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Running title: Land use effects on stream diversity

LOCAL AND REGIONAL DRIVERS OF TAXONOMIC HOMOGENIZATION IN STREAM COMMUNITIES ALONG A LAND USE GRADIENT

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LOCAL AND REGIONAL DRIVERS OF TAXONOMIC HOMOGENIZATION IN STREAM COMMUNITIES ALONG A LAND USE GRADIENT

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ABSTRACT

Aim: The interaction of land use with local vs. regional processes driving biological homogenization (β-diversity loss) is poorly understood. We explored: i) stream β-diversity responses to land cover (forest vs. agriculture) in terms of physicochemistry and physicochemical heterogeneity, ii) whether these responses were constrained by the regional species pool, i.e. γ-diversity, or local assembly processes through local (α) diversity, iii) if local assembly operated through the regional species abundance distribution (SAD) or intraspecific spatial aggregation, and iv) the dependency on body size, dispersal capacity, and trophic level (producer vs. consumer).

Location: United States of America, Canada, and France

Time Period: 1993-2012

Major Taxa Studied: Stream diatoms, insects, and fish

Methods: We analyzed six datasets totaling 1,225 stream samples. We compared diversity responses to eutrophication and physicochemical heterogeneity in forested vs. agricultural streams with regression methods. Null models quantified contribution of local assembly to β-diversity (β-deviance, β_{DEV}) for both land covers and partitioned it into fractions explained by the regional SAD (β_{SAD}) vs. aggregation (β_{AGG}).

Results: Eutrophication explained homogenization and more uneven regional SADs across groups, but local and regional biodiversity responses differed across taxa. β_{DEV} was insensitive to land use. β_{SAD} largely exceeded β_{AGG} and was higher in agriculture.

Main Conclusion: Eutrophication but not physicochemical heterogeneity of agricultural streams underlay β-diversity loss in diatoms, insects and fish. Agriculture did not constrain the magnitude of local vs. regional effects on β-diversity, but controlled the local assembly mechanisms. While the SAD fraction dominated in both land covers, it further increased in agriculture at the expense of aggregation. Notably, the regional SADs were more uneven in agriculture, exhibiting excess common species or stronger dominance. Diatoms and insects diverged from fish in terms of biodiversity, SAD shape, and β_{DEV} patterns, suggesting an overriding role of body size and/or dispersal capacity compared to trophic position.

Key words: β-diversity, biodiversity loss, taxonomic homogenization, diatoms, fish, insects, land use, local assembly, spatial aggregation, species abundance distribution

INTRODUCTION

Landscape transformations from continuous undeveloped expanses to agricultural fields and urban sprawls have accelerated the global biodiversity decline (Newbold, Hudson, Hill, Contu, Lysenko et al., 2015). Human land use (hereafter land use) underlies declines in both regional richness, i.e. γ-diversity (Barlow, Lennox, Ferreira, Berenguer, Lees et al., 2016), and dissimilarity among biological communities, i.e. β-diversity, resulting in taxonomic homogenization across space and time (Petsch, 2016). Biodiversity losses from land use stem from habitat loss, fragmentation, eutrophication, and physicochemical stress, altogether considered among the primary threats facing global biodiversity (Sala, Stuart Chapin, Iii, Armesto, Berlow et al., 2000; Devictor, Julliard, Clavel, Jiguet, Lee et al., 2008). Preventing biodiversity losses and mitigating subsequent homogenization remain a top priority because both can translate into decreased biological integrity and ecosystem resilience (de Juan, Thrush & Hewitt, 2013; Socolar, Gilroy, Kunin & Edwards, 2016). Therefore, it is critical from a conservation planning standpoint to continue investigating how land use affects ecological processes underlying global diversity in order to mitigate the ongoing biodiversity crisis.

Land use effects on biodiversity occur across scales, operating either in a top-down or bottom-up fashion or both (Flohre, Fischer, Aavik, Bengtsson, Berendse et al., 2011). Top-down mechanisms function through the regional species pool (γ-diversity), which is a product of speciation and extinction, large-scale dispersal, climate, and evolutionary, geological, and land use history (Zobel, 2016). Bottom-up mechanisms include local-level assembly processes, e.g. environmental filtering, interspecific interactions, and small-scale dispersal (Márquez & Kolasa, 2013), which constrain local (α) diversity and subsequently affect site-to-site community dissimilarity. Studies across terrestrial and freshwater systems have reported a general decline in γ-diversity because of land use, but divergent patterns of α-diversity, including decreased α-diversity, owing to losses of sensitive and endemic species, and stable, or even increased α-diversity, owing to greater rates of species invasion and colonization (Vellend, Baeten, Myers-Smith, Elmendorf, Beauséjour et al., 2013; Newbold *et al.*, 2015; Gonzalez, Cardinale, Allington, Byrnes, Arthur Endsley et al., 2016). Thus, land use likely exerts differential impact on the species pool and local assembly processes that may cause γ- and α-diversity, respectively, to vary at different rates, which in turn influences β-diversity response (Kraft, Comita, Chase, Sanders, Swenson et al., 2011).

β-diversity is usually treated as a scalar linking average α-diversity with γ-diversity, thus reflecting spatial or temporal differences among localities. One can then measure the influence of α- and γ-diversity as proxies of local and regional drivers of β-diversity, respectively. Specifically, null models that constrain the observed species pool variation (i.e., γ-diversity) can assess the role of local assembly by calculating a β-diversity measure (β_{DEV}) corresponding solely to α-diversity variation (e.g., Kraft *et al.*, 2011) (Fig. 1a). β_{DEV} can be further decomposed into fractions reflecting roles of intraspecific spatial aggregation (i.e., the spatial clumping pattern of individuals within species) and the regional species abundance distribution (SAD, vector of species abundances) (Xu, Chen, Liu & Ma, 2015) (Fig. 1b). Intraspecific spatial aggregation results from dispersal, competitive, and environmental mechanisms that cluster individuals of species across fewer sites, thus bolstering β-diversity (Veech, 2005). However, regional SADs influence β-diversity because rare species are less likely to be locally sampled due to low regional abundance (He & Legendre, 2002). Although examined across latitudes, the two fractions of local assembly have not been studied in other contexts and it is unknown whether these components are responsive to strong ecological influences (e.g., land use).

Studying how local assembly and regional species pool processes interplay is an ongoing area of research in terrestrial systems because it may explain how β-diversity varies with land use (Socolar *et al.*, 2016). Surprisingly, little attention is focused on freshwater systems, even though freshwater biodiversity is more vulnerable to land use relative to terrestrial systems, particularly through habitat modification (Sala *et al.*, 2000; Wiens, 2016) and eutrophication from agriculture (Withers, Neal, Jarvie & Doody, 2014). Although primary productivity in agricultural streams could increase with eutrophication, forest streams, which are usually low in nutrients and have more shading, tend to harbor higher biodiversity stemming from greater physical and environmental heterogeneity that translates into greater ecosystem complexity (Penaluna, Olson, Flitcroft, Weber, Bellmore et al., 2017). Agriculture probably causes changes in physicochemical heterogeneity as well, but this subject is poorly explored. Thus, the scarcity of data, especially for aquatic taxa, has inhibited general understanding of how land use influences local and regional processes driving β-diversity.

Impacts of agricultural eutrophication on β_{DEV} are not understood, although null models have been used to assess environmental disturbance (e.g., Myers, Chase, Crandall & Jiménez, 2015). We hypothesize β-diversity response to eutrophication, including variation in β_{DEV}, depends on trophic level, body size, and dispersal capacity. For example, many unicellular producers, like diatoms, have high nutrient demands and may benefit from increased nutrients (Passy, 2008; Soininen, Jamoneau, Rosebery & Passy, 2016). Diatom microscopic size, high local abundance, and broad geographic distributions, allowing both in-stream and overland passive dispersal (Finlay, 2002), may result in weak β-diversity and β_{DEV} response to agriculture. Smaller bodied macroscopic organisms, such as aquatic insects, may be more constrained in active dispersal capacity during larval stages but exhibit greater overland mobility during winged adult life stages, which could offset some harmful agricultural effects. In contrast, larger consumers with more limited geographic dispersal capacity, such as fish, may be negatively affected by eutrophication due to ammonia toxicity, loss of suitable habitat, and lower quality food sources (Allan, 2004).

In this study, we compared spatial patterns of biodiversity and abundance in streams with watersheds dominated by agriculture vs. forest. Our objectives were to determine: i) how β-diversity and related biodiversity properties respond to agriculture (through nutrient enrichment or physicochemical heterogeneity), ii) if agriculture alters the relative contribution of local assembly effects to β-diversity, iii) whether agriculture differentially constrains the fractions of local assembly explained by spatial aggregation vs. the SAD, and iv) if the relationships outlined in i) to iii) vary across organismal groups (Table 1).

MATERIALS AND METHODS

Data sources and site selection

Our datasets (six in total) comprise stream organisms sampled from the US, France, and Canada (Fig. 2). Each dataset included community data and physicochemistry from watersheds dominated by either forest or agriculture. Only streams with ≥ 50% of their upstream watershed belonging to one of the two land cover categories were included in our analyses. We examined biodiversity patterns across three US datasets (diatoms, insects, and fish), two French datasets (diatoms and fish), and one Canadian dataset (diatoms), constructed as follows.

United States

US community data, spanning 19 latitudinal degrees and 55 longitudinal degrees, were obtained from the National Water-Quality Assessment (NAWQA) Program of the United States Geological Survey and the National Rivers and Streams Assessment (NRSA) of the United States Environmental Protection Agency. Communities were collected in the warm months during low flow conditions (July through September) to constrain seasonal succession and variation in temperature and flow. NAWQA communities (diatoms, insects, and fish) were sampled between 1993-2010, whereas NRSA communities (fish), between 2011 and 2012. Diatoms were collected from the richest-targeted habitats, encompassing hard substrates or macrophytes. Depending on available substrate, a defined area of 25 cobbles, 5 woody snags or 5 macrophyte beds was sampled within a stream reach and the samples were composited. Diatoms were identified generally to species in counts of 400-800 cells. Benthic insects (class Insecta) were composed of combined sieved samples taken from the richest-targeted habitats (i.e., riffles, main-channel, and natural-bed instream habitats). Insects were identified to the lowest possible category (order to species) in counts of 400-800 individuals. Both NAWQA and NRSA fish were generally identified to species in counts of 400-950 individuals taken from riffle, pool, and run habitats using electrofishing equipment with seines.

Land use and cover data were generated by the NAWQA and NRSA using National Land Cover Datasets 1992 and 2006, 30 m resolution. We selected 400 streams for diatoms and 126 streams for insects split equally between both land cover categories. Since fish communities and environmental data in both the NAWQA and NRSA data were sampled with similar methods, we combined both fish datasets into a single dataset comprising 231 streams (116 agricultural and 115 forested streams).

France

French diatom data were sourced from a national dataset including field collections of 200 streams from 2011. Algae were collected from stones during the low flow period in June through September with a standardized sampling method (Afnor, 2007). Diatoms were identified generally to species in counts of about 320-475 cells. The French fish dataset was collected by the French National Agency for Water and Aquatic Environments (ONEMA) during low flow periods between May and October 2011. The dataset comprised 200 streams with fish identified to species in counts of 10-3300 individuals sampled with electrofishers. For both French datasets, we used 100 agricultural and 100 forest streams, spanning 8 latitudinal and 14 longitudinal degrees. Land use cover data were obtained from the CORINE land cover database (European Environment Agency, 2013)

Canada

Canadian diatom data included 46 stream samples (23 streams in both land cover categories) collected in August to September during the low flow period between 2002 and 2009 (Lavoie, Campeau, Zugic-Drakulic, Winter & Fortin, 2014) spanning 3 latitudinal and 6 longitudinal degrees. Samples were composites of rock scrapes (5-10 rocks) per stream reach, targeting riffles and runs. Diatoms were mainly identified to species in counts of at least 400 valves. Land use cover data were compiled from government GIS databases, including the Ecoforestry Information System, Annual Crop Inventory, and the Insured Crop Database.

Environmental data

All datasets had associated physicochemical and coordinate data (i.e., GCS coordinates re-projected with Lambert Conformal Conic). Environmental variables in our analyses included water temperature, air temperature, nitrite + nitrate (or total nitrogen when absent), ammonia, orthophosphate, total phosphorus, specific conductance, and pH (Appendix 1, Table S1.1 in Supplemental Information). Environmental data for the US datasets consisted of the average for the month of sample collection. Environmental data for French diatoms included the median of measurements obtained 30 days before and 15 days after the diatom sample date. The French fish environmental data represented the average of 12 monthly measurements prior to fish sampling. Air temperature for French diatom data were not recorded at the time of sampling and were obtained from the WorldClim database (Hijmans, Cameron, Parra, Jones & Jarvis, 2005), whereas air temperatures for French fish streams were measured at the stream. Canadian environmental data were seasonal averages calculated from water samples collected from July to September.

Diversity, spatial aggregation, and species abundance distribution

We calculated $\overline{\alpha}$-diversity (average richness across samples), γ-diversity (total richness per land use), and β-diversity of stream samples for both land cover categories for each dataset. We used equation (1) to calculate the observed β-diversity (β_{OBS}),

$$\beta_{OBS} = 1 - \frac{\overline{\alpha}}{\gamma} \qquad (1)$$

which indicated the average proportion of the species pool absent from a stream.

We used the null model framework developed by Xu *et al.* (2015) to quantify i) the magnitude of the local assembly effect on β-diversity after controlling for γ-diversity and ii) the contributions of the SAD vs. intraspecific spatial aggregation to local assembly (Fig. 1b). First, the difference (i.e., β-deviance, β_{DEV}) between β_{OBS} and the expected β-diversity (β_{EXP}, i.e., β-diversity expected assuming completely random sampling, see Appendix S2) was taken to quantify local assembly absent the effect of γ-diversity. β_{DEV} is bounded between 0 and 1, with larger β_{DEV} corresponding to greater local control. Secondly, we calculated β-diversity predicted when intraspecific spatial aggregation is constant across all species (β_{PRED}). Then, the difference between β_{PRED} and β_{EXP} reveals what fraction of β_{DEV} is contributed by the SAD (β_{SAD}), while the remaining fraction of β_{DEV} is attributed to spatial aggregation (β_{AGG}). In this model, β_{SAD} can exceed β_{DEV} if β_{PRED} exceeds $\beta_{OBS.}$ The corresponding aggregation fraction will in turn be negative because the sum of the two fractions, β_{SAD} and β_{AGG}, must equal 1, thus meaning that the pattern is less aggregated than expected by the null model. To test whether the two land covers differ in their magnitude of intraspecific spatial aggregation, we used maximum likelihood methods and calculated the aggregation parameter, *k*, across samples within each land cover (Appendix S3). Because smaller *k* corresponded to greater aggregation, we analyzed the reciprocal of the parameter for easier interpretation. In summary, the procedure yielded six measurements: $\beta_{EXP,}$ β_{PRED}, $\beta_{DEV,}$ β_{SAD}, $\beta_{AGG,}$ and 1/*k*.

Regional SADs for both land cover categories was analyzed by summing abundances of each species across all stream samples and calculating the standard deviation (parameter σ) of the Poisson-lognormal distribution fit of the abundance data using the `sads´ R package (Prado, Mirands & Chalom, 2017). Parameter σ reflects SAD evenness with greater σ values corresponding to increased unevenness. To determine if changes in σ were associated with prevalence of rare vs. common species, we also examined the relationship of σ with the skewness (`skewness´ function from R package `moments´, Komsta & Novomestky, 2015) of the log-transformed regional species abundances for each land cover category. Skewness was significant if skewness divided by the standard error of the skewness (i.e., $(6/n)^{0.5}$, where n = number of species) was greater than 2. Significant positive skew indicates greater prevalence of abundant species, while significant negative skew reveals higher number of rare species compared to the lognormal distribution.

Statistical analyses

Resampling scheme

Generally, the described procedures in our study typically produced a single value without any estimate of error, which inhibits statistical comparisons between datasets. Therefore, to test for abiotic and biotic differences between land covers, we conducted a resampling procedure where we randomly selected 50% of the streams within each land cover category for each dataset without replacement 999 times. Each loop calculated the median of each physicochemical variable, an estimate of physicochemical heterogeneity, biodiversity ($\overline{\alpha}$-, β-, and γ-diversity), SAD, and null model measures including the null model β-diversity values, and the within group intraspecific aggregation ($1/k$). This procedure generated six new datasets that contained resampled physiochemistry data and biotic measures, which were used further statistical analyses. R scripts are available as supplementary material for online publication only (see Appendices S3 and S4).

Eutrophication and physicochemical heterogeneity

We employed principal components analysis with all resampled, standardized median physicochemical variables (mean = 0, standard deviation = 1) to create a synthetic variable corresponding to the major physicochemical trend. The first PCA axis represented a eutrophication gradient and explained between 53.1% (French diatom samples) and 94.3% (Canadian diatom samples) of the variation among samples (Appendix 1, Fig. S1.1).

To estimate physicochemical heterogeneity within each land cover, we used permutational analysis of multivariate dispersion on standardized physiochemical data with the `betadisper´ function from R package `vegan´ (Anderson, Ellingsen & McArdle, 2006; Oksanen, Blanchet, Friendly, Kindt, Legendre et al., 2017). In this procedure, physicochemical heterogeneity is calculated as the average distance from a multivariate group median (group = land cover) with larger distances corresponding to greater within-group heterogeneity.

Environmental effects

We determined how land use-driven eutrophication and physicochemical heterogeneity affected diversity components using a combination of univariate and multivariate techniques and variance partitioning. For each dataset, we used permutational MANOVA function `adonis´ from package `vegan´ to test for differences in the multivariate mean of the $\overline{\alpha}$-, β-, and γ-diversity between land covers. If the permutational MANOVA was significant, we followed with permutational ANOVA using the `perm.anova´ function provided in `RVAideMemore´ (999 permutations; Herve, 2018) for each dependent variable. We then used RDA-based variance partitioning models (`vegan´ function `varpart´) on each dataset to identify major explanatory factors underlying diversity patterns, with eutrophication, physicochemical heterogeneity, and land cover (coded as dummy variables) as predictors and the diversity measures ($\overline{\alpha}$-, β-, and γ-diversity) as response variables.

We employed permutational MANOVA and permutational ANOVA to determine if the resampled β_{DEV}, β_{SAD}, β_{AGG}, $1/k$, σ, and skewness differed between land covers. Because total abundance and γ-diversity influence the shape of the regional SAD, we controlled their influences by regressing parameter σ against total abundance and γ-diversity of the resample and obtaining the residuals, which were then used in subsequent analyses. To further explore if β_{DEV} was sensitive to variation in SAD unevenness (residual σ) and intraspecific spatial aggregation ($1/k$), we calculated Pearson correlations within both land cover categories for all datasets. Pearson correlations were also used to assess whether residual σ correlated with skewness and $1/k$. We then implemented variance partitioning to determine if eutrophication, physicochemical heterogeneity, land cover, or their covariance explained the variation in β_{DEV}.

RESULTS

Eutrophication and Environmental Heterogeneity Effects on Diversity and the SAD

Permutational MANOVA and permutational ANOVAs of environmental data showed that all physiochemistry levels were significantly elevated ($P < 0.05$) in agricultural land use across all datasets. Permutational ANOVAs also indicated greater physicochemical heterogeneity among agricultural streams in all but the Canadian diatom dataset (higher in forest land cover) and the US Fish dataset (no differences, Fig. 3). MANOVA of $\overline{\alpha}$-, β-, and γ-diversity against land use revealed that land use significantly affected the diversity measures across all datasets. Following our first objective, we demonstrated that β-diversity declined with agriculture across all datasets. Gamma diversity usually decreased, whereas $\overline{\alpha}$-diversity often increased with agriculture (Table 2). Except for French fish, SADs were generally significantly more uneven for agricultural land use than forest (higher residual σ), although the differences were mainly small (Fig. 4, columns 1-3). Intraspecific aggregation ($1/k$) was always greater in forest than in agriculture and was negatively correlated with residual σ, meaning more even SADs were always associated with higher aggregation (Appendix 1, Table S1.2). Skewness was significantly positive in the insect and all three diatom datasets, but non-significant in the two fish datasets. When positive, skewness correlated positively with residual σ regardless of land cover (although weakly for diatoms), indicating that SAD unevenness was generally characterized by greater abundances of more common species.

Our first objective was to determine how biodiversity explained by land use, eutrophication, and physicochemical heterogeneity. Variation in all diversity measures was primarily explained by covariance effects, while pure land cover, pure eutrophication, and pure physicochemical heterogeneity contributed minorly (Fig. 5). In general, covariance of eutrophication with land cover explained most of the variation, indicating that land use constrained biotic variability mainly through eutrophication rather than physicochemical heterogeneity. However, the insect dataset differed from the rest in that the covariance fraction of land cover, eutrophication, and physicochemical heterogeneity captured most of the variation.

Eutrophication-associated shifts in local assembly across organismal groups

For our second objective, we found local assembly weakly drove diatom and insect β-diversity (β_{DEV} generally less than 0.26 across land covers) but had a relatively greater influence on fish β-diversity (β_{DEV} between 0.38-0.45). β_{DEV} differed significantly between forest and agriculture (permutational ANOVA) in all datasets except insects (no difference). However, the magnitude of the difference in β_{DEV} was usually small (3.49 to 16.04%), with the direction of the difference depending on organismal group and biogeographic region (Fig. 4, column 4).

Contribution of the SAD vs. intraspecific spatial aggregation to β_{DEV}

For objective three, the partitioning of β_{DEV} revealed that β_{SAD} generally exceeded 100% and β_{AGG} was negative, regardless of land cover except for the US and French diatom datasets, which showed β_{SAD} < 100% and positive β_{AGG} for forest land use (Fig. 4, columns 5-6). As changes in β_{SAD} correspond to equal and opposite changes in β_{AGG}, we focus on β_{SAD} for brevity. β_{SAD} represented nearly all of β_{DEV} regardless of dataset and land cover type (~ 90-110% of total deviance) and was significantly (although marginally) larger in agricultural land use than in forest cover. Further, β_{DEV} was generally negatively correlated with residual σ, regardless of land cover or organismal group, implying that increased SAD unevenness was usually associated with greater contribution of the regional species pool (Appendix 1, Table S2). Variance partitioning of β_{DEV} across datasets showed mixed patterns among and within organismal groups over what effects best explained β_{DEV} (Fig. 6).

Variability across organismal groups

Consistent with our fourth objective, we demonstrated that smaller organisms (diatoms and insects) with greater dispersal capacity were more similar in terms of SAD and β_{DEV} patterns, but diverged from fish. However, we also observed divergence in some ecological patterns between datasets within organismal groups (i.e., diatoms and fish) in that $\overline{\alpha}$-diversity, γ-diversity, SAD skewness, and β_{DEV} responses varied between country of origin, which indicated context dependency of our results.

DISCUSSION

In this comprehensive study of stream organisms from two continents, agriculture and subsequent eutrophication were generally associated with reduced β- and γ-diversity and increased $\overline{\alpha}$-diversity. First, covariance of land use with physicochemical gradients, rather than with physicochemical heterogeneity, characterized regional biodiversity loss with land use.

Second, all datasets showed significant shifts in magnitude of β_{DEV} with eutrophication but the direction (i.e., stronger or weaker local assembly effects) depended on organismal group and potentially biogeographical factors. Third, the regional SAD overrode intraspecific spatial aggregation in explaining β_{DEV} and its influence and unevenness increased with agriculture.

Eutrophication and Environmental Heterogeneity Effects on Diversity and the SAD

With respect to objective one, regional biodiversity loss, local diversity gains, and increased community similarity in aquatic taxa were correlated with agricultural land use, consistent with patterns expected for taxonomic homogenization (Petsch, 2016). Recently, Ribiero *et al*. (2015) explored the generality of floral homogenization consequential of agricultural land use and noted that too many studies focus on a single spatial scale or a single taxon. For aquatic taxa, agriculturally-associated changes in β-diversity have been reported, however, we have only begun to examine these changes at broader spatial scales. For example, Winegardner *et al*. (2017) attributed greater temporal β-diversity of diatoms across modified US landscapes to richness gains and losses stemming from disproportionate influence of contemporary vs. past land use, yet observed no changes in spatial β-diversity. In contrast, diatom spatial β-diversity declined with eutrophication in French streams (Jamoneau, Passy, Soininen, Leboucher & Tison-Rosebery, 2018). Our investigation, exploring diatoms, insects, and fish across regional to subcontinental scales, demonstrates that the detrimental effects of agriculture on the regional biodiversity in stream ecosystems are independent of species biology or scale.

We further revealed that biodiversity variation between forest and agriculture was mainly driven by land use differences in physicochemistries rather than physicochemical heterogeneity, a result contrary to conventional wisdom that higher environmental heterogeneity brings greater turnover. While agriculture may homogenize the landscape, we show that it tended to lead to greater stream physicochemical heterogeneity, possibly due to variability in fertilization and landscape management regimes. Heterogeneity is an important mechanism of co-existence because it offsets competitive exclusion (Tilman & Pacala, 1993). However, we observed that physicochemical heterogeneity poorly explained β-diversity, because eutrophication in agricultural streams may have exceeded the physiological thresholds of sensitive species and decoupled compositional and environmental variability (Bini, Landeiro, Padial, Siqueira & Heino, 2014). The lack of a relationship may also be due to our measure of heterogeneity, which did not incorporate other aspects of heterogeneity, such as variability in substrate size, known to diminish with agriculture (Allan, 2004).

Increased prevalence of common species over spatial and temporal scales is a hallmark of taxonomic homogenization (Olden & Rooney, 2006), but our findings are restricted to the spatial dimension. Notably, while across datasets SADs were generally more uneven in agriculture, they were more positively skewed compared to forest only in two datasets, i.e. US insects and French diatoms. In these datasets, homogenization in agriculture was characterized by greater prevalence of common relative to rare species, which has also been observed in terrestrial arthropods (Simons, Gossner, Lewinsohn, Lange, Türke et al., 2015; Komonen & Elo, 2017). However, SADs were more positively skewed in forest cover than in agriculture for two datasets (US and Canadian diatoms), and not skewed for both fish datasets. This suggested that stronger SAD unevenness in agriculture resulted from either buildup of common species or greater regional dominance by a relatively few species. Like recent terrestrial and tropical studies (Vázquez & Gaston, 2004; Lohbeck, Bongers, Martinez-Ramos & Poorter, 2016), we showed that SAD unevenness was associated with agriculturally-driven homogenization. Future research on homogenization should incorporate novel methods and procedures, like we employed, to elucidate how habitat modification and trait distribution contribute to the two forms of unevenness, i.e. asymmetry vs. dominance.

Land use-associated shifts in local assembly across organismal groups

Following objective two, we examined how local assembly (β_{DEV}) varied between forested and agricultural streams. In general, β_{DEV} marginally differed between land covers, suggesting that the strength of local vs. regional mechanisms was relatively unaffected by physicochemical stressors, consistent with prior work, reporting that fire disturbance altered β-diversity but not its causes (Myers *et al.*, 2015). Community comparisons revealed that the magnitude of β_{DEV} usually increased with body size, which here was linked with dispersal capacity. Smaller β_{DEV} values in diatoms and insects indicated that the observed species pool exerted greater influence on β-diversity relative to local assembly. These results are corroborated by earlier research showing that diatom and insect communities are unsaturated, whereby local richness is limited by the size of the regional pool as opposed to local interactions (Passy, 2009; Al-Shami, Heino, Che Salmah, Abu Hassan, Suhaila et al., 2013; but see Thornhill, Batty, Death, Friberg & Ledger, 2017). Therefore, it is possible that regional effects play a greater role in structuring local richness and β-diversity of smaller and more dispersive organisms than of larger and less dispersive organisms, and these relationships are not consistently affected by eutrophication.

In contrast, β_{DEV} in both fish datasets approaching 0.50 suggested relatively similar local and regional control of β-diversity, in agreement with prior observations of comparable contributions of regional and local factors to fish richness (Angermeier & Winston, 1998). Taxonomic homogenization is a particularly prevalent phenomenon among freshwater fish

(Petsch, 2016) and our study elucidated that the possible causes include both local and regional processes.

Other nearly uniform patterns, independent of land use, were the negative correlation of residual σ of the regional SAD and the positive correlation of intraspecific aggregation (1/*k*) with β_{DEV}. These correlations indicated that more even regional SADs and increased intraspecific spatial aggregation were associated with stronger local constraints on β-diversity. Recent work has only begun to explore the relationship of SAD evenness with taxonomic homogenization, showing clear links between the two with implications for conservation (e.g., Simons *et al.*, 2015; Komonen & Elo, 2017). Our study is novel in that it demonstrates that local and regional processes controlling β-diversity are dependent on SAD evenness—a finding that could guide future stream conservation and management decisions, which need to be scale-explicit. For example, if preserving β-diversity, then adopting practices promoting abundance of less common species may be beneficial, given that SAD evenness is positively correlated with β-diversity.

The contribution of the SAD vs. intraspecific spatial aggregation to β_{DEV}

To our knowledge, we are the first to explore how land use affects partitioning of β_{DEV} into SAD vs. spatial aggregation fractions, i.e. β_{SAD} vs. β_{AGG} (objective three). β_{SAD} accounted for most of β_{DEV}, similar to observations for global tree communities (Xu *et al.*, 2015), but opposite to findings, with a different null model, for Czech forests (Sabatini, Jiménez-Alfaro, Burrascano, Lora & Chytrý, 2017). We further discovered that β_{SAD} largely exceeded β_{AGG} across organismal groups, datasets, and land cover types. However, β_{SAD} was significantly higher in agriculture compared to forest in all datasets. The two land covers also diverged in β_{AGG}—less spatial aggregation than predicted by the null model ($\beta_{AGG} < 0$) was detected in agriculture across all datasets, while some aggregation ($\beta_{AGG} > 0$) was observed in forest streams in four out of six datasets. These results suggest that although land use did not constrain the magnitude of local assembly effects (β_{DEV}), it did control the mechanisms of local assembly, i.e. land use increased the role of the SAD, but diminished the influence of aggregation.

Organismal and geographic dependencies in biodiversity response to homogenization

In pursuit of our fourth objective, we found that organismal groups responded differently to land use, as reported by other studies (e.g., Angermeier & Winston, 1998; Thornhill *et al.*, 2017). Insects resembled diatoms in biodiversity, SAD shape, and β_{DEV} patterns, which suggested that body size and dispersal capacity may be more important than trophic position (autotroph vs. heterotroph) in predicting ecological responses to agricultural eutrophication. We generally expected consistent responses of these metrics to agriculture, regardless of country of origin (i.e., diatoms and fish). We reasoned that agriculture, being a major habitat alteration, will override all other influences, yet within both groups, there was divergence depending on region. We ensured that variation in individual counts and mean counts among samples and differences in geographic spread across datasets did not contribute to their dissimilarity (data not shown). Thus, our findings of within-taxon variability with respect to biodiversity and the SAD highlighted the importance of considering context dependency. Histories of land use disturbance among geographic regions can set biodiversity and relative abundance patterns on different trajectories by affecting processes underlying β-diversity (Cramer, Hobbs & Standish, 2008). For example, European fish diversity has been historically depauperate relative to North American fauna owing particularly to differences in glacial influence (Oberdorff, Hugueny & Guégan, 1997).

Furthermore, French aquatic communities have been impacted by agricultural activities far longer than their North American counterparts (Hahn & Orrock, 2015).

In summary, we determined eutrophication is a major driver of β-diversity losses among stream taxa, although the importance of geographic context was shown through the varied biodiversity responses within taxonomic groups. Local assembly generally was weakly affected by agriculture. However, in agriculture the regional SAD became significantly more uneven and its effect on local assembly significantly increased compared to forest, which may be the underlying causes of taxonomic homogenization. Biodiversity, SAD shape, and β_{DEV} depended more strongly on body size and/or dispersal than trophic position. Future research should explore how local and regional processes operate in tandem with the SAD to uncover whether homogenization drivers are specific to organismal groups and the regions from which they were sampled. Although we examined β-diversity loss from a taxonomic perspective, we recommend future investigations on whether agriculture leads to phylogenetic and functional homogenization across space and time. Then, taxonomic, phylogenetic, and functional diversity responses to agriculture could be compared to generate more holistic understandings of the causes and patterns of biotic homogenization.

ACKNOWLEDGEMENTS

We thank W. Xu for helpful comments on the null model. Support by the National Science Foundation (grant NSF DEB-1745348) to SIP is gratefully acknowledged.

DATA AVAILABILITY STATEMENT

Community and environmental datasets for the US are available for download from the USGS NAWQA Program via the Water Quality Portal (https://www.waterqualitydata.us/contact_us/) and EPA NRSA (https://www.epa.gov/national-aquatic-resource-surveys/data-national-aquatic-resource-surveys) databases. DOI with associated URLs for all community and environmental datasets analyzed for this project will be made freely available for download from Dryad Digital Repository upon publication.

REFERENCES

Afnor, N.F. (2007) T90-354, Qualite de l'eau. Determination de l'Indice Biologique Diatomees (IBD). 1-79.

Al-Shami, S.A., Heino, J., Che Salmah, M.R., Abu Hassan, A., Suhaila, A.H. & Madrus, M.R. (2013) Drivers of beta diversity of macroinvertebrate communities in tropical forest streams. *Freshwater Biology*, **58**, 1126-1137.

Allan, J.D. (2004) Landscapes and Riverscapes: The Influence of Land Use on Stream Ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, **35**, 257-284.

Anderson, M.J., Ellingsen, K.E. & McArdle, B.H. (2006) Multivariate dispersion as a measure of beta diversity. *Ecology Letters*, **9**, 683-693.

Angermeier, P.L. & Winston, M.R. (1998) Local vs. regional influences on local diversity in stream fish communities of Virginia. *Ecology*, **79**, 911-927.

Barlow, J., Lennox, G.D., Ferreira, J., Berenguer, E., Lees, A.C., Mac Nally, R., . . . Oliveira, V.H.F. (2016) Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. *Nature*, **535**, 144.

Bini, L.M., Landeiro, V.L., Padial, A.A., Siqueira, T. & Heino, J. (2014) Nutrient enrichment is related to two facets of beta diversity for stream invertebrates across the United States. *Ecology*, **95**, 1569-1578.

Cramer, V.A., Hobbs, R.J. & Standish, R.J. (2008) What's new about old fields? Land abandonment and ecosystem assembly. *Trends in Ecology & Evolution*, **23**, 104-112.

de Juan, S., Thrush, S.F. & Hewitt, J.E. (2013) Counting on β-diversity to safeguard the resilience of estuaries. *Plos One*, **8**, e65575.

Devictor, V., Julliard, R., Clavel, J., Jiguet, F., Lee, A. & Couvet, D. (2008) Functional biotic homogenization of bird communities in disturbed landscapes. *Global Ecology and Biogeography*, **17**, 252-261.

European Environment Agency (2013) Corine Land Cover 2006 seamless vector data (Version 17). In. European Environment Agency, Kopenhagen, Denmark.

Finlay, B.J. (2002) Global dispersal of free-living microbial eukaryote species. *Science*, **296**, 1061-1063.

Flohre, A., Fischer, C., Aavik, T., Bengtsson, J., Berendse, F., Bommarco, R., . . . Eggers, S. (2011) Agricultural intensification and biodiversity partitioning in European landscapes comparing plants, carabids, and birds. *Ecological Applications*, **21**, 1772-1781.

Gonzalez, A., Cardinale, B.J., Allington, G.R.H., Byrnes, J., Arthur Endsley, K., Brown, D.G., . . . Loreau, M. (2016) Estimating local biodiversity change: a critique of papers claiming no net loss of local diversity. *Ecology*, **97**, 1949-1960.

Hahn, P.G. & Orrock, J.L. (2015) Land-use history alters contemporary insect herbivore community composition and decouples plant–herbivore relationships. *Journal of Animal Ecology*, **84**, 745-754.

He, F. & Legendre, P. (2002) Species diversity patterns derived from species–area models. *Ecology*, **83**, 1185-1198.

Herve, M. (2018) RVAideMemoire: Testing and plotting for biostatistics. R Package version 0.9-69-3.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965-1978.

Jamoneau, A., Passy, S.I., Soininen, J., Leboucher, T. & Tison-Rosebery, J. (2018) Beta diversity of diatom species and ecological guilds: Response to environmental and spatial mechanisms along the stream watercourse. *Freshwater Biology*, **63**, 62-73.

Komonen, A. & Elo, M. (2017) Ecological response hides behind the species abundance distribution: Community response to low-intensity disturbance in managed grasslands. *Ecology and Evolution*, **7**, 8558-8566.

Komsta, L. & Novomestky, F. (2015) moments: Moments, Cumulants, skewness, kurtosis, and related tests. R package version 0.14.

Kraft, N.J.B., Comita, L.S., Chase, J.M., Sanders, N.J., Swenson, N.G., Crist, T.O., . . . Myers, J.A. (2011) Disentangling the Drivers of β Diversity Along Latitudinal and Elevational Gradients. *Science*, **333**, 1755.

Lavoie, I., Campeau, S., Zugic-Drakulic, N., Winter, J.G. & Fortin, C. (2014) Using diatoms to monitor stream biological integrity in Eastern Canada: An overview of 10 years of index development and ongoing challenges. *Science of The Total Environment*, **475**, 187-200.

Lohbeck, M., Bongers, F., Martinez-Ramos, M. & Poorter, L. (2016) The importance of biodiversity and dominance for multiple ecosystem functions in a human-modified tropical landscape. *Ecology*, **97**, 2772-2779.

Márquez, J.C. & Kolasa, J. (2013) Local and regional processes in community assembly. *Plos One*, **8**, e54580.

Myers, J.A., Chase, J.M., Crandall, R.M. & Jiménez, I. (2015) Disturbance alters beta-diversity but not the relative importance of community assembly mechanisms. *Journal of Ecology*, **103**, 1291-1299.

Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., . . . Purvis, A. (2015) Global effects of land use on local terrestrial biodiversity. *Nature*, **520**, 45-50.

Oberdorff, T., Hugueny, B. & Guégan, J.F. (1997) Is there an influence of historical events on contemporary fish species richness in rivers? Comparisons between Western Europe and North America. *Journal of Biogeography*, **24**, 461-467.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., . . . Wagner, H. (2017) vegan: Community Ecology Package. R Package Version 2.4-2.

Olden, J.D. & Rooney, T.P. (2006) On defining and quantifying biotic homogenization. *Global Ecology and Biogeography*, **15**, 113-120.

Passy, S.I. (2008) Continental diatom biodiversity in stream benthos declines as more nutrients become limiting. *Proceedings of the National Academy of Sciences*, **105**, 9663-9667.

Passy, S.I. (2009) The relationship between local and regional diatom richness is mediated by the local and regional environment. *Global Ecology and Biogeography*, **18**, 383-391.

Penaluna, B.E., Olson, D.H., Flitcroft, R.L., Weber, M.A., Bellmore, J.R., Wondzell, S.M., . . . Reeves, G.H. (2017) Aquatic biodiversity in forests: a weak link in ecosystem services resilience. *Biodiversity and Conservation*, **26**, 3125-3155.

Petsch, D.K. (2016) Causes and consequences of biotic homogenization in freshwater ecosystems. *International Review of Hydrobiology*, **101**, 113-122.

Prado, P.I., Mirands, M.D. & Chalom, A. (2017) "sads": Maximum Likelihood Models for Species Abundance Distributions. R package Version 0.4-1.

Sabatini, F.M., Jiménez-Alfaro, B., Burrascano, S., Lora, A. & Chytrý, M. (2017) Beta-diversity of central European forests decreases along an elevational gradient due to the variation in local community assembly processes. *Ecography*, **41**, 1038-1048.

Sala, O.E., Stuart Chapin, F., Iii, Armesto, J.J., Berlow, E., Bloomfield, J., . . . Wall, D.H. (2000) Global Biodiversity Scenarios for the Year 2100. *Science*, **287**, 1770-1774.

Simons, N.K., Gossner, M.M., Lewinsohn, T.M., Lange, M., Türke, M. & Weisser, W.W. (2015) Effects of land-use intensity on arthropod species abundance distributions in grasslands. *Journal of Animal Ecology*, **84**, 143-154.

Socolar, J.B., Gilroy, J.J., Kunin, W.E. & Edwards, D.P. (2016) How Should Beta-Diversity Inform Biodiversity Conservation? *Trends in Ecology & Evolution*, **31**, 67-80.

Soininen, J., Jamoneau, A., Rosebery, J. & Passy, S.I. (2016) Global patterns and drivers of species and trait composition in diatoms. *Global Ecology and Biogeography*, **25**, 940-950.

Solar, R.R.d.C., Barlow, J., Ferreira, J., Berenguer, E., Lees, A.C., Thomson, J.R., . . . Oliveira, V.H.F. (2015) How pervasive is biotic homogenization in human-modified tropical forest landscapes? *Ecology Letters*, **18**, 1108-1118.

Thornhill, I., Batty, L., Death, R.G., Friberg, N.R. & Ledger, M.E. (2017) Local and landscape scale determinants of macroinvertebrate assemblages and their conservation value in ponds across an urban land-use gradient. *Biodiversity and Conservation*, **26**, 1065-1086.

Tilman, D. & Pacala, S. (1993) The maintenance of species richness in plant communities. In R.E. Ricklefs & D. Schulter (Eds.), *Species Diversity in Ecological Communities* (pp. 13-25). Chicago, IL: Chicago Press.

Vázquez, L.B. & Gaston, K.J. (2004) Rarity, commonness, and patterns of species richness: the mammals of Mexico. *Global Ecology and Biogeography*, **13**, 535-542.

Veech, J.A. (2005) Analyzing patterns of species diversity as departures from random expectations. *Oikos*, **108**, 149-155.

Vellend, M., Baeten, L., Myers-Smith, I.H., Elmendorf, S.C., Beauséjour, R., Brown, C.D., . . . Wipf, S. (2013) Global meta-analysis reveals no net change in local-scale plant biodiversity over time. *Proceedings of the National Academy of Sciences*, **110**, 19456-19459.

Wiens, J.J. (2016) Climate-Related Local Extinctions Are Already Widespread among Plant and Animal Species. *PLOS Biology*, **14**, e2001104.

Winegardner, A.K., Legendre, P., Beisner, B.E. & Gregory-Eaves, I. (2017) Diatom diversity patterns over the past c. 150 years across the conterminous United States of America: Identifying mechanisms behind beta diversity. *Global Ecology and Biogeography*, **26**, 1303-1315.

Withers, P.J.A., Neal, C., Jarvie, H.P. & Doody, D.G. (2014) Agriculture and eutrophication: where do we go from here? *Sustainability*, **6**, 5853-5875.

Xu, W., Chen, G., Liu, C. & Ma, K. (2015) Latitudinal differences in species abundance distributions, rather than spatial aggregation, explain beta-diversity along latitudinal gradients. *Global Ecology and Biogeography*, **24**, 1170-1180.

Zobel, M. (2016) The species pool concept as a framework for studying patterns of plant diversity. *Journal of Vegetation Science*, **27**, 8-18.

Table 1. Summary of procedures and analyses performed with corresponding expectations and observations.

Procedures	Analyses	Expectations	Observations

1) Determine the differences in physicochemistry and physicochemical heterogeneity between land covers.	PCA, PERMDISP, MANOVA	Land cover would be characterized effectively by physicochemical parameters and potentially by physicochemical heterogeneity.	1) All analyses clearly separated streams into two groups, corresponding to forest and agriculture; 2) Agricultural streams had elevated nutrient levels, suggestive of eutrophication; 3) Physicochemical heterogeneity was greater among agricultural streams except in the Canadian diatom dataset.

2) Reveal the responses of $\overline{\alpha}$-, γ-, and β-diversity, SAD evenness, and SAD skewness to physicochemistry and physicochemical heterogeneity.	MANOVA, Variance partitioning	The responses of biodiversity components to physicochemistry and physicochemical heterogeneity may differ depending on body size, dispersal capacity, and trophic level (autotroph vs. heterotroph).	1) In general, β- and γ-diversity were negatively related to eutrophication, whereas $\overline{\alpha}$-diversity increased. SADs tended to be more uneven in agricultural streams due to buildup of common species and/or increased dominance; 2) Covariance of land use with physiochemistry explained most of the diversity variation across datasets, whereas environmental heterogeneity poorly explained diversity; 3) Pure land cover and pure physicochemistry generally explained some additional variation in the diversity components.

3) Determine if land use influences the relative roles of local assembly and the regional species pool in driving β-diversity.	Null models, Permutational ANOVA, Variance partitioning	The contribution of local assembly should be responsive to agricultural land use, however, the magnitude and direction of the response may vary across organismal groups.	1) The role of local assembly was generally weakly affected by land use, and not in a consistent way across datasets, suggesting a potential influence of organismal type and biogeography.

4) Determine if β-deviation (β_{DEV}) is explained by the species abundance distribution (SAD) or intraspecific spatial aggregation.	Null models, Permutational ANOVA	It is unknown how land use may influence the fractions of β_{DEV} explained by the SAD and intraspecific spatial aggregation.	1) The SAD was the dominant fraction of β_{DEV} and this pattern was independent of land use and organismal group. However, the SAD fraction was significantly higher in agriculture across all datasets, which may be the underlying factor of taxonomic homogenization; 2) Intraspecific spatial aggregation fraction was negative for agricultural streams and positive for forest streams, indicating that intraspecific aggregation was lower than expected across disturbed streams;

Table 2. Summary of the impact of agricultural land use on resampled diversity measures as positive or negative percent change relative to forest cover. Significant differences between land covers were detected in all comparisons (permutational MANOVA and ANOVA, *P* < 0.05).

		% Change from agriculture		
Taxonomic group	Country	$\bar{\alpha}$	γ	[1]β_{OBS}
Diatoms	US	+20.71	−3.54	−1.09
	France	+13.33	−7.46	−2.22
	Canada	−12.15	−23.14	−4.64
Insects	US	−20.42	−22.98	−0.59
Fish	US	+9.55	+12.97	−2.29
	France	+54.99	+26.91	−6.41

[1] β-diversity = $1 - \frac{\bar{\alpha}}{\gamma}$

FIGURE LEGENDS

Figure 1. a. Conceptual model depicting the land use effect on the species abundance distribution (SAD) and intraspecific spatial aggregation, which in turn interact with local (α) and regional (γ) diversity. β-diversity is calculated as a function of average α-diversity and γ-diversity. Interactions that were controlled for by the null models of Kraft *et al.* (2011) and Xu *et al.* (2015) are marked with a thick dotted line. **b.** Diagram summarizing the Xu *et al.* (2015) partition of β_{DEV} into fractions explained by the SAD and intraspecific spatial aggregation using an occupancy-abundance based null model procedure. The null model β_{DEV} is taken as the raw difference between expected β-diversity (β_{EXP}) and observed β-diversity (β_{OBS}). The fraction of β_{DEV} explained by the SAD, β_{SAD}, is the difference between predicted β-diversity (β_{PRED}) and expected β-diversity (β_{EXP}), whereas the fraction of β_{DEV} explained by intraspecific aggregation (β_{AGG}) represents the difference between β_{OBS} and β_{PRED}.

Figure 2, a-f. Maps of diatom, macroinvertebrate, and fish sampling localities in the US, France, and Canada. Grey triangles represent agriculture samples, whereas black circles represent forest samples. a = US diatoms, b = US insects, c = US fish, d = French diatoms, e = French fish, f = Canadian diatoms.

Figure 3, a-f. Boxplots showing differences in resampled physicochemical heterogeneity between land covers for each dataset. a = US diatoms, b = French diatoms, c = Canadian diatoms, d = US insects, e = US fish, f = French fish. Points indicate resamples that fall outside the interquartile range. Different letters denote significant differences in mean heterogeneity (permutational ANOVA, $P < 0.05$).

Figure 4, a-f. Boxplots of resampled SAD and null model metrics showing the differences between land covers for each dataset. a = US diatoms, b = French diatoms, c = Canadian diatoms, d = US insects, e = US fish, f = French fish. Significant differences were observed in all comparisons (permutational ANOVA, $P < 0.05$) except β_{DEV} for US insects (panel D3, denoted by asterisk).

Figure 5, a-f. Venn diagrams showing output of redundancy analysis-based variance partitioning of diversity measures ($\overline{\alpha}$-, β-, and γ-diversity). Values represent model adjusted R^2 values. Values in intersections represent covariance fractions, whereas values in circles represent pure fractions.

Figure 6, a-f. Venn diagrams showing output of regression-based variance partitioning of β_{DEV}. Values represent model adjusted R^2 values. Values in intersections represent covariance fractions whereas values in circles represent pure fractions.

Figures

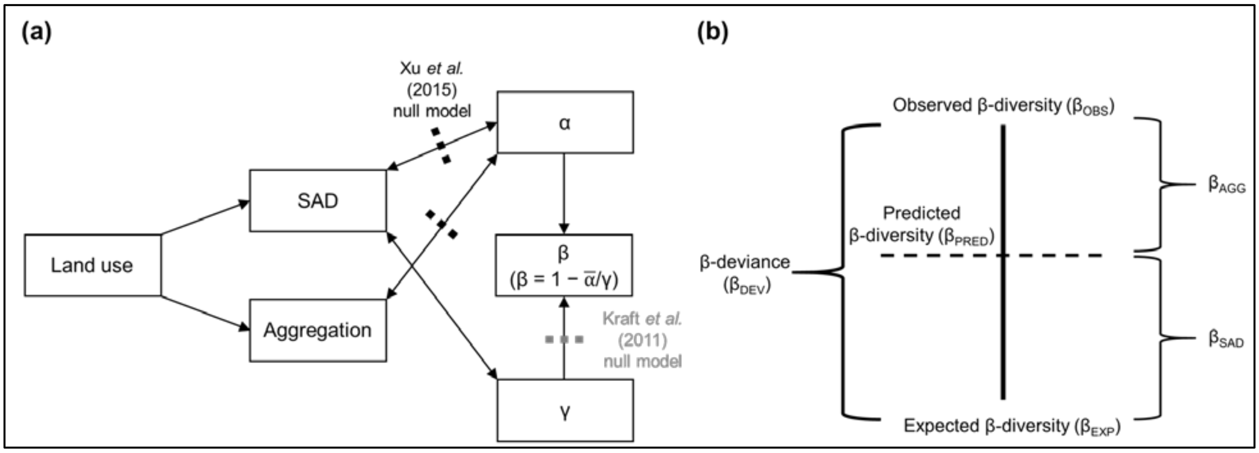


Figure 1

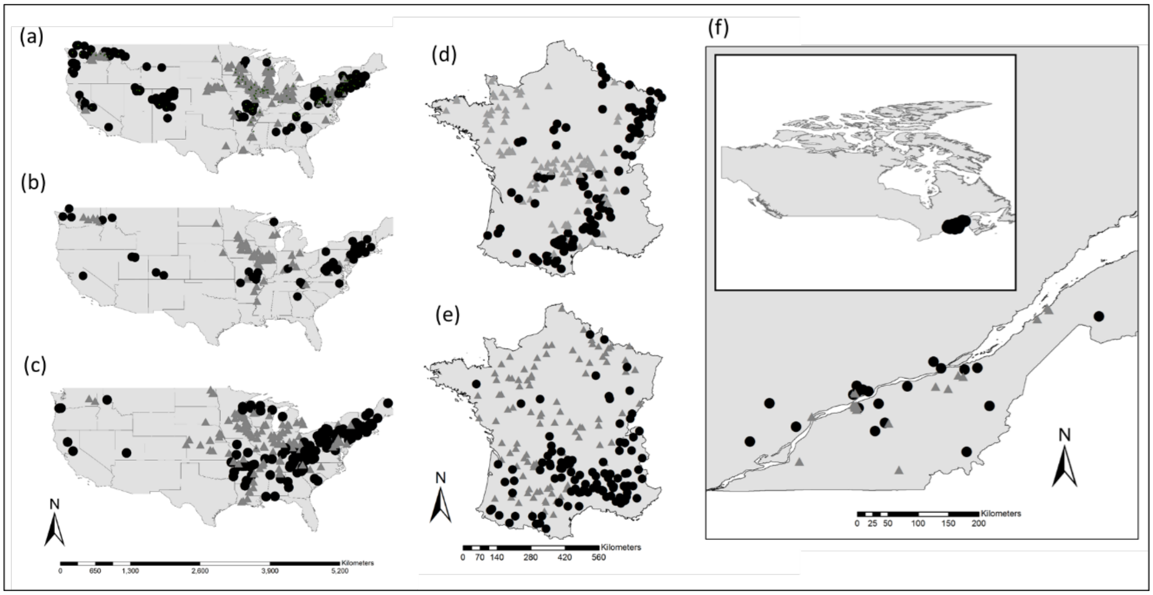
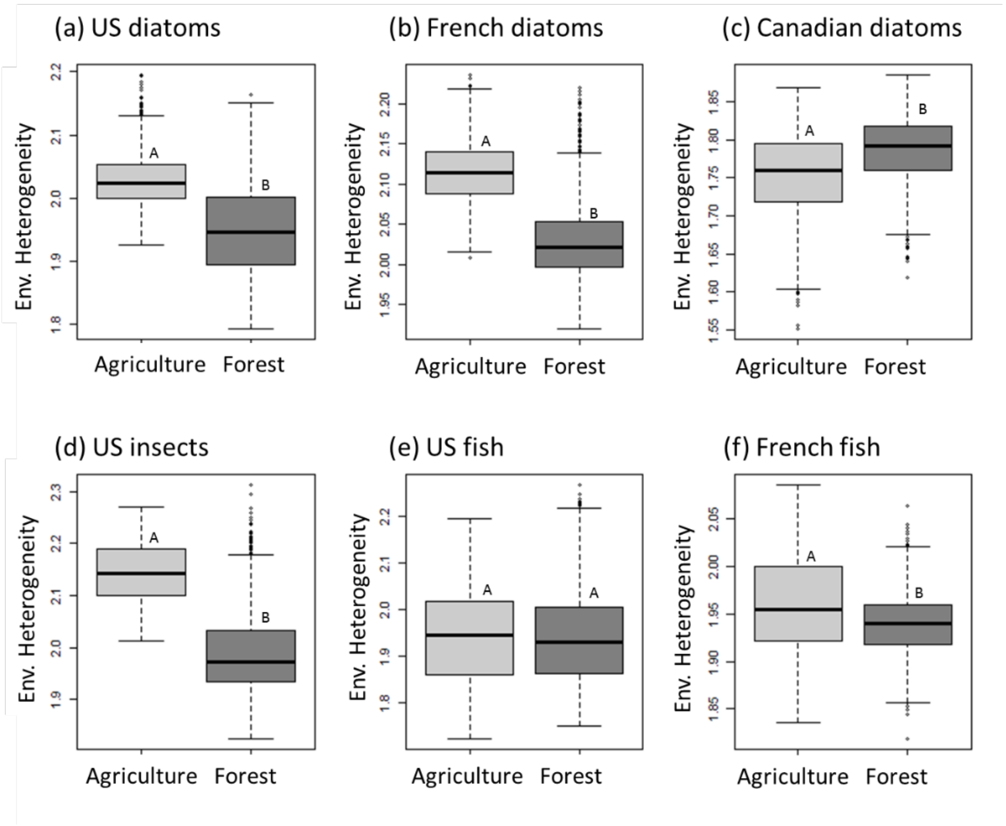


Figure 2


(a) US diatoms
Env. Heterogeneity
1.8
1.9
2.0
2.1
2.2
A
B
Agriculture
Forest
(b) French diatoms
Env. Heterogeneity
1.95
2.00
2.05
2.10
2.15
2.20
A
B
Agriculture
Forest
(c) Canadian diatoms
Env. Heterogeneity
1.55
1.60
1.65
1.70
1.75
1.80
1.85
A
B
Agriculture
Forest
(d) US insects
Env. Heterogeneity
1.9
2.0
2.1
2.2
2.3
A
B
Agriculture
Forest
(e) US fish
Env. Heterogeneity
1.8
1.9
2.0
2.1
2.2
A
A
Agriculture
Forest
(f) French fish
Env. Heterogeneity
1.85
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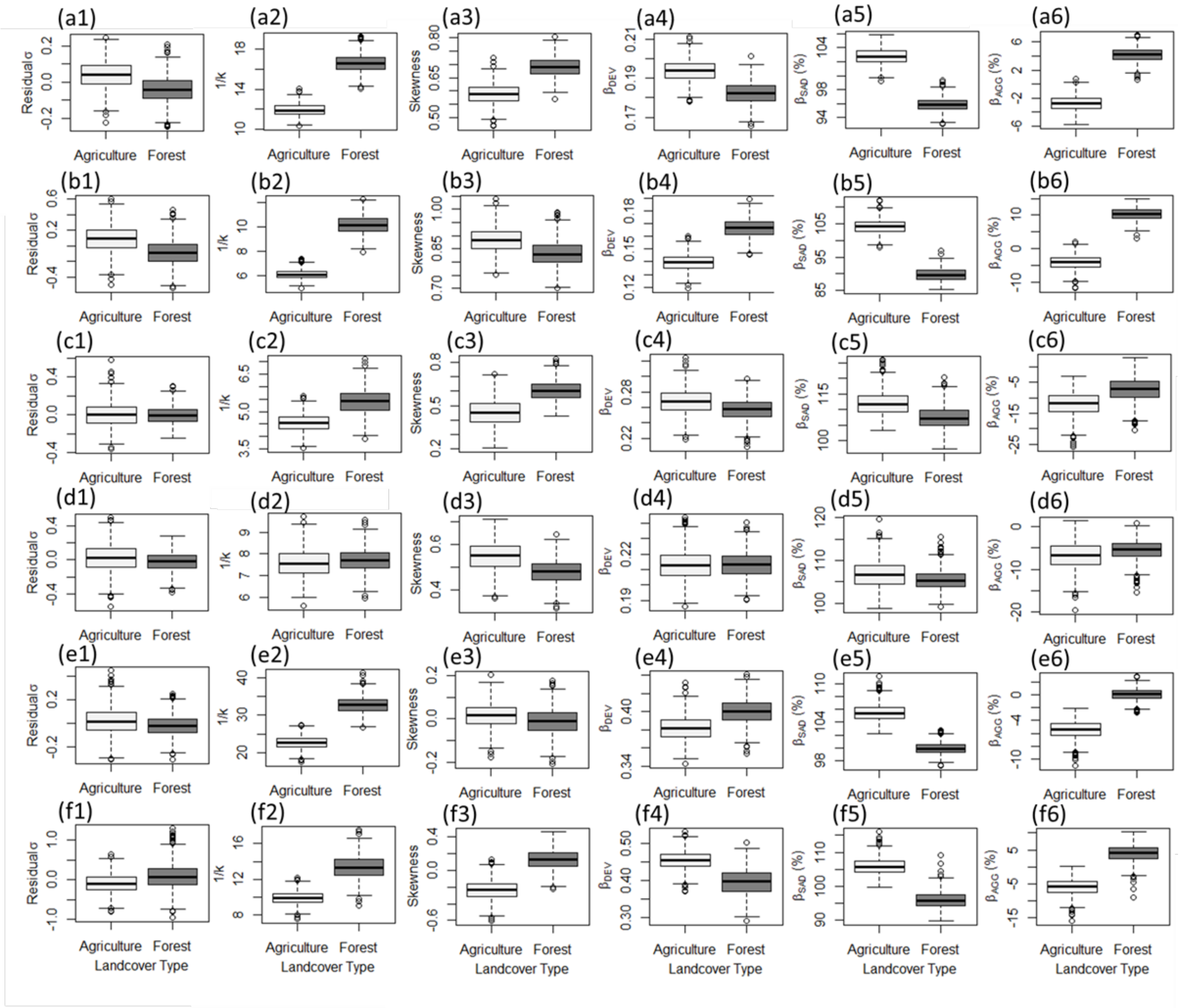
Agriculture
Forest

Figure 3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(f4)
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Residualσ
1/k
Skewness
β_{DEV}
β_{SAD} (%)
β_{AGG} (%)
Agriculture
Forest
Landcover Type

Figure 4

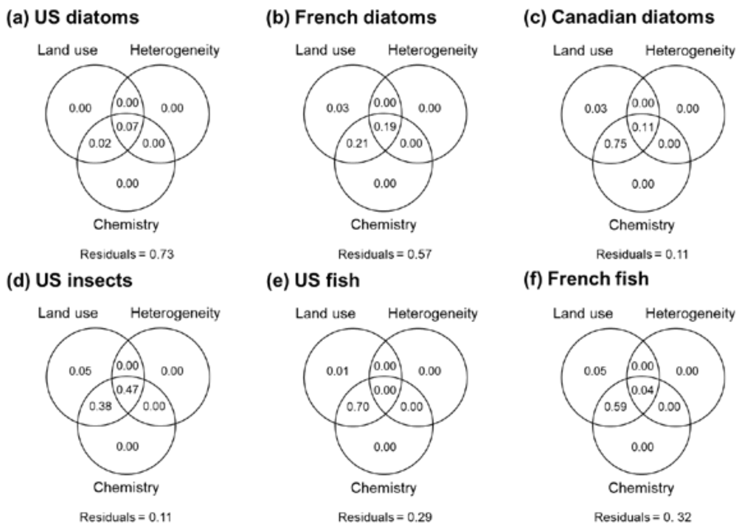

Figure 5

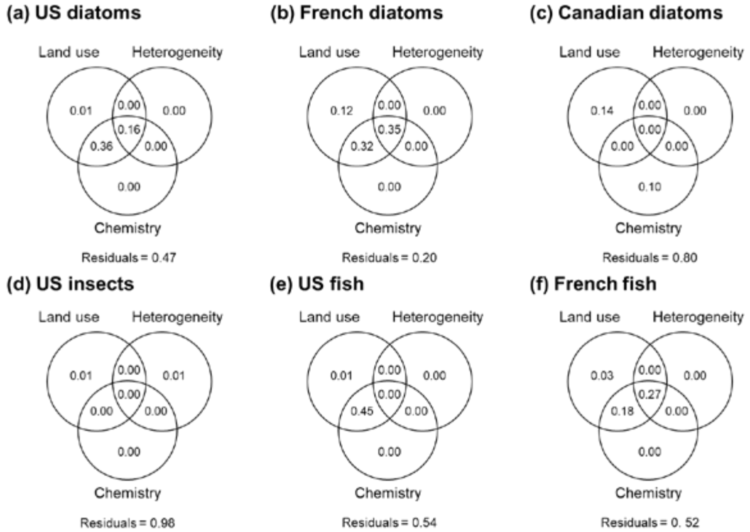

Figure 6

Supporting Information Appendix Short Titles

Appendix 1: Expanded description of environmental data and null model correlation results

Appendix 2: Description of Null Model Machinery

Appendix 3: R-code script for looping procedures

Appendix 4: R-code script for analyses of loop output