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Combining potentially incompatible community datasets when harmonizing forest inventories in subarctic Alaska, USA

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Abstract

Aims: Plant responses to disturbances and environmental variation can manifest in communities as compositional nestedness (i.e., one community is a subset of another) and/or turnover (two communities represent different compositional gradient spaces). Yet, different sampling designs can artificially give an illusion of such compositional differences among two datasets, making it problematic to harmonize them in multi-species analysis. We test the prediction that sampling differences which increase beta-diversity components (nestedness and turnover) among two vegetation datasets will decrease their exchangeability.

Location: Boreal forests of Tanana River region, interior Alaska, USA.

Methods: We develop novel methods for comparing compositional variation among two datasets in nonmetric multidimensional scaling (NMDS) ordination. Resampled NMDS establishes internal sampling variability for each dataset independently, and reciprocal NMDS determines external exchangeability when the two are mutually exchanged. We first compare simulated data with specified beta-diversity differences, then evaluate two forest inventories based on local vs regional sampling designs in Alaska's boreal forests.

Results: As simulated species turnover and nestedness increased, internal sampling variability remained essentially constant, but external exchangeability progressively declined. Species turnover (not nestedness) had the larger negative effect on exchangeability. Among the boreal forest inventories, internal sampling variability was relatively similar, and exchangeability was weakly moderate, but the regional inventory exhibited much better fit to broad-scale environment. Species turnover (not nestedness) contributed the majority of beta-diversity differences among the two forest inventories, suggesting that strong environmental gradients were unequally represented.

Conclusions: Species turnover alters multivariate outcomes more drastically than species nestedness. Therefore, combining two vegetation datasets may be inadvisable when turnover prevails. Instead, a multi-scale perspective, with separate but complementary forest inventory analyses, can portray local and regional variation at appropriate scales. Our method is tractable for assessing exchangeability of potentially inconsistent sampling designs, like those that are common in synthesis studies and long-term ecological monitoring.

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KEYWORDS
beta-diversity, bootstrapped ordination, boreal forests, community compositions, cross-validation, forest ecology, interior Alaska, national forest inventory, nonmetric multidimensional scaling, procrustes analysis, species abundance distributions, species pools

1 | INTRODUCTION

Forest vegetation databases now provide unprecedented amounts of information used to test ecological theories and inform forest management (Dengler et al., 2011). Chief among them, design-based forest inventories with standardized plot measurements are uniquely informative for providing statistically defensible estimates of forest biomass and carbon, evaluating forest health and biodiversity, and tracking trends in forest disturbances and land uses (Corona, Chirici, McRoberts, Winter, & Barbati, 2011; Gray & Whittier, 2014; Powell, Cohen, Kennedy, Healey, & Huang, 2014). National and regional forest inventories typically feature extensive sampling designs intended to be geographically representative of large areas. By contrast, local "purposive" inventories may use intensive sampling designs covering much smaller geographic areas, which could nevertheless hold rich information for making inferences to surrounding landscapes. The prospect of combining two kinds of forest inventories into one vegetation analysis is attractive, but also presents a challenge: how best to combine unrelated and potentially incompatible datasets?

Problems inherent to combining potentially incompatible datasets are common in ecological meta-analyses and long-term monitoring programs. Meta-analytic methods commonly integrate many disparate datasets to estimate an effect size (Koricheva & Gurevitch, 2014) or its variability (Nakagawa et al., 2015). Yet, many meta-analyses explicitly consider only univariate outcomes such as plant growth (Wu, Dijkstra, Koch, Peñuelas, & Hungate, 2011), forest productivity (Zhang, Chen, & Reich, 2012) or species richness (Whittaker, 2010), which suggests a need for ways to combine multivariate datasets across different spatial or temporal domains. Paul et al. (2008) suggested combining data that exhibit similar univariate probability distributions and correlation structures, though this doesn't directly address the multivariate nature of multi-species datasets. Combining multivariate datasets is also a common problem in comprehensive long-term monitoring because monitoring programs often measure multi-attribute (plant/animal/nutrient) outcomes in the face of ever-evolving research questions and sampling methods that change over time (Lindenmayer & Likens, 2010). These changes can complicate interpretation of real ecological changes in vegetation when sampling design changes were concurrent (Lintz, Gray, & McCune, 2013). Lindenmayer and Likens (2018) remark on the urgent need for methods to integrate and combine data from large-scale monitoring programs with smaller-scaled "question-driven" research sampled at different temporal and spatial scales.

The boreal region of Alaska, encompassing some 45 million ha of forest lands, is of key importance for global change monitoring due to potential for permafrost degradation, massive releases of soil organic carbon, widespread vegetation shifts, and accelerating wildfire cycles (Jorgenson et al., 2013; Turetsky et al., 2015). This region remains the largest area of the United States lacking baseline measurements for a comprehensive, design-based forest inventory (Barrett & Gray, 2011), although two recent initiatives of the US Forest Service's Forest Inventory and Analysis program have begun to remedy the knowledge gap. The first initiative is the Interior Alaska Inventory, a large-footprint, regional inventory begun in 2014 to report the status and trend of key ecosystem attributes (Pattison et al., 2018). The second initiative, centered on the Bonanza Creek Long-Term Ecological Research (LTER) site, is a small-footprint, intensified sample from 2011 which aimed to leverage existing long-term data and infrastructure to provide early warning of climatic changes (FIA, 2012). It is unclear whether two forest inventories like these might provide similar information about how vegetation composition relates to regional climate. Resolving this requires a way to harmonize and evaluate the two inventories.

Harmonizing forest inventories is an ongoing challenge (McRoberts, Tomppo, Schadauer, & Ståhl, 2012) complicated by potential mismatches. For example, community ecology datasets may differ in the number and identity of included taxa, spatial coverage or extent, size of sample units, measurement technique, and/or degree of sampling effort (Anderson, Ellingsen, & McArdle, 2006; Paavola et al., 2006). Given different plot sizes, for example, a collection of smaller plots often has higher beta-diversity (more plot-to-plot heterogeneity) than a collection of larger plots that exhibits more compositional homogeneity (De Cáceres et al., 2012), implying that smaller plots may capture only a nested subset of an available species pool. Inconsistent sampling designs lead to weaker detection of compositional gradients and greater disagreement among ordination scores (Økland, Eilertsen, & Økland, 1990; Otýpková & Chytrý, 2006; Smith, Jovan, & McCune, 2017). Therefore, results from algorithms that are sensitive to variation in community compositions (i.e., beta-diversity) could be especially vulnerable to misinterpretation when two sampling designs capture apparently different collections of species.

Variations in community compositions can be decomposed into "nestedness-resultant" and "turnover" components of beta-diversity (Baselga, 2010, 2013). Nestedness-resultant components of beta-diversity increase to the extent that one collection of species is a (nested) subset of another. Turnover components increase to the extent that two collections of species represent different portions of a compositional gradient. Community ecology theory predicts that geographical distance, environmental divergence, or differing colonization histories among two collections of species will contribute to beta-diversity (Vellend, 2016). Interpreting variation in species

compositions is the domain of unconstrained ordination methods, which capitalize on compositional variation to relate community structure to, e.g., climate processes, land-use changes, and forest disturbances in boreal forests and elsewhere (Gibson et al., 2016; MacDonald et al., 2015; Nelson, McCune, Roland, & Stehn, 2015). Data-driven ordination algorithms like nonmetric multidimensional scaling (NMDS; Kruskal, 1964) are particularly appropriate for ecological data that exhibit strong departures from multivariate normality, yet these algorithms are also clearly sensitive to beta-diversity (Anderson et al., 2011). Currently, it is unresolved how the nestedness and turnover components of beta-diversity might complicate the interpretation of NMDS solutions derived from two possibly inconsistent datasets.

Our aim was to resolve whether a local and a regional forest inventory yielded exchangeable multivariate outcomes based on vegetation attributes sampled across a large boreal forest landscape in the US state of Alaska. We predicted that increasing beta-diversity components (nestedness-resultant and turnover) would increase species differences (and hence decrease exchangeability) among pairs of vegetation datasets. To test this, we used resampled NMDS (to assess internal sampling variability) in combination with a novel reciprocal cross-fitting method for NMDS (to assess external exchangeability). We first apply the concept to a series of simulated datasets with specified degrees of species nestedness and turnover, then use it to evaluate exchangeability among two real forest inventories from the boreal region of interior Alaska.

2 | MATERIALS AND METHODS

Calculations were done in R version 3.5.1 (R Development Core Team, 2018) with supplemental packages noted below. To reproduce analyses, we provide all data (described in Supporting information Appendix S1, and provided in Supporting information Appendix S2) and computer code (described in Supporting information Appendix S3, and provided in Supporting information Appendix S4). We also created an original R software package named *fitNMDS* to implement the newly proposed methods, freely available at https://github.com/phytomosaic/fitNMDS. We assessed both simulated and real datasets.

2.1 | Simulated data: manipulating beta-diversity components

One goal was to evaluate how performance may change under differing degrees of beta-diversity components: nestedness-resultant and turnover. We first generated one reference dataset using function 'coenoflex' from the package of the same name (Roberts, 2016). This consisted of a matrix containing $\log_{10}(x + 1)$ transformed abundances of 50 species sampled at regular intervals along two synthetic, orthogonal environmental gradients (49 sample units on a 7 × 7 grid). Gradients ranged from 0 to 100 arbitrary units, with productivity held constant, and species maximum total abundance was 100 arbitrary units (i.e., 100% plot cover). We simulated weak sampling noise by adding uniformly random values ±1% of original values, and by incorporating 10% probability of absence in suitable sites. Species responses followed the integrated rate methodology of individual gradient responses, with species centroids uniformly randomly distributed across the two gradients. Species' niche widths had a variance 60% of the mean niche width (which was 50% of the gradient length), and were specified to be uncorrelated with maximum abundances. The distribution of maximum species abundances was approximately log-normal (specified skew factor = 3.0). We simulated a moderate competitive advantage for larger organisms (specified competition asymmetry coefficient = 10). To systematically vary beta-diversity components (nestedness and turnover), we iteratively modified species from the 50-species reference dataset. To simulate nestedness, we randomly deleted 10, 20, 30, or 40 species from the 50-species reference dataset, yielding strict subsets. To simulate turnover, we randomly replaced 10, 20, 30, or 40 of the reference species with simulated "new" species from further along gradients, keeping species richness constant. To confirm that our simulations had intended beta-diversity components, we quantified nestedness-resultant or turnover components using multi-site Sørensen dissimilarity decomposition (Baselga, 2013) to species lists from each dataset pair. In total, we considered 40 manipulated datasets (=2 beta-diversity components ×4 species modification levels ×5 replicates each) in relation to the original reference.

2.2 | Real forest vegetation data: two inventory types

Another goal was to evaluate the exchangeability of real vegetation data from two alternative forest inventories sampled as part of the US Forest Service's Forest Inventory and Analysis program. The first, large-footprint, regional inventory was the Interior Alaska Inventory ("FIA" hereafter; Pattison et al., 2018). The second, small-footprint, local inventory was an intensified, purposive sample from the Bonanza Creek Long-Term Ecological Research site ("BNZ" hereafter; FIA [Forest Inventory and Analysis Program], 2012). Both were based on surveys of 672-m^2 sample units in which trained technicians recorded the abundance of trees, shrubs, forbs, graminoids, and terrestrial mosses on lands that qualified as forested (currently or recently ≥10% tree cover). For our analysis, the measure of abundance for trees was plot basal area standardized by all-species maximum (therefore bounded [0,100]). The measure of abundance for shrubs, forbs, graminoids, and terrestrial mosses was vertically projected canopy cover (also bounded [0,100]) to the nearest whole percentage point. Moss species were aggregated into functional groups. The FIA and BNZ inventories differed in the completeness of species sampling (simplified vs exhaustive species capture), criteria for locating plots (systematic on fixed grid vs systematically randomized within cells of a pre-defined hexagonal grid covering the study area), plot density (1 plot per 9,712 ha vs 270 ha), and geographic footprints (~1 million ha vs 15,000 ha).

Both inventories were conducted in the Tanana River region of interior Alaska, at elevations ranging from 15 to 650 m above sea

level, on all accessible slopes and aspects (Figure 1). The regional climate is considered subarctic continental, with long, extremely cold winters and brief, warm summers; on average most precipitation falls in late summer. Regional topography is characterized by paludified peat-dominated wetlands, poorly drained north-facing slopes underlain by discontinuous permafrost, drier south-facing slopes, subxeric uplands, and a wide alluvial floodplain draining the Alaska Range to the south and the Yukon-Tanana uplands to the north. The boreal forest tree layer is dominated by *Picea mariana* and *Betula neoalaskana*, along with *Picea glauca*, *Populus balsamifera*, *Populus tremuloides* and *Larix laricina*. Common tall shrubs include *Alnus viridis*, *Salix glauca*, *S. bebbiana* and *S. scouleriana*. Low shrubs include *Vaccinium vitis-idaea*, *Vaccinium uliginosum*, *Ledum groenlandicum* and *Betula nana*. Ground layer moss vegetation is dominated by nitrogen-fixing feather mosses *Pleurozium schreberi* and *Hylocomium splendens* in uplands, and *Sphagnum* spp. peat-mosses in lowlands.

2.3 | Harmonization

Prior to analysis, we resolved taxonomic concepts among the forest inventories (for example, all *Betula papyrifera* records were reassigned to the modern name *Betula neoalaskana*), and we aggregated subspecific ranks (varieties and subspecies) to species rank. Because the BNZ "Phase 3" sampling protocol was more inclusive of species than the FIA "Phase 2" protocol, we filtered observations from the BNZ dataset to mimic FIA's sampling design – specifically, we included only the top four species per growth form (tree/shrub/forb/graminoid) that exceeded 3% canopy cover in each of four 168-m^2 area subplots per 672-m^2 plot, following FIA's Phase 2 protocol (FIA, 2017). Therefore, species abundances in the FIA dataset were sampled in the field, while species in the BNZ dataset were "sampled" computationally using the identical inclusion criteria in identically-sized plots. To minimize observations contributing little to overall community structure, we removed very rare species (<1% relative frequency), species-poor plots (<4 species), and plots that were extreme outliers in community composition (average Bray-Curtis dissimilarity >3 standard deviations from the grand mean). Under these constraints there were roughly twice as many FIA plots as BNZ plots (196 vs 84). Therefore we downsampled the FIA dataset by selecting only those FIA plots that were compositionally most similar (smallest Bray-Curtis dissimilarities) to the BNZ plots, yielding a balanced, equal number of co-regional plots for each. The final products for analysis were two boreal forest vegetation abundance matrices: FIA (84 plots × 87 species) and BNZ (84 plots × 76 species).

2.4 | Modeling approach

With two approaches, we sought to answer the question: relative to inherent sampling variability, to what degree are two candidate datasets exchangeable under the null hypothesis of having been sampled from an identical species abundance distribution? Resampled NMDS gives a collective measure of internal sampling variability ($R_{P\text{internal}}$) of an ordination configuration, by resampling the original data with replacement (for the bootstrap version) or by omitting single observations in turn (for the jackknife version), then iteratively calculating new ordination scores which are compared to the reference ordination using Procrustes analysis (Gower, 1966; Peres-Neto & Jackson, 2001). Reciprocal NMDS gives a relative measure of external exchangeability ($R_{P\text{external}}$) of an ordination configuration, by using each of two competing datasets to calibrate a model, reciprocally swapping each dataset into the opposing calibration model (i.e., two-fold cross-validation using each dataset as a "training" or "test" set in turn), then comparing each ordination using Procrustes analysis. Just like a traditional R^2 statistic, the $R_{P\text{external}}$ statistic can be interpreted subjectively, but we recommend as a rule-of-thumb that at $R_{P\text{external}}$ >0.9 groups are relatively exchangeable, 0.9–0.7 moderately exchangeable, 0.7–0.5 weakly exchangeable, and <0.5 would require serious inspection. Comprehensive descriptions of algorithms follow.

2.5 | Internal sampling variability of a single dataset: resampled NMDS algorithm

First:

1. Reference ordination: obtain NMDS configuration based on complete reference data.

   Then, for each {1, …, *B*} replicate:

2. Resampling: draw with replacement *n* sample units from the reference dataset (for the bootstrap version) or draw *n*–1 sample units (for jackknife version) to create a replicate dataset. Resampling sample units (instead of species or species abundance values) preserves dependencies among the abundances of co-occurring species (Knox & Peet, 1989).
3. Resampled ordination: obtain NMDS configuration based on the resampled replicate, keeping settings identical to reference.
4. Alignment: perform Procrustean reflection/rotation/dilation to align the replicate and original reference configurations to maximum similarity. This step corrects arbitrary reversals of axis directions while retaining the relative rank order of site scores.
5. Scores: save site scores, then calculate weighted average species scores.
6. Site score statistic: calculate Procrustean sums-of-squares and symmetric Procrustean fit statistic of the aligned replicate configuration relative to the reference configuration.
7. Species score statistic: calculate the variance of species ranks along all ordination axes.

   Across all *B* replicates:

8. Internal sampling variability statistic ($R_{P\text{internal}}$): calculate median of all *B* Procrustean fits from Step 6, to obtain $R_{P\text{internal}}$, a measure of sampling variability of site scores.

9. Summarize species scores: calculate median observed species rank variance (from Step 7) divided by expected rank variance to obtain scaled rank variance, *SRV*, a measure of sampling variability of species scores (Knox & Peet, 1989).

2.6 | External exchangeability of two datasets: reciprocal NMDS algorithm

1. Enforce balanced sample sizes: downsample the larger dataset by keeping only the "nearest neighbors" of the smaller dataset, based on minimizing geographic, environmental, or species dissimilarities.
2. Check: stop if no species are shared in common among the two datasets (i.e., disconnected).
3. Calibration models: with each dataset as a "training set," obtain two independent NMDS configurations.
4. Reciprocal models: reciprocally exchange each dataset as a "testing set" into each calibration model, obtaining new predicted site scores for each combined pair (training + testing).
5. Partial fit statistic: *for each dataset separately*, calculate partial Procrustean fit among the two models (aka "intermodel fit" of Smith et al., 2017), as a relative measure of how much each dataset contributes to final agreement between models.
6. Alignment: perform Procrustean reflection/rotation/dilation to maximize similarity among the two *complete* reciprocal models from Step 4.
7. External exchangeability statistic ($R_{P\text{external}}$): calculate symmetric Procrustean fit among the two complete aligned models, as a measure of how well the two models agree. Complete mutual exchangeability ($R_{P\text{external}} = 1$, on a 0–1 scale) would result if observations were drawn from an identical species abundance distribution.
8. Optional statistics: for each of the reciprocal models, calculate nonlinear adjusted-R^2 from a generalized additive model regressing axis-wise NMDS scores on a set of explanatory variables (climate, disturbance, resource availability, etc.).

For each combination of modified vs reference datasets (simulated data) or FIA vs BNZ datasets (real data), we performed resampled NMDS (jackknife version) and reciprocal NMDS per the procedures described above. Prior to ordinations, species abundance matrices were converted to zero-adjusted Bray-Curtis dissimilarities (Clarke, Somerfield, & Chapman, 2006) to account for otherwise incomparable sample units (no shared species) possibly generated during resampling (although the *fitNMDS* software package permits most commonly-used dissimilarity indices, and has options to use or not use zero-adjustments). Because Bray-Curtis dissimilarities tend to provide ambiguous information at maximally dissimilar values, adjustments were needed (Smith, 2017). Therefore, we applied shortest-path stepacross adjustment (Williamson, 1978) using function 'stepacross' in R package *vegan* (Oksanen et al., 2018). For all NMDS runs (function 'metaMDS' using engine 'monoMDS' in *vegan*), we specified a maximum of 99 random starting configurations, a maximum of 200 iterations, weak tie treatment, and final configurations rotated to orthogonal principal axes. We requested 2-dimensional solutions for the simulated data (to reflect the 2-dimensional synthetic grid) and 3-dimensional solutions for the more complex boreal forest vegetation. The reciprocal step relied in part on custom function 'addpoints.nmds.R' authored by David W. Roberts (http://ecology.msu.montana.edu/labdsv/R/labs/lab9/), which iteratively fits predicted scores for all NMDS axes simultaneously while leaving existing points unchanged. In the univariate case, this would be roughly analogous to obtaining new values by fitting new observations to an existing regression model, except in our multivariate case for NMDS, the algorithm seeks to minimize differences between ranked pairwise dissimilarities of sample units and their Euclidean distances in the ordination space, while holding existing points in place. In all cases, we specified symmetric Procrustes statistics (Gower, 1966; Peres-Neto & Jackson, 2001) using *vegan* function 'protest'.

Given that the reciprocal NMDS step is a special case of two-fold cross-validation using two independent datasets as partitions, we were also curious how our larger FIA dataset would perform when partitioned and compared to itself, with the expectation of high "exchangeability". For this, we performed 999 iterations of two-fold cross-validation of the FIA dataset (partitioning it into two halves for reciprocal NMDS), then compared the median cross-validated $R_{P\text{external}}$ value to the $R_{P\text{external}}$ value observed when using both the FIA and BNZ datasets independently. We also determined the percentile of the observed FIA–BNZ $R_{P\text{external}}$ with reference to the FIA-only distribution of randomly split values. Cross-validation methods may underestimate prediction error in the presence of dependence structures (Roberts et al., 2017); therefore, whenever nearby sites have more similar community compositions than distant sites (i.e., data are spatially structured), then performing reciprocal NMDS on spatially blocked subsets may be advisable to avoid biased estimates of exchangeability.

To partition total beta-diversity into species nestedness and turnover components, we applied multi-site Sørensen dissimilarity decomposition (Baselga, 2013) to species lists compiled from the two forest inventories. We tested for differences in average alpha-diversity (mean species richness) by fitting a fixed-effects linear model with orthogonal *F*-tests of coefficients. We assessed the strength of fit to climatic environmental gradients by regressing NMDS scores on the known synthetic gradients (for simulated data), or by regressing NMDS scores on principal component scores (PCs) of the environmental variables (for real data). For this, the principal components analysis (PCA) of environmental variables was based on the correlation matrix (centered and standardized by standard deviation), and the regression was a generalized additive model using thin-plate spline smoothing functions of the PCs selected by generalized cross-validation in R package *mgcv* (Wood, 2011). Climatic environmental variables for the Alaska data were seasonal 30-year normals for minimum and maximum temperatures, precipitation, radiation, reference

evapotranspiration and climatic moisture deficit following Wang, Hamann, Spittlehouse, and Carroll (2016).

3 | RESULTS

3.1 | Simulated data

For the 40 simulated datasets, stress of the final 2-dimensional NMDS configurations ranged from 0.09 to 0.27. The two beta-diversity components had divergent effects on internal and external attributes. For internal sampling variability (assessed by jackknife resampled NMDS), species nestedness had very little effect (0.99 = minimum $R_{P\text{internal}}$ on a 0–1 scale), while species turnover had a slightly larger negative effect (0.88 = minimum $R_{P\text{internal}}$) (Figure 2a). For external exchangeability (assessed by reciprocally fitting reference and modified datasets in opposing NMDS models), both nestedness and turnover had negative effects, but turnover was more strongly negative (Figure 2b,c). Resampled NMDS configurations showed greater sampling variability for turnover than for nestedness (Figure 3). Likewise, reciprocal NMDS configurations showed lower exchangeability as more species were modified to simulate turnover than nestedness (Figure 4). Fit to environment declined with both species nestedness and turnover, although turnover had the larger negative effect (Supporting information Appendix S5).

3.2 | Real boreal forest vegetation data

From a collective species pool of 104 observed species, the two forest inventories in the lower Tanana River region of interior Alaska shared 59 species (57% of the collective species pool) after downsampling

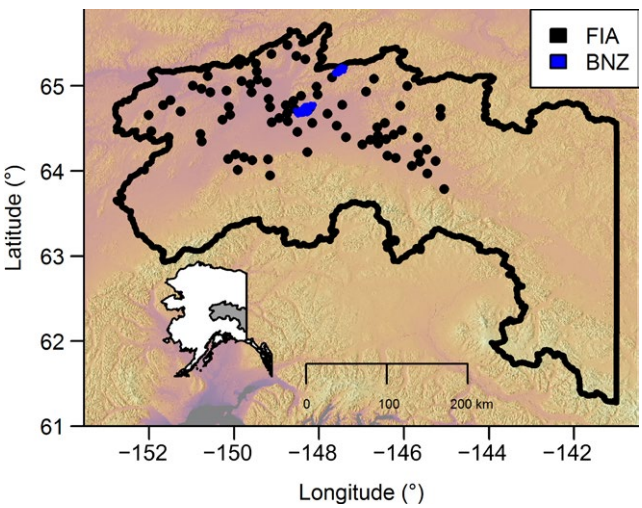

FIGURE 1 Approximate plot locations from two forest inventories in the Tanana River study area. Both inventories were conducted in subarctic boreal forests of interior Alaska, which is dominated by a wide alluvial floodplain draining the Alaska Range to the south and the Yukon-Tanana uplands to the north. Regional FIA inventory covers most of the study area, while local BNZ inventory was an intensified purposive sample [Colour figure can be viewed at wileyonlinelibrary.com]

FIA plots based on maximum similarity with BNZ plots. Of the 87 species in the regional FIA dataset, 28 (32%) were unique. Of the 76 species in the local BNZ dataset, 17 (22%) were unique. The most common shared species, exceeding 50% relative plot frequency, were nitrogen-fixing mosses (e.g., *Pleurozium schreberi* and *Hylocomium splendens*), *Picea glauca*, *Betula neoalaskana*, *Picea mariana*, *Vaccinium vitis-idaea*, *Rosa acicularis*, *Ledum groenlandicum*, and *Alnus viridis*. Of unshared species unique to each dataset, none were very common (none >8% plot frequency). Unshared species primarily included members of *Salix*, *Carex*, and other difficult-to-identify graminoid genera. Notable exceptions included woody shrubs *Dasiphora fruticosa* and *Betula glandulosa*, which were present only in the FIA inventory. Average alpha-diversity did not differ among the forest inventories ($F_{1,166}$ = 2.18, p = 0.14 from a linear fixed-effects model). Based on multi-site Sørensen dissimilarity decomposition (Baselga, 2013) comparing species lists from the two forest inventories, species turnover accounted for much more of the total beta-diversity than nestedness (turnover = 0.224, nestedness = 0.052, total = 0.276).

The FIA and BNZ vegetation datasets had very similar internal sampling variability and moderate external exchangeability, but quite dissimilar fit to regional climate, where FIA outperformed BNZ (Supporting information Appendix S5). Internal sampling variability, as measured by resampled NMDS statistics, was qualitatively similar among the FIA and BNZ datasets ($R_{P\text{internal}}$ = 0.974 vs 0.831, median stress = 0.151 vs 0.132, scaled rank variance for species scores = 0.445 vs 0.380). External exchangeability, as measured by reciprocal NMDS statistics, was only moderate among the FIA and BNZ datasets (partial $R_{P\text{external}}$ = 0.824 vs 0.830, overall $R_{P\text{external}}$ = 0.825; Supporting information Appendix S6). By comparison, 999 iterations of two-fold cross-validation of the FIA dataset (repeatedly randomly splitting it into two halves for reciprocal NMDS) yielded higher "exchangeability" ($R_{P\text{external}}$ = 0.894 = cross-validated median) than for the FIA–BNZ comparison (overall $R_{P\text{external}}$ = 0.825 = cross-validated 7th percentile). The reciprocal model calibrated with FIA data had greater fit to regional environmental variables (first axis R^2 = 0.13 vs 0.07, second axis R^2 = 0.10 vs 0.12, third axis R^2 = 0.20 vs 0.01).

4 | DISCUSSION

The flood of forest inventory and vegetation plot information now publicly available means that ecologists must increasingly consider weaving together inconsistent datasets for their analyses (Brunner et al., 2017; Jetz, McPherson, & Guralnick, 2012; Pacifici et al., 2017). We identified the relative contributions of beta-diversity components on NMDS ordination outcomes, finding a stronger influence of species turnover than nestedness. This implies that meta-analysis and synthesis studies should carefully consider the effects of sampling designs that portray community compositions differently, particularly if datasets share few species in common and encompass different portions of species compositional gradients. Among boreal forest vegetation of interior Alaska, we found only

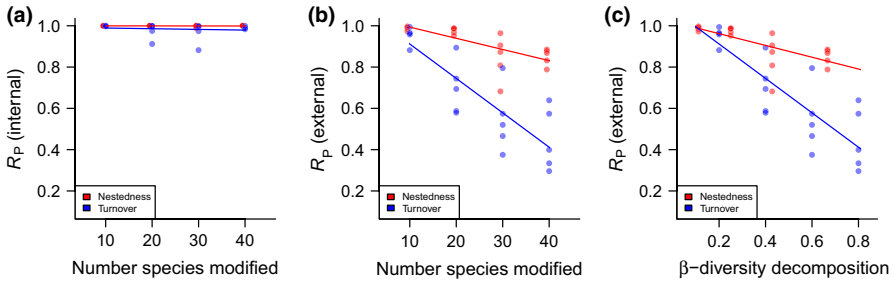

FIGURE 2 Species turnover had a larger negative effect than species nestedness. One simulated reference dataset (49 plots × 50 species) had varying numbers of species modified by random removal (nestedness component) or else random replacement with new species (turnover component), with 5 replicates per modification. Internal sampling variability (from jackknife resampled NMDS, Figure 2a) remained relatively high for both beta-diversity components. External exchangeability (from reciprocal NMDS, Figures 2b, 2c) was more sensitive to these modifications, where turnover had the larger negative effect. This held true whether considering the number of modified species (Figure 2b) or the nestedness-resultant and turnover components of Sørensen dissimilarities from beta-diversity decomposition (Figure 2c) [Colour figure can be viewed at wileyonlinelibrary.com]

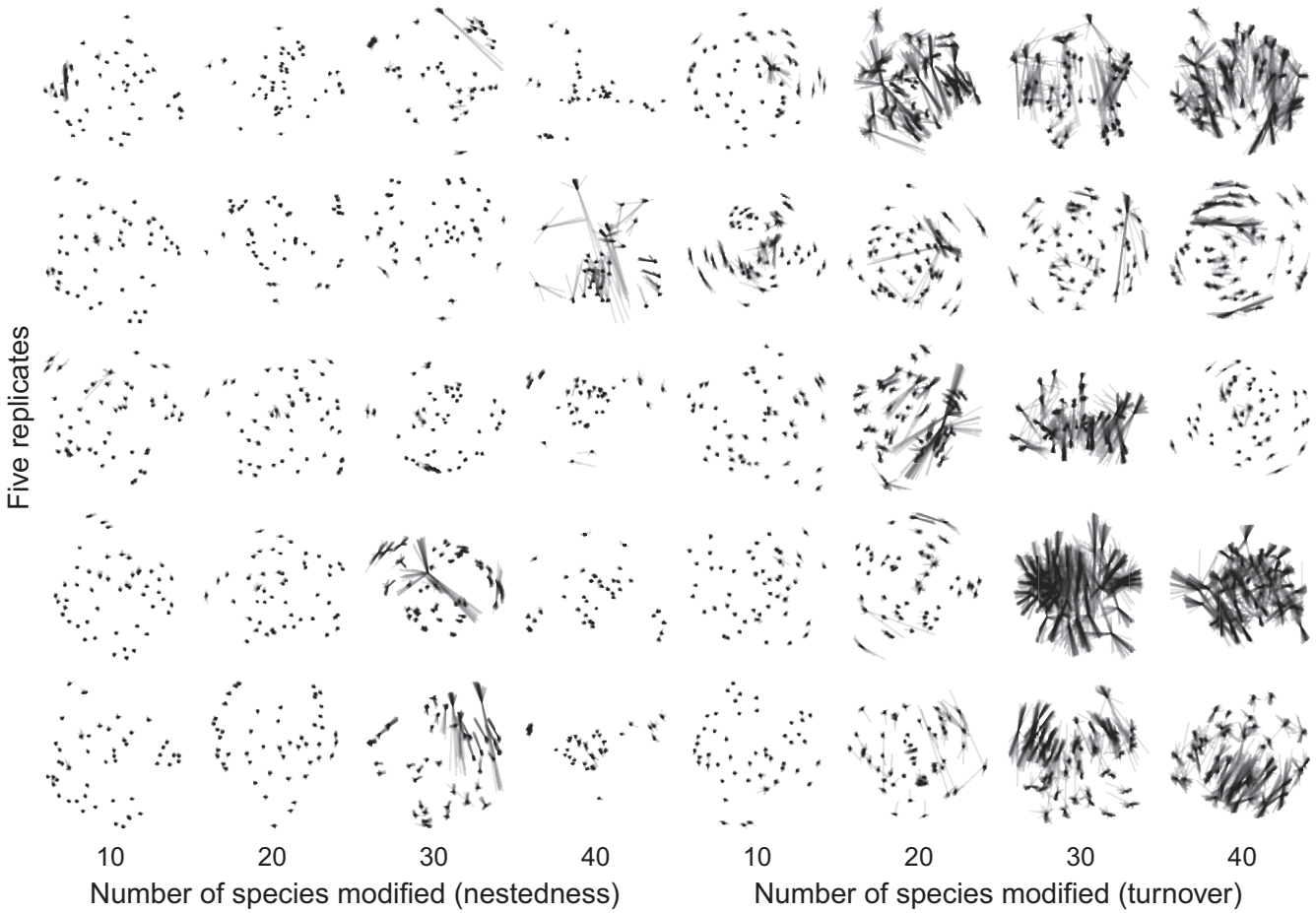

FIGURE 3 Resampled NMDS configurations exhibit greater sampling variability for species turnover than for nestedness. Each configuration is a 2-dimensional NMDS ordination of 49 sample units based on community compositions generated by resampling original data with replacement. Each sample unit has an original score (centroids of each star-like cluster per configuration) and associated replicate scores (line tips radiating from each cluster). Longer lines indicate relatively worse solutions (greater internal sampling variability, lower $R_{Pinternal}$)

moderate exchangeability among a local and a regional forest inventory, likely driven by a low proportion of shared species and a non-trivial amount of apparent species turnover. In addition, the regional model had better fit to environment, suggesting that combining the two forest inventories into one ordination may not be advisable for portraying how plant communities respond to regional climate gradients in Alaska's boreal forests. Instead, we advocate a multi-scale strategy in which inference on local and regional ecological processes are matched to sampling designs at appropriate spatial scales. When field sampling has concluded (and therefore sampling design

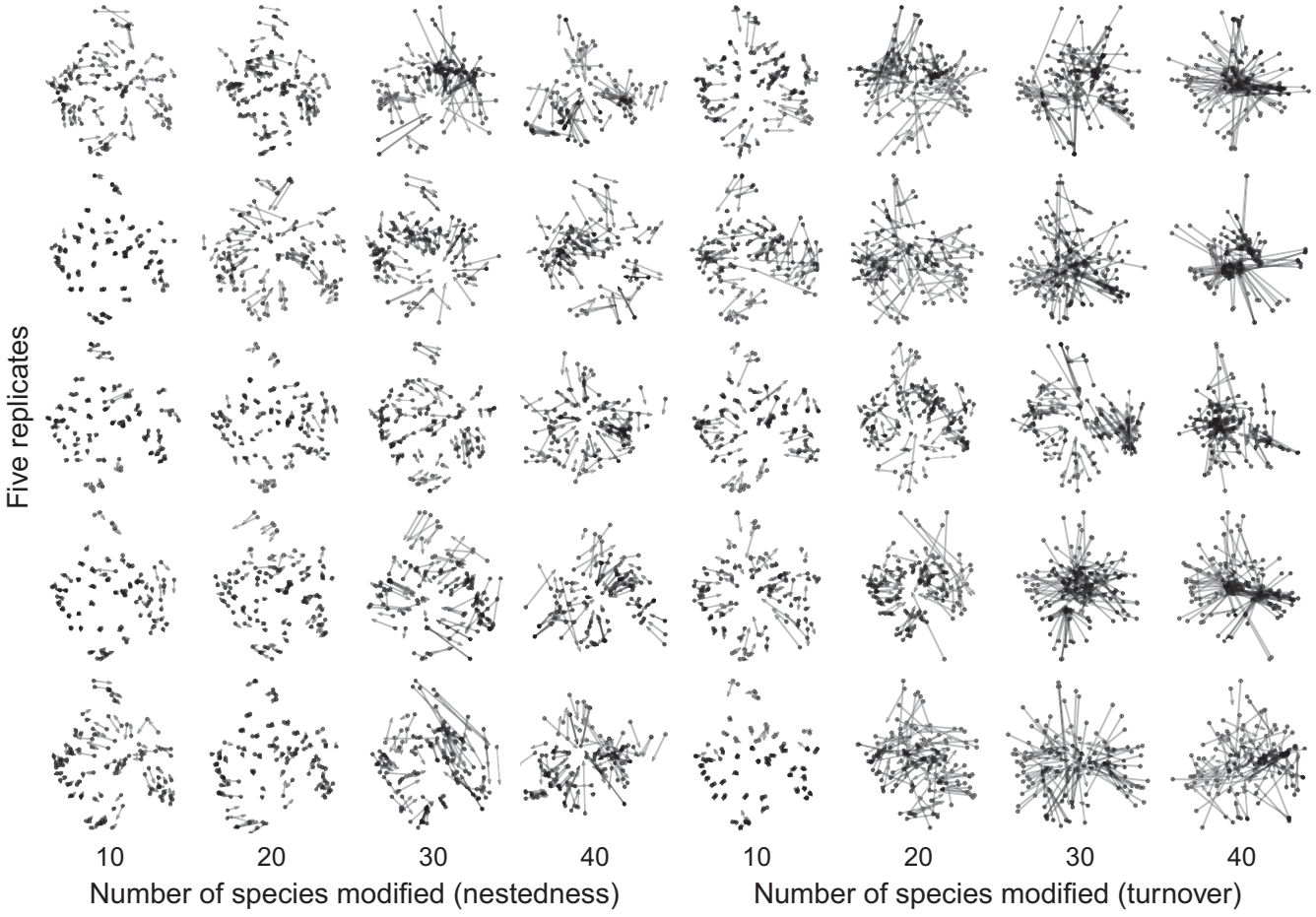

FIGURE 4 Reciprocal NMDS configurations exhibit lower exchangeability for species turnover than for nestedness. Each configuration is a 2-dimensional NMDS ordination based on community compositions of 49 sample units from a reference dataset (black circles) and 49 sample units from a modified dataset (arrow tips), rotated to maximum similarity. Procrustes errors (black arrows) show differences between reference and modified configurations, where longer lines indicate relatively worse solutions (lower external exchangeability, lower $R_{Pexternal}$)

changes are not possible), such a multi-scale approach can occur during analysis where different datasets are considered separately, or otherwise accounted for in hierarchical analysis.

Through simulation, we found support for the expectation that increasing beta-diversity components (nestedness and turnover) would decrease the exchangeability of vegetation datasets. Specifically, species turnover altered ordination outcomes more drastically than nestedness, suggesting that combining vegetation datasets may not be advisable when turnover prevails. Even when turnover is relatively minor, nestedness may still strongly influence NMDS outcomes (Baeten et al., 2012). This highlights the need to clearly identify the ecological causes (after accounting for sampling disparities) that generate beta-diversity. Several ecological processes, such as differential species' tolerances to environmental or resource conditions, may generate true species turnover (Vellend, 2016). For example, environmental changes during vegetation succession have contributed to species turnover based on consistent repeat sampling (Heinrichs & Schmidt, 2017; Vanhellemont, Baeten, & Verheyen, 2014). By contrast, inconsistent sampling designs may generate artificial ordination configurations that could be confused with having ecological origins (Økland et al., 1990; Otýpková & Chytrý, 2006). Hierarchical model-based ordination approaches (e.g., Ovaskainen et al., 2017) may be adapted to help reconcile these issues; however their statistical model, depending on (link-) linear functions and assumptions of multivariate normality, may disagree with the biological reality of often noisy, nonlinear, multi-modal species response functions and dependence structures which strongly depart from multivariate normality even after transformation or other manipulation. Our dissimilarity-based approach makes no such assumptions. Our proposed approach, based on resampled and reciprocal NMDS ordinations, provides an avenue to detect when the effects of real ecological processes may be confounded by differences in sampling designs, especially spatial scale differences.

Resampled ordination has previously been used to determine the number of interpretable ordination dimensions (Peres-Neto, Jackson, & Somers, 2003; Pillar, 1999), to estimate confidence regions for site scores (Jacoby & Armstrong, 2014), and to test the variability of species scores (Knox and Peet, 1989). However, we know of only one other attempt to explicitly quantify sampling variability of an ordination configuration in its entirety by pairing resampling techniques with Procrustes analysis (Manjarrés-Martínez, Gutiérrez-Estrada, Hernando, & Soriguer, 2012). We are also unaware of any attempts

to quantify ordination exchangeability subject to the null hypothesis of having been sampled from an identical species abundance distribution. Given a pair of candidate datasets, it is tempting to simply combine both into one single "joint" ordination, or else to somehow average two independent solutions into a "consensus" configuration (Blanchet, Legendre, Bergeron, & He, 2014; Carroll & Chang, 1970; Gower, 1975). However, our findings imply that these practices are questionable when compositional variation originates from different sampling designs. This is consistent with the observation that combining two datasets which differ in sampling effort into one ordination will yield an artificial configuration that more represents the relative sampling differences rather than true differences in community compositions (Otýpková & Chytrý, 2006). Therefore, prior to combining or averaging datasets, we suggest that workers first evaluate their relative exchangeability using the reciprocal ordination approach.

Forest inventories and long-term vegetation monitoring are foundational to informed decision-making in forestry and the natural resources. Unfortunately, long-term monitoring is rife with inconsistent and potentially incompatible data because of recurrent changes to management goals and survey techniques over time. Changes to forest inventory sampling designs over time can affect tree species' niche models (Lintz et al., 2013) and multivariate ordination scores (Smith et al., 2017). While scaling or correction factors could help correct univariate estimates (e.g., species richness) for differing sampling designs, it is not strictly possible to "adjust" entire multivariate community compositions, since these implicitly rely on sampling from identical species abundance distributions. Analysts may choose to aggregate species at higher taxonomic ranks (family or genus) or to use functional group categories, but this may degrade any information contained in species' individualistic responses. Estimating the degree to which candidate datasets are exchangeable can help account for design changes in the course of long-term monitoring, and can guide workers in selecting the scale of analysis that is most appropriate to their level of inference.

Harmonization (producing comparable estimates among unstandardized datasets) is of central interest for forest inventories since sampling designs and measurements can vary dramatically among regions and countries (McRoberts et al., 2012; Verheyen et al., 2017; Winter, Chirici, McRoberts, Hauk, & Tomppo, 2008). We attempted harmonization by resolving species names, by filtering observations to mimic identical criteria for species inclusion, and by retaining "most similar" sample unit pairs among the two forest inventories. Despite these corrections, we found only moderate exchangeability in ordinations, suggesting that the two forest inventories capture different portions of a complex species compositional gradient. We initially expected the relative floristic simplicity of boreal forests (Qian, 2002) to yield similar ordination outcomes, but instead found that dissimilar outcomes may be the product of sampling discrepancies between the two forest inventories. Harmonization was not a perfect remedy for the inconsistent sampling designs, since it did not greatly improve the low proportion (57%) of species shared among the two forest inventories. Few shared species likely led to the moderate exchangeability we observed. Furthermore, the poor fit of the local model to regional climate suggests that the small-footprint inventory may not have encompassed enough climatic variation to accurately infer how plant communities are associated with regional or global atmospheric processes.

We argue that a multi-scale perspective, separately evaluating both local and regional sampling designs, can reveal forest trends at the appropriate spatial scales. For example, a small-footprint inventory is appropriate to capture high local variation (e.g., vegetation driven by soil nutrients and permafrost, localized herbivory, plant interactions, intensive land-use practices), while a large-footprint inventory is appropriate to depict vegetation responses to broad regional processes (e.g., drought and climatic variation, large wildfires, major pest and pathogen outbreaks). Currently, the US Forest Service's Forest Inventory and Analysis program is conducting a large-footprint inventory, the Interior Alaska Inventory, with the goal of providing a baseline for measuring broad trends in subarctic boreal forest vegetation. This inventory concluded surveys in the Tanana River region in 2018, and over the next decade will install an additional 3,700 forested plots throughout other major Alaskan watersheds (Copper-Susitna, Southwest, Lower Yukon, Upper Yukon, and North Slope). Coupled with intensive local monitoring at the Bonanza Creek Long-Term Ecological Research site, this multi-scale perspective will provide a strong baseline for measuring status and trends in forest attributes throughout the major portion of Alaska that is north of the Alaska Range.

In summary, we reiterate the need to distinguish true ecological processes from sampling artifacts when assessing potentially inconsistent datasets. Sampling artifacts have the most substantive effects on ordination outcomes when they generate species turnover, and to a lesser degree, species nestedness. Pathways to determining how well two datasets are exchangeable include resampled and reciprocal ordination. These can help determine when it is advisable to take a multi-scale approach, using datasets separately to address complementary phenomena at the appropriate physical scale. Given that an ever-expanding array of vegetation plot and relevé data are now freely available, this strategy may help prevent mistaken attribution of effects to ecological processes rather than to artifacts of sampling. This should help strengthen large-scale synthesis, meta-analysis and long-term monitoring efforts that draw together many disparate vegetation data sources.

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AUTHOR CONTRIBUTIONS

R.S. and A.G. designed the research; the USFS-FIA program and cooperators collected data; R.S. performed statistical analyses and software development, R.S. and A.G. together wrote the paper, discussed the results and commented on the manuscript.

DATA ACCESSIBILITY

All data are freely available in Supporting Information, with actual plot locations withheld for privacy.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Description of data file in Supporting information Appendix S2.
Appendix S2. Data file for simulated and real vegetation communities.
Appendix S3. Description of computer code in Supporting information Appendix S4.
Appendix S4. Computer code to read data file and reproduce all analyses.
Appendix S5. Summary statistics for simulated data and boreal forest vegetation data.
Appendix S6. Reciprocal NMDS results of exchangeability of boreal forest datasets.

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