

Response diversity, nonnative species, and disassembly rules buffer freshwater ecosystem processes from anthropogenic change

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Abstract

Integrating knowledge of environmental degradation, biodiversity change, and ecosystem processes across large spatial scales remains a key challenge to illuminating the resilience of earth's systems. There is now a growing realization that the manner in which communities will respond to anthropogenic impacts will ultimately control the ecosystem consequences. Here, we examine the response of freshwater fishes and their nutrient excretion – a key ecosystem process that can control aquatic productivity – to human land development across the contiguous United States. By linking a continental-scale dataset of 533 fish species from 8100 stream locations with species functional traits, nutrient excretion, and land remote sensing, we present four key findings. First, we provide the first geographic footprint of nutrient excretion by freshwater fishes across the United States and reveal distinct local- and continental-scale heterogeneity in community excretion rates. Second, fish species exhibited substantial response diversity in their sensitivity to land development; for native species, the more tolerant species were also the species contributing greater ecosystem function in terms of nutrient excretion. Third, by modeling increased land-use change and resultant shifts in fish community composition, land development is estimated to decrease fish nutrient excretion in the majority (63%) of ecoregions. Fourth, the loss of nutrient excretion would be 28% greater if biodiversity loss was random or 84% greater if there were no nonnative species. Thus, ecosystem processes are sensitive to increased anthropogenic degradation but biotic communities provide multiple pathways for resistance and this resistance varies across space.

Keywords: biodiversity, ecosystem function, resilience, stream, urbanization

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Introduction

The human enterprise has led to conspicuous changes to biological diversity with often unexpected and profound impacts on ecosystem structure and function (Hooper *et al.*, 2005, 2012; Estes *et al.*, 2011). Experimental evidence suggests that decreases in species richness associated with the random loss of native species can reduce rates and stability of ecosystem processes (Loreau *et al.*, 2001; Hooper *et al.*, 2005; Tilman *et al.*, 2006). However, it is well recognized that human activities do not simply reshuffle biodiversity in a random manner; instead communities are being disassembled according to heterogeneous rates of species losses (i.e., sensitive species) and gains (i.e., opportunistic or tolerant species) across the landscape (Byrnes *et al.*, 2007; Zavaleta *et al.*, 2009; Dirzo *et al.*, 2014; Dornelas *et al.*, 2014). Species invasions are also contributing to

ongoing community shifts (Blanchet *et al.*, 2010; Dornelas *et al.*, 2014) where changes in species composition and not systematic reductions in species richness are being witnessed (Dornelas *et al.*, 2014). Accordingly, there have been recent and repeated calls for science that advances our understanding of how non-random species change in the future may impact ecosystem processes across large spatial scales (Loreau *et al.*, 2001; Kremen, 2005; Srivastava & Vellend, 2005).

Species communities could resist or ameliorate the impacts of anthropogenic change on ecosystem processes via several mechanisms. First, the differential responses of species to environmental degradation, termed response diversity (Mori *et al.*, 2013), can confer stability to the abundance or biomass of the aggregate community (Karp *et al.*, 2011) or metapopulation (Anderson *et al.*, 2015) as well as the collective ecosystem processes they control (Elmqvist *et al.*, 2003; Winfree & Kremen, 2009; Mori *et al.*, 2013). By contrast, ecosystem processes in communities with low response

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diversity and limited redundancy may decline precipitously with degradation. Through contributing to this response diversity, nonnative species likely play an important, yet underappreciated and rarely quantified role in maintaining ecosystem processes in the face of environmental change (Schlaepfer *et al.*, 2011; Bertness & Coverdale, 2013; Lagrue *et al.*, 2014; Twardochleb & Olden, 2016). Second, disassembly rules describing the relationship between the sensitivity of a species (response) and its contribution to ecosystem function (effect) can control the resistance of ecosystems to environmental change (Solan *et al.*, 2004; Bunker *et al.*, 2005; Gross & Cardinale, 2005; McIntyre *et al.*, 2007; Zavaleta *et al.*, 2009). For example, large-bodied dung beetles and bees are the most sensitive to habitat fragmentation yet concurrently are the most efficient processors and pollinators, suggesting that small biodiversity changes may translate into large decreases in ecosystem function (Larsen *et al.*, 2005). Accordingly, disassembly rules shed insight on the linkages between response diversity and ecosystem effect.

Freshwater ecosystems are strongly influenced by the animals that inhabit them, such as through the process of nutrient recycling via fish excretion (Vanni, 2002; Capps *et al.*, 2015). Nutrient excretion by fishes can transform nitrogen (N) and phosphorus (P) that are sequestered in the organic matter of prey and then, through excretion, mobilize the nutrients and make them available for uptake by primary producers (Vanni, 2002). Fish excretion is often a large component of N and P budgets in freshwater environments, stimulate primary production by elevating local nutrient levels, and even create biogeochemical hotspots where nutrient release by fish exceeds uptake by other organisms (McIntyre *et al.*, 2008; Small *et al.*, 2011). In some circumstances, nutrient recycling by fish can have larger impacts on food webs than their trophic impacts (Leroux & Loreau, 2010). Recent syntheses of fish excretion studies have revealed that traits describing body size and trophic (or feeding) guild largely control species-specific excretion rates (Sereda *et al.*, 2008; Sereda & Hudson, 2011). Similarly, body size is an important response trait linked to environmental change; fish body size is a strong predictor of extinction risk (Olden *et al.*, 2007), and size-biased changes in fish assemblages have been attributed to nonnative species (Blanchet *et al.*, 2010). Given these linkages, community structure, both in terms of native and nonnative species, may strongly influence the response of ecosystems to environmental degradation.

Here, we present a broad-scale investigation of whether fish community structure buffers freshwater ecosystem processes, specifically nutrient recycling, from environmental change associated with human

activities. We focus on land degradation associated with urban land development because it is a leading driver of freshwater ecosystem change that decreases water quality, alters hydrologic regimes and physical habitat, and causes shifts in biological communities (Paul & Meyer, 2001; Allan, 2004; Vörösmarty *et al.*, 2010). Our study integrates an extensive database on hundreds of fish species from thousands of streams from across the United States to existing information on ecological traits, excretion rates, and anthropogenic land degradation to address the following three questions. First, what is the geographic footprint of fish nutrient excretion across the contiguous United States? Second, what is the linkage between native and nonnative species sensitivity to human land use and their ecosystem role with respect to nutrient excretion? Third, what are the contributions of nonnative species and disassembly rules in defining ecosystem resistance to land degradation? By addressing these questions, our study sheds novel insight into how human land development influences ecosystem processes through biodiversity shifts across continental scales, and how species communities comprised of both native and nonnative fishes may modulate these outcomes.

Materials and methods

Fish community database

We compiled a comprehensive database of 8100 fish surveys (representing 533 species) from stream and river ecosystems across the contiguous United States from a variety of standardized sources that included the national and regional EPA Environmental Monitoring and Assessment Programs, the USGS National Water Quality Assessment Program, numerous state agency biomonitoring programs, and large-scale sampling efforts by other organizations and researchers (see Appendix S2). The database included survey sites that were either selected using a systematic, randomized approach or were synoptic in scope and sampled sites from a broad range of stream types and sizes during the period 1990–2012, thus providing an accurate national-scale representation of present-day fish communities. Fish sampling methods for all sources included standardized electrofishing and seining of defined stream length during the Northern Hemisphere spring or fall months, and the identification and enumeration of all captured individuals allowed for robust estimates of species density. We determined native and nonnative (both domestic and foreign introductions) status for all species at each site according to the United States Geological Society (USGS) Nonindigenous Aquatic Species Database (2012). We also compiled information on developed land use and other important environmental factors for each of the 8100 stream sites. Percent of the local contributing watershed in developed land use (summed across low-, medium-, and high-intensity categories) was calculated according to the National Land

Cover Database referenced to 2006 (which represents the average year the fish surveys were conducted). Accordingly, land development included urban and suburban development, but not agricultural practices. In addition, we compiled stahler stream order, mean annual discharge, elevation (m), mean annual air temperature (°C), and mean annual precipitation (mm) (see Appendices S1 and S2) for each site, which represent well-known surrogates for habitat size, productivity, and predictors of fish communities (Jackson *et al.*, 2001). See Appendix S2 for more details.

Predicting nutrient excretion

We quantified patterns of stream fish nutrient excretion at local and continental scales by estimating nutrient excretion by individual fish species and fish communities at each of the 8100 sites. The per-capita excretion ($\mu\text{g h}^{-1}$ individual $^{-1}$) of species j was calculated as

$$E_j = 10^{b+a \log_{10} M_j}$$

where M is the mass of species j , and a and b are empirically estimated parameters that differ for N and P and for the detritivore and nondetritivore trophic guilds (Sereda *et al.*, 2008). These parameters were obtained from a previous meta-analysis that found strong empirical relationships ($R^2 > 0.87$) for individual fish excretion rates ($\mu\text{g h}^{-1}$ individual $^{-1}$) of total dissolved N and P as a function of log wet mass and trophic guild (Sereda *et al.*, 2008). We classified fish species as detritivores or nondetritivores following a recent compilation of traits of North American freshwater fishes (Mims *et al.*, 2010). Species classifications can be found in the previously published trait database (Mims *et al.*, 2010). Rarely did the fish surveys include values of fish size, thus we used species-specific length at maturation data for fish species (Mims *et al.*, 2010) and converted these lengths to masses based on species- or genus-specific published length-weight scaling relationships (Froese & Pauly, 2011).

We calculated the community-level aggregate excretion rate ($\mu\text{g h}^{-1}$ site $^{-1}$) at each sampling reach as the sum, across all S species present, of the products of the per-capita excretion and the abundance of species j :

$$E_c = \sum_{j=1}^S E_j n_j$$

Abundances of each species at each site (n_j) were obtained from the fish survey data (see Appendix S2).

These estimates of community- and species-level nutrient excretion should be viewed as approximations of relative nutrient excretion rather than precise quantifications. Specifically, nutrient excretion rates are based on species-level size traits rather than observed individual size measurements. However, average length within fish species has been found to not systematically vary as a function of anthropogenic disturbance (Murphy *et al.*, 2013), suggesting that this approach would not generate systematically biased estimates of fish nutrient excretion across gradients of land development. Regardless, this approach is necessary in providing

quantitative predictions of fish nutrient excretion given that fish were not consistently measured across the large datasets we integrated. Furthermore, given that fish surveys represent a single snapshot in time, it is likely that fish nutrient excretion rates vary across time (although all surveys were conducted primarily in spring or fall). This type of approach, linking observed fish communities to nutrient excretion rates to predict aggregate nutrient excretion, has previously been used on smaller scales to highlight fine-scale heterogeneity in fish nutrient excretion (i.e., for <50 channel units within a single river (McIntyre *et al.*, 2008)). We quantified relationships between site fish species richness, total abundance, and community P excretion using linear models, log-transforming both response and predictor variables to improve normality. We focus on P given that it is often the key limiting nutrient in fresh waters (Schindler, 2006), but the results are qualitatively similar for N (see Appendix S1).

Quantifying sensitivity to land development and response diversity

We quantified the sensitivity of freshwater fishes to land-use change to determine possible response diversity across species. For each fish species, we quantified how land development influenced their abundance and statistically accounted for other important environmental factors. Although we focus on developed land (in 2006) as a factor, each model also included elevation, stream order, mean annual precipitation, and air temperature to account for important environmental differences across sites.

We used negative binomial regression to quantify relationships between fish abundance and watershed land development (Martin *et al.*, 2005). Negative binomial regression is appropriate for dealing with count data that can be overdispersed. We modeled the abundance of each species by restricting the model to only the freshwater ecoregions (Abell *et al.*, 2008) where the species was present, thus avoiding spurious relationships based on biogeographic boundaries. Predictor variables were normalized to standardize measurement units and improve model performance. The coefficients for land development were used as an index of the sensitivity of each species. Negative coefficients indicate that those species less likely to occur and be abundant in streams with higher levels of developed land use, whereas the opposite is true for species models containing positive coefficients. This sensitivity metric thus quantifies the relationships between species and developed land across space while controlling for the influence of other abiotic conditions. This metric integrates multiple potential pathways, ranging from both indirect (e.g., species interactions such as predation) and direct (e.g., habitat loss and modification) pathways, by which land development may impact species occurrence. Species were omitted if they had <15 records of occurrence (leaving 283 species). We used Spearman rank correlations to examine the relationships across species sensitivities and effect in order to avoid assumptions of normality and relationship shape.

Linking components of community change to ecosystem resistance

We aimed to quantify the degree to which nonnative species and disassembly rules provide resistance to ecosystem processes. Using a simulation-based approach, we examined how these different components of community change modulate the impacts of land-use development on aggregate fish nutrient excretion (E_c). This approach used sensitivities derived from the negative binomial regression models to infer response to land development; previous studies have found that such space-for-time substitutions provide accurate predictions of community change (Blois *et al.*, 2013). As freshwater ecoregions represent distinct fish taxonomic pools with distinct evolutionary and ecological histories (Abell *et al.*, 2008), we focused these simulations on the ecoregion scale. For each of the 41 freshwater ecoregions, we identified the species that were present in each ecoregion. Using this species pool, and the coefficients of each species from the negative binomial models, we predicted changes in community composition with increasing land development. Specifically, we set the environmental variables to be the mean observed values for all sites within each ecoregion, systematically increased watershed development from 0% to 10%, and predicted the abundance of each species using the previously estimated models. Four-fifths (80%) of sites had <10% development. Thus, we focused on 0–10% development to avoid extrapolating beyond the domain of the data. The National Land Cover Database has calculated that urban impervious surface has increased from 6.04% to 6.34% from 2001 to 2011 (Homer *et al.*, 2015). Forecasts of urbanization are for similar incremental increases over the next several decades (Theobald, 2005). Even though watersheds are experiencing only incremental urbanization, it is possible that fish communities are sensitive to these modifications and that these small changes in watershed urbanization may lead to subsequent changes in the ecosystem processes that fish control. We translated these shifts in community composition into changes in aggregate P excretion (E_c) through the previously quantified estimates of species-specific nutrient excretion (E_p). We retained species that were present in at least 20 sites. Using this general procedure, we examined three components of community disassembly:

1. Baseline (predicted). This scenario uses the full species pool for each ecoregion and their linked sensitivities and ecosystem effects (E_p). Thus, this scenario represents a realistic estimate of how P excretion changes in response to land development.
2. Native species only. This scenario predicts the change in community P excretion with land development based solely on native fish species. Species were classified as nonnative if they were designated 'nonnative' status in at least one survey site in the ecoregion.
3. Random disassembly. This scenario estimates P excretion change with land development assuming no relationship between species sensitivity and species contribution to nutrient excretion. For each ecoregion, the relationship between species effect (E_p) and sensitivity was randomized,

bootstrapping with replacement. We present the median predicted change (based on 1000 iterations) for each ecoregion.

For each scenario, we calculated the % change in the estimated aggregate community nutrient excretion (E_c) with increased land development, using 0% development as the reference state. We focus on the % change in nutrient excretion from 0% to 10% development as a key response variable. To examine how nonnative species and disassembly rules contribute to resistance of aggregate nutrient excretion, we compared the change in nutrient excretion for these scenarios with the baseline scenario for each ecoregion. These scenarios focused on the taxonomic pool from each ecoregion and did not include species from other ecoregions that could potentially but unpredictably be introduced or move across biogeographic boundaries.

Results

We projected nutrient excretion by 533 fish species in 8100 stream sites across the contiguous United States to explore community excretion rates across local and regional scales. Streams ranged widely in their environmental characteristics (see Appendix S1). Of the 533 fish species, 8% were herbivores–detritivores, 59% were invertivores, 9% were invertivore–piscivores, 19% were omnivores, and 5.4% were piscivores. Predicted community P excretion at each site varied more than five orders of magnitude, from 5.1 to 747 420 $\mu\text{g P h}^{-1}$ (median 6058 $\mu\text{g P h}^{-1}$) (Fig. 1). Community P excretion was higher in sites with higher total abundance of fish ($R^2 = 0.56$, $P < 0.001$), higher average body mass ($R^2 = 0.32$, $P < 0.001$), and higher total richness ($R^2 = 0.34$, $P < 0.001$). In addition, sites with higher mean annual discharge tended to have higher community P excretion ($R^2 = 0.13$, $P < 0.001$) while the proportion of herbivore–detritivores explained little of the variation in community P ($R^2 = 0.008$, $P < 0.001$) (see Appendix S1).

Sites varied greatly in fish species richness, from 1 to 51 species at a single site (average 11.2 species), as well as fish total abundance, from 2 to 4959 individuals, and richness and abundance were positively associated ($R^2 = 0.43$, $P < 0.001$). There was substantial unexplained variation across sites in estimated community nutrient excretion, likely due to the myriad factors that control local fish community composition, including species interactions such as predation and competition. On the continental scale, fish communities in western United States generally had lower predicted P excretion compared to communities in eastern and south-central streams, such as those within the Mississippi River Basin (Fig. 1). At watershed scales, community nutrient excretion rates were predicted to be generally lower in higher elevation streams. Spatial patterns in

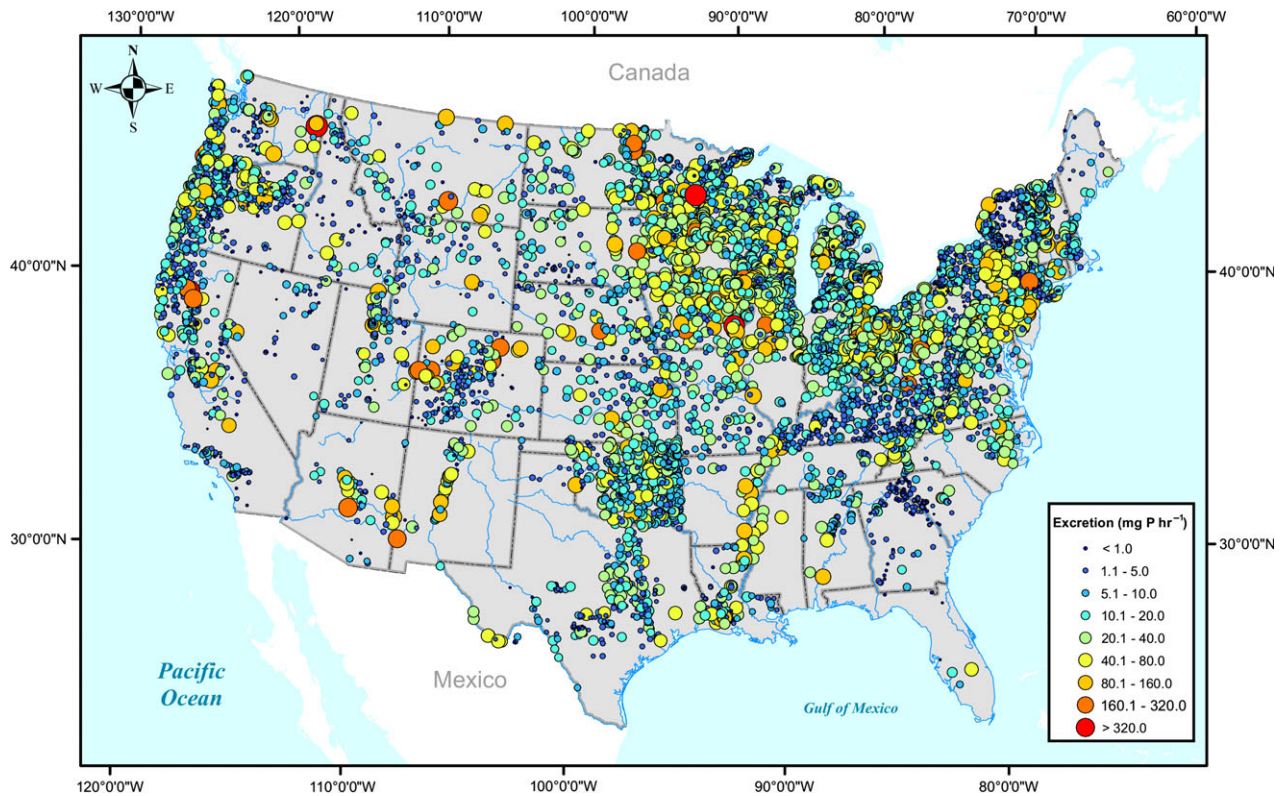


Fig. 1 Quantitative predictions of aggregate fish excretion of P across the contiguous United States. Point size and color scales to the predicted excretion (E_c) for each site.

community N excretion were qualitatively similar to the results reported above for P (see Appendix S1).

Freshwater fishes exhibited pronounced response diversity in their sensitivity to land development (Fig. 2). Although fish species tended to display overall negative associations with land development (median slope = -0.19), we found variation in species responses ranging from highly negative to positive. Nonnative fishes generally were more tolerant of land development than native fishes (nonnative median slope = -0.02 ; native median slope = -0.31); half (50%) of nonnative species displayed positive associations (e.g., many basses and sunfishes: family Centrarchidae), compared to one quarter (25%) of native species (Fig. 2). There were trends that different functional groups may be differently tolerant of land development, but these were not statistically significant ($P > 0.05$; Fig. S7 in Appendix S1). While previous research has found that body size in native freshwater fishes is negative correlated to extinction risk (Olden *et al.*, 2007); we did not find strong evidence of a relationship between tolerance and body size for both native fish (Spearman rank correlation, $\rho = 0.12$, $P = 0.15$) and nonnative fishes (Spearman rank correlation, $\rho = 0.76$, $P = 0.49$) (Appendix S1). Together, our

results provide strong evidence that fish species exhibited differential sensitivity to land development.

Fish species also varied enormously both in their contribution to community nutrient excretion and their sensitivity to land development, providing evidence of linkages between species sensitivity and their ecosystem effect (Fig. 3). We assessed the average contribution of a species to community nutrient excretion as the product of their average abundance and per-capita excretion rate. Native species demonstrating higher P excretion rates tended to be more tolerant to land development (Spearman rank correlation, $\rho = 0.19$, $P = 0.002$); this included a number sucker species (family Catostomidae). This relationship suggests a connection between species sensitivity to land-use modification and their contribution to nutrient recycling. More generally, fish species ranged greatly in their average P excretion, with the vast majority of fish species contributing little (e.g., *Etheostoma* spp, common name: darters) and a few species contributing a great deal (e.g., *Ictiobus* spp, common name: buffalo) to community P excretion (Fig. 3). Across all species, native and nonnative fishes had similar P excretion rates (Fig. 3). In contrast to native species, the sensitivity of nonnative species to land development was not related

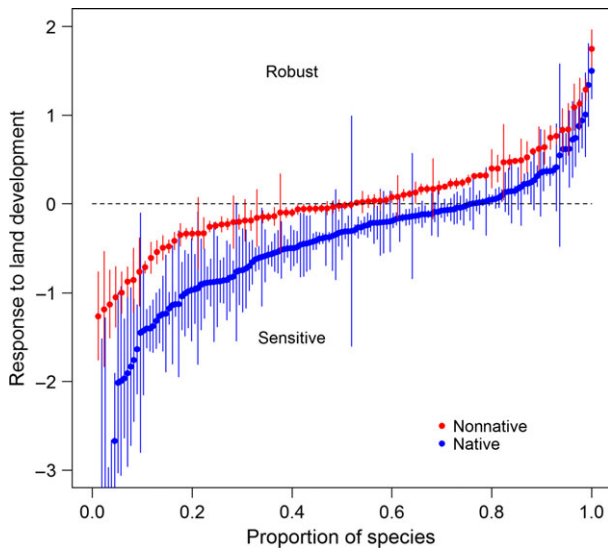


Fig. 2 Response diversity of freshwater fishes to land development. Sensitivity values to land development (i.e., the slope of the negative binomial model relating species abundance to watershed development) are shown for native (blue) and nonnative species (red) and are arranged in increasing order along the x -axis. Shown are best estimated parameters ± 1 SE. Values above 0 indicate that watershed development is positively associated with species occurrence ('tolerant' species), whereas values below 0 indicate a negative species development relationship ('sensitive' species).

to their species-level excretion for P (Spearman rank correlation, $\rho = 0.08$, $P = 0.44$). Thus, unlike native species that exhibited disassembly rules, nonnative species displayed an idiosyncratic pattern of apparent random disassembly.

Increased land development by human activities is predicted to often decrease fish community nutrient excretion in freshwater ecosystems (Fig. 4). Using our empirically derived estimates of species nutrient excretion and their sensitivity to human land use, we examined how increasing developed land (e.g., increased urbanization and impervious surfaces) of watersheds influences fish community nutrient excretion for ecoregions across United States. According to the baseline scenario containing present-day fish communities, increasing developed land from 0% to 10% is predicted to decrease P excretion in the majority of ecoregions (63%, 25 of 40 ecoregions), with an average decline in community P excretion of 6.8% (median = -5% change). However, fish community composition varies substantial across the United States, which resulted in ecoregions exhibiting profoundly different patterns of nutrient excretion change with land development (Fig. 4). For some ecoregions, the aggregate P excretion was predicted to increase by over a third (37%) when

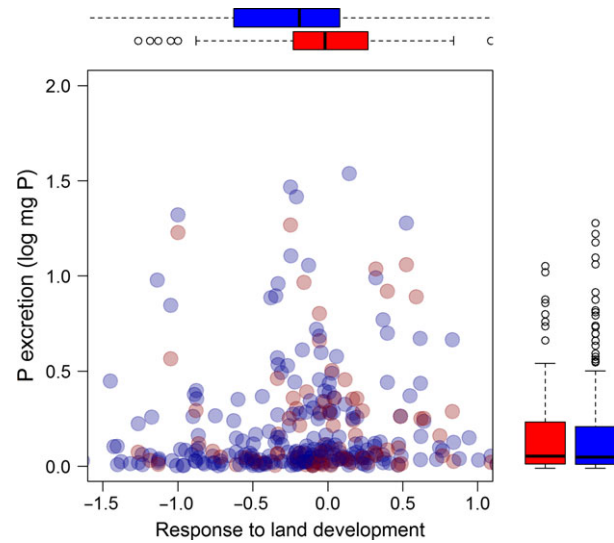


Fig. 3 Disassembly rules of freshwater fish communities. Response to land development, as quantified by the slope of relationship with watershed development, varies with a species' average P excretion ($\log(\text{mg P h}^{-1} + 1)$). Each point represents a different species, including native (blue) and nonnative (red) species. Positive response values indicate species that are more positively associated with land development. For translocated species, we present their P excretion separately for sites where they are native and sites where they are nonnative. Summary boxplots of sensitivity (top) and P excretion (right) display the median and inner quartiles.

developed land use was increased from 0% to 10%, whereas in other ecoregions, P excretion from the fish communities was predicted to be almost completely lost (-90%). This predicted change in community P excretion was related to the invaded status of the fish community of the ecoregion; ecoregions with a higher proportion (by abundance) of nonnative fish were generally more resistant to land development (linear model: $R^2 = 0.12$, $P = 0.02$).

Nonnative fishes can buffer changes to community nutrient excretion in response to human land development (Fig. 4). When considering only the native species of fish communities, we found that aggregate nutrient excretion decreased by an average of 13% (median = -9% change, range = -92% to 27%) with increased land development from 0% to 10%. Thus, loss of nutrient excretion would be 84% greater on average if there were no nonnative species. The native species scenario predicted a larger negative decrease in P excretion (with 0–10% land development) for almost three-quarters (73%) of the ecoregions compared to the baseline scenario, with an average difference in relative excretion loss of -6% (range: 4% to -43%). Nonnative species can buffer excretion from land-use change in

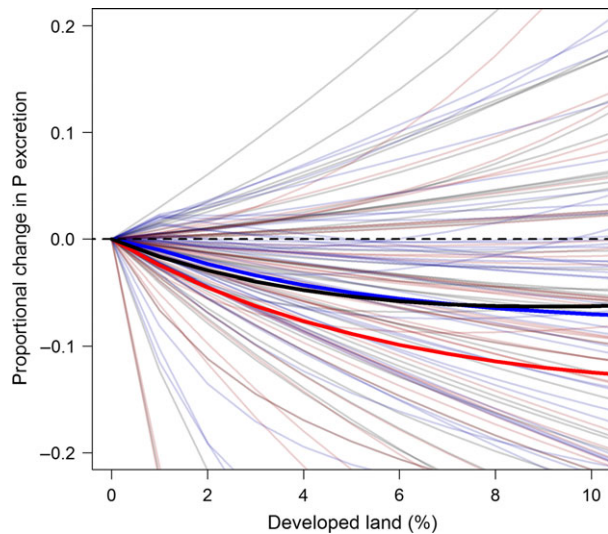


Fig. 4 Scenarios of community disassembly and nutrient excretion. Lines show the predicted nutrient excretion change from the aggregate community (E_c), relative to the undeveloped reference state (0% human development), as a function of increased developed land use. Partially transparent lines represent predictions for each ecoregion and thick solid lines depict the average response across all ecoregions. Black lines indicate the base scenario, red lines indicate the native species only scenario, and blue lines indicate the random disassembly scenario.

the majority of ecoregions, likely due to their relative insensitivity to land development and ability to compensate numerically and functionally for dwindling sensitive native taxa.

Disassembly rules also can confer resistance to community nutrient excretion from land-use change (Fig. 4). Through a randomization procedure that severed the link between species response (i.e., sensitivity to land use) and effect (i.e., contribute to nutrient recycling), we found that random disassembly can exacerbate declines in community P excretion. Thus, the predicted loss of nutrient excretion with land-use development would be 28% greater on average if biodiversity change was random. On average, the random disassembly scenario predicted a 9% decrease (range: -55% to 19%) in P excretion with increased land development from 0% to 10%. There were greater losses in community nutrient excretion for almost three-quarters (70%) of ecoregions in the random disassembly scenario compared to the baseline scenario, with a mean difference of -2% (range: 39% to -61%). This finding is supported by our observation that native fishes that are less sensitive to land development tended to contribute more to nutrient excretion and illustrates that the disassembly rule that links species effect and species sensitivity can buffer nutrient excretion from environmental change.

Discussion

Our study provides insight into the different pathways that influence the vulnerability of communities and the ecosystem processes that they control. First, our results demonstrate that fish species exhibited differential sensitivity to land development (Fig. 2) and support an emerging appreciation for response diversity in biological communities (Elmqvist *et al.*, 2003; Karp *et al.*, 2011; Cariveau *et al.*, 2013; Mori *et al.*, 2013) and the role it may play in ecosystem processes and resistance to anthropogenic change (Mori *et al.*, 2013). Second, we provide evidence that the relationship between species vulnerability and impact (i.e., disassembly rule) plays a role in determining the vulnerability of ecosystem processes to anthropogenic change. The species that contributed the most to ecosystem processes tended to be more tolerant of anthropogenic change than species that contributed less (Fig. 3). Accordingly, in most cases, fish community responses to human land use resulted in lower loss of nutrient excretion compared to random disassembly, evidence of the role of disassembly rules in buffering ecosystems from community change (Kremen, 2005; Larsen *et al.*, 2005; Zavaleta *et al.*, 2009). Third, our results provide insight into the potential roles of nonnative species in ecosystem resistance. Intriguingly, nonnative species did not exhibit a relationship between their sensitivity and their impact. This random disassembly of nonnative species is likely because the invasion process selects for a different suite of traits (i.e., high dispersal), thereby potentially disrupting the relationship between determinants of excretion rates and sensitivity to land-use change observed in native species (Olden *et al.*, 2004). Accordingly, we found that nonnative species were generally more tolerant of anthropogenic change than native species. Our simulations found that ecoregions with more nonnative fishes were more resistant to land development impacts on nutrient excretion. These results provide new evidence of the potential important contribution of nonnative species to ecosystem processes in a changing world (Schlaepfer *et al.*, 2011; Gribben *et al.*, 2013; Twardochleb & Olden, 2016).

Our study provides evidence that the vulnerability of biodiversity and ecosystem processes to anthropogenic change can be context-dependent. Perhaps not surprisingly, fish communities and their predicted nutrient excretion varied widely across the United States. These findings support previous research demonstrating that fish can produce local biogeochemical hotspots (McIntyre *et al.*, 2008). More striking is that across the thousands of sites that we examined, different fish communities and their ecosystem processes exhibited

different vulnerability to anthropogenic change – at some ecoregions, increased anthropogenic land use is predicted to increase nutrient excretion while at other ecoregions, it is predicted to decrease nutrient excretion. Forecasting the resistance of ecosystem processes to anthropogenic perturbations may be challenging, yet exciting opportunities exist to merge our understanding of how landscapes shape species traits (Mims *et al.*, 2010; Poff, 2012) and how these traits define ecosystem effects and sensitivities of those species (Zavaleta *et al.*, 2009). Our study represents a step toward forging these linkages at broad spatial scales using novel datasets of empirical field surveys and species traits.

Although much research has focused on carefully controlled field experiments to quantify the ecosystem consequences of random biodiversity change (Hooper *et al.*, 2005), predicting the ecosystem consequences of environmental degradation also requires empirical research that incorporates the realities of community change across large spatial scales (Kremen, 2005; Srivastava & Vellend, 2005). This approach necessarily requires some assumptions. For example, while previous work has highlighted that diversity itself can influence ecosystem processes (Hooper *et al.*, 2012), our approach did not explicitly consider diversity effects per se nor compensatory dynamics. However, our estimates of species sensitivities reflect empirical patterns of abundance and occurrence and thus would subsume strong species interactions and compensatory dynamics. Furthermore, previous studies have found that response diversity is more important than compensatory dynamics at landscape scales (Winfree & Kremen, 2009; Karp *et al.*, 2011). Our results quantify how land development will decrease nutrient excretion by fishes in streams, yet it is important to note that this land-use conversion is also directly associated with increased nutrient runoff due to human activities (Paul & Meyer, 2001). Previous studies have found that at high levels of urbanization, anthropogenic nutrient loading can swamp nutrient cycling [e.g., above 10% impervious surface (Meyer *et al.*, 2005)]; our analyses focused on a lower range of development (0–10%) and thus systems that were likely not saturated by anthropogenic nutrients. Fish can be sensitive to even low levels of watershed development (Paul & Meyer, 2001).

Other types of land development, such as agricultural, also contribute to stream nutrient budgets. For example, one ha of corn agriculture loads $0.22 \text{ kg ha}^{-1} \text{ yr}^{-1}$ of dissolved phosphorus (P) and $3.02 \text{ kg ha}^{-1} \text{ yr}^{-1}$ of dissolved nitrogen (N) (Harmel *et al.*, 2006; Christianson & Harmel, 2015). We can compare these estimates of the nutrients that are lost from different types of agriculture to the amount of nutrients excreted by fish in each of our 8100 study reaches. Fish excrete

more nutrients than is lost from one ha of corn agriculture in 15.7% and 47% of sites for P and N, respectively. We note that this exercise necessitates some assumptions regarding scaling up estimates; for instance, fish excretion is estimated for stream reaches that are approximately 500 m long and we assume that fish excretion rates remain constant across the year, but these basic comparisons reveal that fish excretion is relevant to stream nutrient dynamics in watersheds with some level of agricultural nutrient loading. Thus, the net nutrient availability in streams of urbanizing watersheds will be a function both of contributions from the local flora and fauna, increased human inputs (Paul & Meyer, 2001), cascading trophic interactions (Leroux & Loreau, 2010), as well as in-stream processes and stoichiometry (Mulholland *et al.*, 2008).

Our approach estimates fish nutrient excretion as a function of abundance and static species-specific estimates of body size and trophic guide – previous meta-analyses have found that these three factors explain the vast majority of variability in excretion (Sereda *et al.*, 2008; Sereda & Hudson, 2011). However, it is important to note that a range of other factors undoubtedly contribute to nutrient excretion such as temperature, prey stoichiometry, consumption rates, and life stage (Moody *et al.*, 2015). In addition, our work highlights the potential importance of nonnative species in contributing to ecosystem processes. However, those same nonnative species may negatively impact native species through various mechanisms (Cucherousset & Olden, 2011). Thus, rather than provide specific conservation targets for stream ecosystems, our study illustrates the fundamental, yet underappreciated, linkages between community assemblages of mixed species origins and resistance of ecosystem processes.

The relationship between species sensitivities and their ecosystem effects will control the resistance of natural systems (Kremen, 2005; Larsen *et al.*, 2005; Zavaleta *et al.*, 2009). The emerging literature on this subject is intriguing – in most cases, it appears that the ecosystem consequences of biodiversity loss are worse than expected with random extirpation based on simulations (Solan *et al.*, 2004; McIntyre *et al.*, 2007), observational studies (Kremen, 2005; Larsen *et al.*, 2005), and experiments (Zavaleta & Hulvey, 2004; Selmants *et al.*, 2012). By contrast, our research for freshwater environments indicate that empirically predicted ecosystem consequences of biodiversity loss can be smaller than expected based on random extirpation (Schlapfer *et al.*, 2005). In our case, this difference may be because small freshwater fish species are generally more sensitive than large fishes to anthropogenic land-use change whereas for other systems and processes large-bodied species contribute the most to ecosystem processes and

are the most sensitive (Larsen *et al.*, 2005, 2008). Thus, different drivers of environmental change and ecosystem processes may have different disassembly rules and species responses (Solan *et al.*, 2004; Bunker *et al.*, 2005; McIntyre *et al.*, 2007; Zavaleta *et al.*, 2009).

A key challenge to illuminating the resilience of earth's systems is the integration of understanding of environmental degradation, biodiversity change, and ecosystem processes across large spatial scales. Through linking biological and environmental data for freshwater ecosystems across the USA, our study discovered that ecosystem processes are sensitive to increased anthropogenic degradation and that this sensitivity varies across space, but that biotic communities provide multiple pathways for resistance. Given these ecological complexities, a precautionary approach would be to maintain connectivity and full assemblages of biodiversity to support the resistance of ecosystems to diverse human stressors.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Supplementary results, including the results of nitrogen excretion analyses.

Figure S1 Histograms of site characteristics for the 8100 sites.

Figure S2 Histogram of pseudo R^2 (McFadden's) for species-specific negative binomial regression models—each count is a different species.

Figure S3 Quantitative predictions of aggregate fish excretion of N across the contiguous United States.

Figure S4 Disassembly rules of fish communities.

Figure S5 The relationship between maximum body size (mm, log-scale) and sensitivity to land development.

Figure S6 The relationship between total community P excretion as a function of different variables.

Figure S7 The response of species from different trophic guilds to land development.

Appendix S2 Additional information on data sources, methodological approach, and statistical approach.

Table S1 National fish survey database including the number of survey locations (N) and source (reference or agency providing the data).