of the most important philosophical and methodological discriminating characteristics between network inference approaches.

The second axis encapsulates the capacity to account for different covariates such as environmental gradients, phylogenetic relatedness, and functional traits of species (Morales-Castilla et al. 2015). Approaches along this spectrum can be sorted based on covariates, like environmental conditions, being either absent or present (again, either implicitly or explicitly) when inferring the associations in a network. The importance of including this information has been demonstrated through climatological conditions altering the persistence of competing species (Usinowicz and Levine 2021) and the role of functional traits in governing interactions between forest tree species (Kunstler et al. 2012). Still, most ecological network inference approaches do not incorporate such information (Blanchet et al. 2020), most likely due to data availability constraints, concerns of collinearity, or complexity of analyses.

Lastly, ecological networks are affected by the species richness of their corresponding ecosystems (Poisot et al. 2012), a property determined by the assessment scale (e.g., larger areas contain larger species pools, Conor & McCoy, 2013). The occurrence and magnitude of a link between species may thus differ across geographic scales due to changes in species pool. While such effects of species turnover have been studied for in-situ quantified networks and demonstrated to alter 1-1 links, no such assessment exists for inferred ecological networks.

Practitioners of ecological network inference are faced with many decisions when selecting an appropriate approach and data sources for their respective study. The philosophical and methodological distinctions between approaches raise an important question: *How comparable are different methods of ecological network inference*? The necessary comparisons of modern ecological network inference methods at a scale relevant to quantifying the broader impacts of global environmental change are missing. Here, we focus on the comparability of inferred networks rather than their accuracy for three reasons. First, locally in-situ measured networks often fail to describe all existing links and hence cannot be used to benchmark interference accuracy. Second, existing frameworks to generate "virtual" networks fail to incorporate the two dimensions that differentiate between ecological network inference approaches and variable scales. Last, we aim to showcase the need to align the inference approach with the research questions and the scale applicability of the method. Doing this will give necessary context to the interpretation of the inferred links, network topology, and ecological processes governing network assembly.

In this study, we compare and quantify similarities between four methods of ecological network inference. By doing so, we investigate how consistent inferred ecological networks are when quantifying links (1) at the same scale using different inference approaches and (2) across ecologically relevant scales using the same inference approach. We expect networks corresponding to opposing sides of the occurrence-performance spectrum to differ notably in their structure, with lower dissimilarities between approaches leveraging similar input types.

We also expect that the largest differences between approaches will be between those that account for abiotic factors and those that do not. We postulate that such differences will be amplified at regional and continental spatial scales where environmental gradients are the main determinants of species distributional patterns (Stephan et al. 2021). Lastly, we expect ecological networks inferred with the same approach, but varying species-pools, to differ across geographic scales. Within this comparison across scales, we expect changes in species pools to contribute to overall network dissimilarity but not sufficiently to explain total dissimilarities of networks.

MATERIAL & METHODS

ECOLOGICAL NETWORK INFERENCE METHODOLOGY

We inferred horizontal (i.e., non-trophic) ecological networks using four methods that encapsulate the variability in statistical principles, data requirements, and ecological interpretation (Table 1). A verbose description of each inference method is provided in the supplementary material. These methods have been used primarily to infer associations between bird species (Griffith et al. 2016, Tikhonov et al. 2020) and plant species (Morueta-Holme et al. 2016, Bimler et al. 2022) at scales ranging from local to continental applications. While other inference methods have been established (e.g.: Damgaard et al., 2018; Lamonica et al., 2021; Swain et al., 2021), we have selected this set of four methods as distinct examples of the occurrence-performance axis, as well as their differences in considering environmental conditions (Figure 1).

Data handling, network inferences, and analyses were carried out in R (R Core Team 2021). The packages cooccur (Griffith et al. 2016), netassoc (Blonder and Morueta-Holme 2017), and hmsc (Tikhonov et al. 2020) were used for the COOCCUR, NETASSOC, and HMSC methods, respectively. NDD-RIM was implemented via custom R code. The workflow diagrams of data handling and network inference are presented in Figures S1 and S2.

DATA SOURCES & DATA HANDLING

We inferred networks based on two datasets of North American woody plants: the Forest Inventory Analysis Database (FIA, Burrill *et al.*, 2018) and the Yosemite Forest Dynamics Plot (YFDP, Lutz *et al.*, 2012). These were aggregated to describe a pool of possibly interacting species at three scales: local (0.256 km^2), regional (3,030.17 km^2), and macro (1,508,451 km^2).

The local scale pool of interacting species was defined using the YFDP data, which is a 25.6 ha study area within which all trees ≥1 cm diameter at breast height (dbh) are measured according to the protocols of the Smithsonian ForestGEO network (Davies et al. 2021). We used a subset of the YFDP data set containing 34,589 records of dbh of 11 woody plant species measured in a grid of 640, 20 m × 20 m quadrats which we subsequently treated as individual plots. For consistency with the FIA, we considered only those stems ≥2.5 cm dbh (Gray et al. 2012), retaining the records of 34,444 individuals and their dbh, as a measurement of resource allocation to growth, for network inference. These data were further aggregated to express species' abundances and occurrence in the 640 quadrants of the YFDP.

Species pools at the regional and macro scales were defined by aggregating FIA-plot data. This dataset summarizes information on tree species' presence, abundance, and size/biomass across the forested portion of the United States of America (Gray et al. 2012). To remove possible biases in inferred association matrices introduced by rare species, we removed all species present in less than 10% of all locations for our analyses. We used the FIA-contained records of biomass per species per plot as proxies for species' performances. The regional scale species pool was defined by limiting FIA-plot data to the region encompassing Yosemite National Park as defined by the U.S. National Park Service (National Park Service 2009). This selection resulted in 291 observations (i.e., biomass and abundance of a species at an FIA-plot) at 101 plots containing 13 species. The macro scale species pool was defined by limiting FIA-plot data to the Temperate Conifer Forests Biome polygon (World Wildlife

Fund 2020). This masking resulted in 96,169 observations across 46,328 plots containing 15 species.

Functional Trait Data

The YFDP dataset also includes species-specific measurements of multiple functional traits. We selected specific leaf area, leaf carbon content, and leaf nitrogen content for our analyses. These traits describe important trade-offs in plant investment in photosynthetic organs and storage of resources (Wright et al. 2004). The FIA dataset does not record functional trait measurements for its respective scales. While functional trait data is available for our target species from functional trait repositories like BIEN (Enquist et al. 2009), functional leaf trait expression is modulated by the environment (Wright et al. 2005), potentially leading to an inaccurate representation of local realities at large scales (Violle et al. 2012). We therefor chose to use functional trait means exclusively when implementing HMSC at local scale (Table 1).

Environmental Data

To quantify plot-level environmental conditions experienced by species/individuals, we matched air temperature, soil moisture in a depth of 0-7 cm, total precipitation, and potential evaporation to our data using the KrigR package (Kusch and Davy 2022). We chose these climate parameters due to their link to vegetation performance (Kusch et al. 2022). To reduce biases introduced by climate regime changes, we aggregated environmental conditions to 10-year climatologies leading up to the sampling date of each plot.

Phylogenetic Relatedness

We established phylogenetic relatedness by pruning a phylogenetic mega tree supplied with the V.PhyloMaker package (Jin and Qian 2019). All species in our data not represented in this backbone phylogeny were removed from our analyses which resulted in the above-mentioned 11, 13, and 15 species at plot-, regional-, and macro-scale respectively.

Species Distributions

We obtained species range maps (for use with NETASSOC, Table 1) using the BIEN package (Maitner et al. 2018) to inform null expectations of species co-occurrences at FIA scales (i.e., regional and macro). At the YFDP scale, null models for NETASSOC were established by resampling the observed species-by-site matrix.

Network Consistency Quantification

To quantify dissimilarities of inferred ecological networks at the level of individual links (interactions/associations) and node sets (species composition), we calculated interaction beta-diversity (a relative measure of how many species-species links and/or species identities are shared between two networks) using the betalink (Poisot et al. 2012) R package. This comparison evaluates whether link patterns or species turnover drive changes in the identity and sign of links. For this analysis, we reduced link sets to statistically significant links (p-value < 0.05 for COOCCUR and NETASSOC; 90% credible interval not overlapping 0 for HMSC and NDD-RIM) in the inferred weighted ecological networks. To ensure comparability across methods, we collapsed opposing links in NDD-RIM networks into mean links when computing topological metrics and assigned statistical significance only when both underlying directed links were identified as statistically significant. Additionally, we changed link weights to -1 and 1 based on their original sign. The pairwise associations common to all inferred networks owing to the shared species are highlighted with black outlines in Figures 2 and 3.

Results

To assess the effects of ecological network inference method choice and specification along the occurrence-performance axis and with explicit or implicit adjustments for climate gradients, we focus on plot scale YFDP data (Figure 2) because most data types are available at this scale (Table 1). Furthermore, the trends observed at plot-scale are mirrored at regional and macro-scales (Figure S3 & Figure S4).

Neither association strength nor sign of 1-1 links showed consistent patterns across methods for the YFDP dataset (Figure 2). This pattern holds even for different specifications of the HMSC approach (Figure 2D to F). Inference methods focused on performance data (NDD-RIM and HMSC in Figure 2F) identify more statistically significant links between species pairs than those focused only on occurrence or abundance data (Figure 2A, B, D, E).

As expected, the network matrices for the eight-species pairings shared across all scales (black outlined tiles in Figure 3) show no scale consistency within the evaluated methods. The magnitude and statistical significance of links change across scales for all methods. In the case of HMSC (Figure 3C), we infer a heterogenous network matrix at the plot scale (containing negative and positive statistically significant links) which changes to an exclusively positive, statistically significant link matrix at the macro scale. This scale-inconsistency can also be seen for COOCCUR (Figure 3A) and NETASSOC (Figure 3B), where we fail to detect any statistically significant associations at the regional scale. Lastly, using NDD-RIM, there is little consistency in the sign and magnitude of statistically significantly identified directed links at the plot scale (Figure 1C), regional scale (Figure S3C) and macro scale (Figure S4C). These inconsistencies remain when collapsing opposing directed links inferred by NDD-RIM into undirected links (Figure 3D).

Quantifying network dissimilarity via decomposition of network-dissimilarities into node-set and link-pattern changes reflects the overall lack of inference consistency across scales and approaches. Network dissimilarities within scales (Figure 4, Table S2) are high and cannot be traced back to species turnover (by definition, each network for the same scale consists of the same node set). Instead, these must be attributed to each method input data or statistical philosophy. In line with our expected differences due to the use of occurrence and performance data, the lowest dissimilarity scores within-scales can be found between HMSC and NDD-RIM outputs. As for abiotic factors governing ecological interactions and their inference, we find comparatively low link dissimilarity of individual links between HMSC and NETASSOC at the macro scale, for which we hypothesised climatological gradients to

play crucial roles. When investigating cross-scale consistencies, we find that network dissimilarity is driven by changes in links between species present across the plot, regional, and macro scale instead of added or removed link structures introduced by species turnover (Table S3). This dissimilarity may be reduced by large amounts of data (Figure S5). This finding is consistent for all inference methods assessed here. Finally, these inconsistencies extend beyond comparisons of individual link structures and lead to a lack of consistency in network topology as described by modularity and node centrality (see supplementary material and Figures S6 & S7).

DISCUSSION

We have identified a lack of consensus among networks inferred using COOCCUR, NETASSOC, HMSC, and NDD-RIM. This discrepancy could be attributed to (1) differences in philosophy of methods (e.g., occurrence vs. performance input data, accounting for abiotic conditions and niche preferences), (2) scale-dependant applicability of different methods and data availability/richness, (3) realised biological interactions change across scales due to differences in species pools, and (4) changes in the ecological processes driving community assembly across scales.

CHOICE OF NETWORK INFERENCE APPROACH ACROSS SCALES

Choice of network inference method should be driven by method applicability given study's spatial extent and data availability. Our results highlight two factors that require careful consideration when choosing which method to implement: (1) biological inputs being analysed and (2) data integration and availability.

First, the traditional reliance on occurrence data for network inference has been criticised as being too simplistic to measure ecological process outcomes (Blanchet et al. 2020). As seen in Figure 2 and Figure 3, methods of network inference that leverage abundance or performance data identify more statistically significant associations than their occurrence-driven counterparts. We postulate that difference in identified statistically significant

ecological associations is partially driven by the amount of biologically relevant information in abundance and performance data compared to occurrence datasets (i.e., quantification of species performances implicitly and explicitly vs. qualitative information). Indeed, performance-based networks reported the lowest dissimilarity scores (Figure 4). Such differences in information content have already resulted in null model analyses to discriminate community assembly rules being augmented with abundance data (Ulrich and Gotelli 2010). We suggest that network inference approaches also be subjected to this paradigm shift, thus leveraging performance or abundance data wherever available despite the considerable data collection efforts this entails, particularly at large geographic scales.

Second, macroecological research has long recognised the relevance of environmental conditions on species presence (Wilkinson et al. 2019), abundance (Johnson and Sinclair 2017), and performance (Coutts et al. 2016). Thus, the scale applicability of ecological network inference depends on whether or not climatological gradients ought to be considered in a given study. Of the four evaluated methods, COOCCUR and NDD-RIM do not account for climatological gradients, while NETASSOC does so implicitly through range expectations, and HMSC does so explicitly through direct use of climate data to quantify contributions of bioclimatic niches and environmental conditions to species performance. By accounting for environmental gradients, which alter species co-occurrence potential, NETASSOC and HMSC address recurring criticisms of ecological network inference (Blanchet et al. 2020). The effect of climatological data integration into ecological network inference manifests in lower network dissimilarity scores for networks inferred with NETASSOC and HMSC at macro scales.

In addition to including climatological patterns, there are calls to account for the shared evolutionary history of species pairs as well as their functional trait expressions (Ovaskainen et al. 2017, Blanchet et al. 2020). Meta-analyses of networks across geographic scales, regions, link types, and trophic levels have revealed that a combination of these information criteria is required to uncover mechanisms explaining network structure (Xing & Fayle,

2021). However, this information is unavailable at some geographic scales (Table 1). Our results clearly show that data sparsity can also affect network inference at the regional scale (Figure 3), where NDD-RIM was the only capable method. This capability is likely due to the response-impact model component of the method, designed to infer rare/unobserved links. While complex methods like HMSC are seemingly the only ones capable of inferring ecological networks at macroecological scales with respect to integration of additional confounding variables, this scale is also where selective data sparsity problem is the strongest, and inference may still be limited as the sampling of relevant information is costly at such scales.

Lastly, the methods of ecological network inference assessed here focus on representing networks emerging from different ecological processes. While COOCCUR and NETASSOC aim to identify species associations and their outcome on space-utilisation by association partners, HMSC is primarily aimed at disentangling community assembly processes with link-inference as a side-product of residuals. In contrast, NDD-RIM considers asymmetries in species associations and aims to identify the effect of one association partner on the performance of the other. In addition, the response-impact model component of NDD-RIM may prove helpful in predicting novel interactions as communities reshuffle, thus giving a valuable set of testable hypotheses for experimental macroecology (Alexander et al. 2016). The ecological mechanism supporting a given methodology and the biological interpretation of network-links must thus align with the research questions being investigated to ensure the results' reliability and interpretation. This consideration should be prioritised over the other factors mentioned above.

SCALE-CONSISTENCY & BIOLOGICAL PROCESSES

Biological processes revealed by ecological networks are conditional on the choice and scale of the inference method. Figure 3 and Figure S5 illustrate that 1-1 associations are inconsistent across geographic scales when inferred using the same approach. These scale-inconsistencies are not necessarily a flaw in the methods of network inference but instead a

feature of (1) the inference method applicability at varying scales, (2) the scale-dependence of species-interactions, and (3) which biological processes are being captured at geographic scales.

Inferred species links can be considered data-driven hypotheses about realised biological interactions (Ovaskainen et al. 2016), which have been demonstrated to change in strength and sign when additional species are introduced/removed (Bartomeus et al. 2021). Our analyses of network link beta diversity suggest that scale-inconsistencies of 1-1 associations are partially driven by variation in realised interactions but cannot be explained by changes in species pools alone. Therefore, while there is a precedent for using ecological networks measured/inferred at one scale to draw conclusion at other scales (Guimarães 2020), our findings indicate that neither 1-1 associations nor whole-network topology measures should be transferred between scales. We recommend ecological networks be inferred and interpreted at the scales at which they are to be used for further analyses.

CONCLUSION

Methods of network inference provide a tool for ecological studies. They allow identifying biological interactions which are extremely difficult to observe in nature (e.g., large communities with many potential and realised interactions). We demonstrate however, that scale inconsistencies are considerable for pairwise species links. We show how focusing on the “best” or “most” consistent ecological network inference is a disingenuous goal. Instead, the choice of method needs to consider: (1) alignment of link-interpretation with research questions, (2) applicability of the network inference method at the geographic scale of study, (3) data availability and information content at the geographic scale of study, and (4) biological mechanisms which are identifiable using network inference at the scale of study.

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AUTHOR CONTRIBUTIONS

EK and AO conceptualised this study. EK led the analysis. EK created all R scripts necessary for the analyses. NDD-RIM integration was aided by MB. Results were interpreted by EK and AO. YFDP data was provided by JAL. Manuscript writing was led by EK. All authors contributed critically to the drafts and gave final approval for publication.

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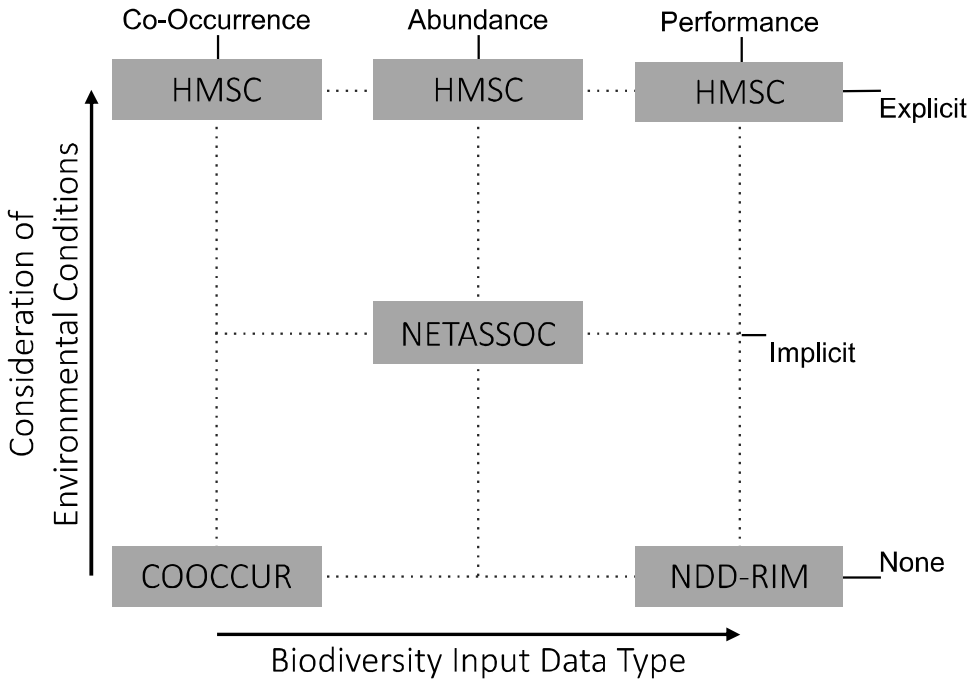

FIGURE 1 – VARIATION ACROSS APPROACHES OF ECOLOGICAL NETWORK INFERENCE – Network inference approaches can be distinguished with regards to their biodiversity input data type (corresponding to the occurrence-performance spectrum, see Figure S1) and their consideration of environmental conditions. The network inference approaches we selected for our study were chosen due to their comprehensive coverage of the resulting spectrum of data type use.

TABLE 1 - METHODS OF NETWORK INFERENCE - Description of statistical principles, data requirements, and ecological interpretation of outputs of the four methods of network inference used in this study. The evaluated methods are: **Probabilistic Species Co-Occurrence Analysis in R** (COOCCUR**,** Griffith et al., 2016), **Inference of Species Associations from Co-Occurrence Data** (NETASSOC**,** Blonder & Morueta-Holme, 2017), **Hierarchical Model of Species Communities** (HMSC**,** Tikhonov et al., 2021), and **Neighbour-Density Dependent - Response Impact Model** (NDD-RIM**,** Bimler et al., 2022). In our implementation of NETASSOC, range estimates for local-scale data were not used in our analyses as they did not represent informative null models. In our implementation of HMSC**,** trait means for each species were only used locally for our analyses as functional trait expressions become too diverse at regional scales to be expressed with a mean value.

Method	Principle	Input	Output	Interpretation of Links
COOCCUR	Probability of species-pair co-occurrence being higher or lower than random.	• Species-by-Site occurrence	Association matrix	Spatial aggregation/disaggregation of species-pairs
NETASSOC	Frequency of species-pair co-occurrence compared to null model.	• Species-by-Site occurrence or abundance • Species-by-Site expectation of range estimates as occurrence		
HMSC	Hierarchical modelling of community assembly processes were residual species-species correlations are treated as association metrics.	• Species-by-site occurrence, abundance, or performance • Environmental conditions at each site • Phylogeny of species • Trait means for each species		Aggregation/disaggregation (in space, abundances, or performance) of species-pairs that aren't explained through other community assembly processes
NDD-RIM	Neighbour-density dependent regression and deconstruction of species interactions into response and effect coefficients for inference of rare interactions.	• Individual/species performance at each site • Species-by-Site matrix of abundance	Interaction matrix	Change in performance of interaction subject with increase in abundance of interaction actor

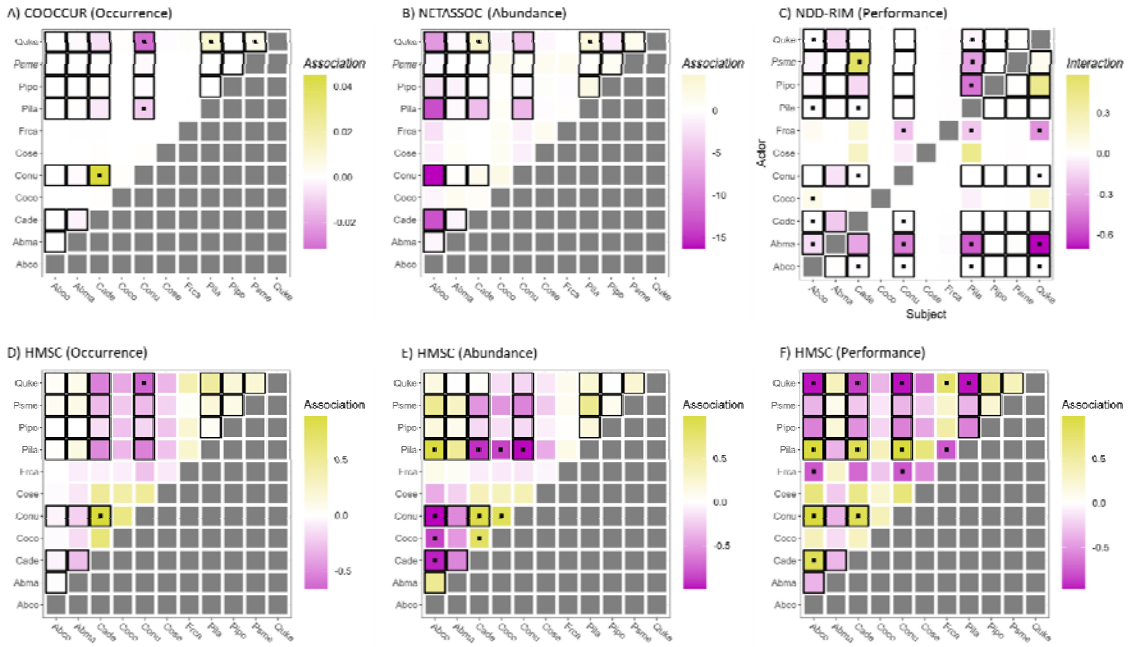

FIGURE 2 - MODEL SPECIFICATION DRIVES NETWORK INFERENCE – Ecological network adjacency matrices inferred at plot scale using the four methods of network inference with differing specifications of spatial products (i.e., occurrence, abundance, performance). COOCCUR (A), NETASSOC (B), NDD-RIM (C) represent use-cases for occurrence, abundance, and performance data. HMSC (D-F) can incorporate occurrence (D), abundance (E), or performance (F) data. Black outlines highlight species pairings shared across all scales of assessment. Black squares in the network matrices signify statistically significant inferred connections between species. See table S1 for an overview of four-letter abbreviations and corresponding species identities.

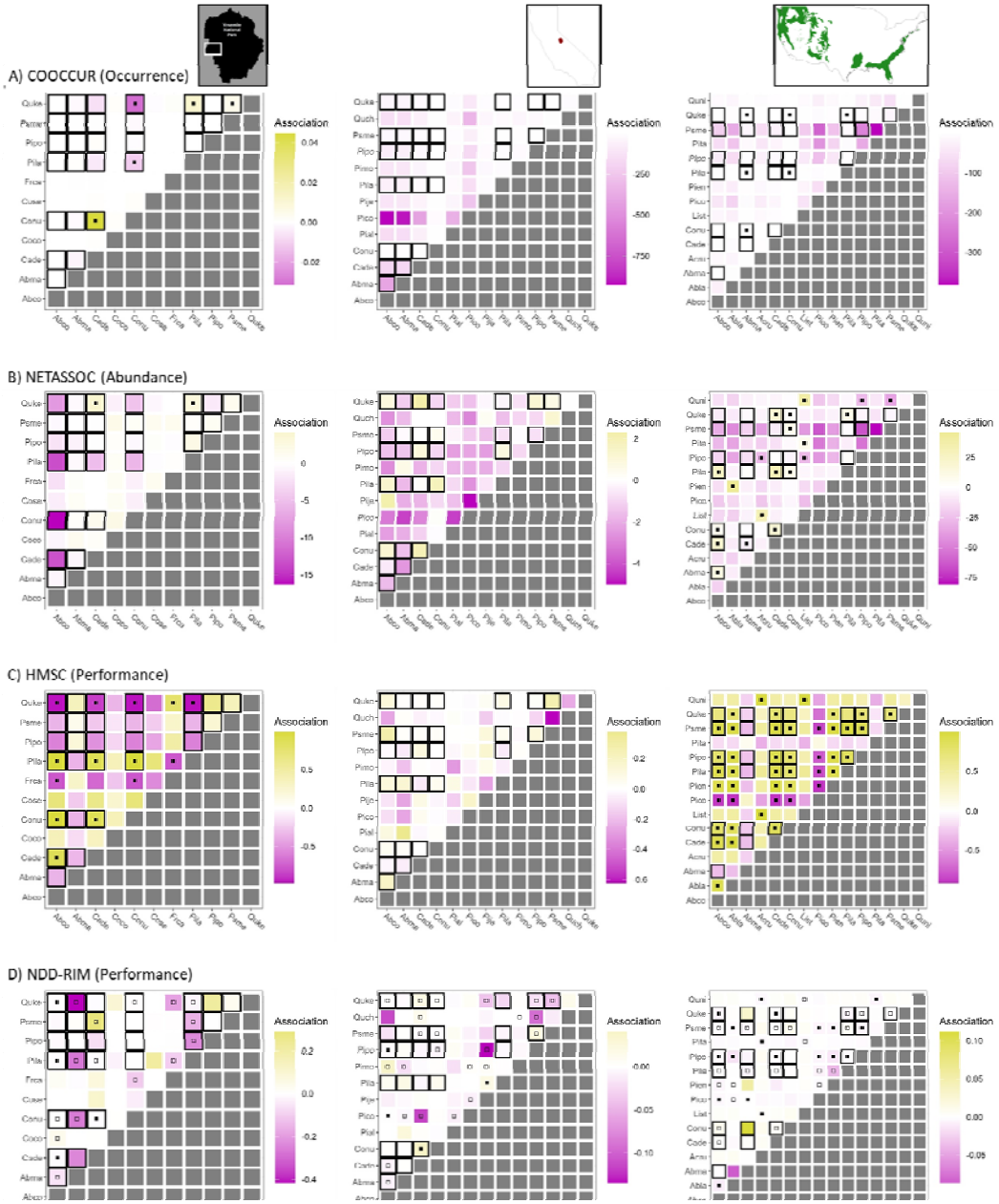

FIGURE 3 - NETWORK INFERENCE IS NOT CONSISTENT ACROSS METHODS OR SCALES – Contrasting the ecological networks inferred using four separate methods (A-D) reveals a lack of scale-consistency when assessing species-species links across geographic scales (i.e., plot scale – left column, region scale – centre column, and macro scale – right column). Black outlines highlight species pairings shared across all scales of assessment. Black outlines highlight species pairings shared across all scales of assessment. Black squares in the network matrices signify statistically significant inferred connections between species. White squares indicate in NDD-RIM visualisation (D) indicate that only one of the underlying directed links was identified statistically significantly. See table S1 for an overview of four-letter abbreviations and corresponding species identities.

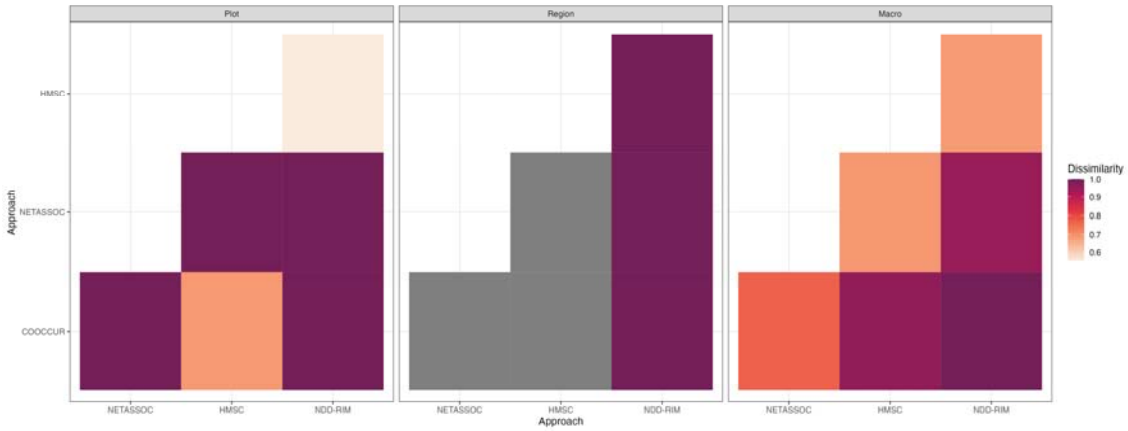

FIGURE 4 – NETWORK BETADIVERSITY ACROSS APPROACHES WITHIN SCALES OF ASSESSMENT – There exists considerably dissimilarity between ecological networks made up of statistically significant links inferred by the four target approaches within each scale of assessment. Notably, inference at region scale (centre panel) was held back by low data availability.