Threshold responses of riverine fish communities to land use conversion across regions of the world

Kai Chen1,2 | Julian D. Olden2

1Department of Entomology, Nanjing Agricultural University, Nanjing, Jiangsu, P.R. China
2School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA, USA

Correspondence
Julian D. Olden, School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA 98103, USA.
Email: olden@uw.edu

Funding information
China Scholarship Council, Grant/Award Number: 201806855012; Nanjing Agricultural University; University of Washington

Abstract
The growing human enterprise has sparked greater interest in identifying ecological thresholds in land use conversion beyond which populations or communities demonstrate abrupt nonlinear or substantive change in species composition. Such knowledge remains fundamental to understanding ecosystem resilience to environmental degradation and informing land use planning into the future. Confronting this challenge has been largely limited to inferring thresholds in univariate metrics of species richness and indices of biotic integrity and has largely ignored how land use legacies of the past may shape community responses of today. By leveraging data for 13,069 riverine sites from temperate, subtropical, and boreal climate zones on four continents, we characterize patterns of community change along diverse gradients of urbanization and agricultural land use, and identity threshold values beyond which significant alterations in species composition exists. Our results demonstrate the apparent universality by which freshwater fish communities are sensitive to even low levels of watershed urbanization (range of threshold values: 1%–12%), but consistently higher (and more variable) levels of agricultural development (2%–37%). We demonstrated that fish community compositional thresholds occurred, in general, at lower levels of watershed urbanization and agriculture when compared to threshold responses in species richness. This supports the notion that aggregated taxon-specific responses may better reflect the complexity of assemblage responses to land use development. We further revealed that the ghost of land use past plays an important role in moderating how current-day fish communities respond to land use intensification. Subbasins of the United States experiencing greater rates of past land use change demonstrated higher current-day thresholds. Threshold responses of community composition, such as those identified in our study, illustrate the need for globally coordinated efforts to prioritize country-specific management and policy initiatives that ensure that freshwater fish diversity is not inevitably lost in the future.

Keywords
agriculture, composition change, conservation, global scale, legacies, urbanization
1 | INTRODUCTION

Human societies rely on land for food, energy, and inhabitance; thus, it comes at little surprise that land use conversion remains a primary driver of biodiversity loss and degradation of ecosystem services (Ellis et al., 2013; Foley et al., 2005; Newbold et al., 2015). Mounting evidence supports the fact that biological communities are undergoing dramatic reassembly in response to agricultural expansion, urbanization, deforestation, and an array of other human activities (Zavaleta et al., 2009). Changes in species composition and not necessarily systematic reductions in local-scale species richness are becoming increasingly recognized (Dornelas et al., 2014; Gonzalez et al., 2016), resulting in ecosystem impacts manifested across large spatial scales (Elmqvist et al., 2003; Moore & Olden, 2017). Human population and exploitation of land resources are expected to only increase in the future (Popp et al., 2017), suggesting that threats to biodiversity will continue to persist (Leclere et al., 2018).

Scientists remain interested in identifying ecological thresholds that define points at which populations or communities demonstrate abrupt nonlinear or substantive change in relation to environmental degradation (Barnosky et al., 2012; Folke et al., 2004; Groffman et al., 2006). Although the practical utility of applying ecological thresholds to conservation decision-making remains a topic of debate (Johnson, 2013), such thresholds can help recognize and then impose limits on levels of land use degradation beyond which substantial impacts are expected. For example, the identification of ecological thresholds at the scale of continents or countries is critical to inform national policies and regulatory frameworks that integrate land use planning into post-2020 strategic goals for the Convention on Biological Diversity (Convention on Biological Diversity, 2011; Mace et al., 2018). As such, testing for the existence and consistency of possible threshold responses of species communities to land use change remains paramount to better ensure the future resilience of ecosystems (Burdon, McIntosh, & Harding, 2013; Carreño-Rocabado et al., 2016).

Land use conversion is a pervasive threat to freshwater ecosystems that compromises water quality, increases water temperature, and alters hydrologic regimes and physical habitat (Reid et al., 2019; Tickner et al., 2020). Changes in land use have demonstrable effects on fish composition and diversity (Booth, Roy, Smith, & Capps, 2016; Dala-Corte et al., 2016; Giam, Olden, & Simberloff, 2018; Utz et al., 2016) that vary by the type of land use modification (Allan, 2004; Paul & Meyer, 2001; Titeux et al., 2016). Although not universal, studies suggest that fish species persistence is more sensitive to changes associated with urbanization compared to agriculture (Trautwein, Schinegger, & Schmutz, 2012; Utz, Hilderbrand, & Raesly, 2010). Projected human population growth and associated changes in land use practices in the future is expected to further threaten freshwater fishes and may fundamentally modify the functioning of freshwater ecosystems (Januchowski-Hartley et al., 2016; Martinuzzi et al., 2014; Radinger et al., 2017).

Evidence for threshold responses of riverine fish communities to land use change remain primarily limited to catchment-level scales (Paul & Meyer, 2001); whereas investigations at larger biogeographic scales are scarce (Clapcott et al., 2012; Daniel et al., 2015; Feld, 2013). Catchment studies have reported threshold values ranging up to 50% agricultural land use, beyond which fundamental shifts in fish community structure and biodiversity (e.g., species richness and index of biotic integrity) were observed (e.g., Allan, 2004; Feld, 2013; Kovalenko et al., 2014; Zhang et al., 2019). Threshold responses of fish community structure to urban land use appear less variable, and generally occur at lower levels ranging from 5% to 25% (e.g., Clapcott, Young, Goodwin, & Leathwick, 2010; Dahm et al., 2013; King, Baker, Kazyak, & Weller, 2011; Lisi et al., 2018). Compositional shifts in fish communities that occur across gradients of land use change may ultimately compromise ecosystem functioning (Moore & Olden, 2017).

Given heterogeneous patterns in the intensity and spatial extent of land use practices across the world, a systematic understanding of broad-scale ecological thresholds has been identified as a critical conservation challenge (Booth et al., 2016; Sutherland et al., 2009). Confronting this challenge in fresh waters has proven difficult for three main reasons. First, the physical complexities of riverine ecosystems over both time and space often result in many contingencies that limit the identification and prediction of nonlinear dynamics (Dodds, Clements, Gido, Hilderbrand, & King, 2010). Second, community threshold responses have been almost exclusively inferred from patterns in aggregate univariate metrics (e.g., fish species richness) and multimetric indices of biotic integrity; both of which may provide little insight into species composition change and turnover (Olden, Joy, & Death, 2006). These approaches have been shown to be relatively insensitive to synchronous threshold declines of numerous individual taxa, and thus underestimate nonlinearities in community responses (King et al., 2011). Third, land use legacies of the past are often important drivers of current ecosystem structure and function (Harding, Benfield, Bolstad, Helfman, & Jones, 1998; Perring et al., 2016). However, addressing thresholds related to land use legacies has received little consideration (Ziter, Graves, & Turner, 2017), and it remains unclear whether, and if so how, past land use conversion influences current threshold responses of fish assemblages (Foster et al., 2003; Utz et al., 2016).

Exploring patterns in fish community reassembly along gradients of land use change will enhance our understanding of the vulnerability of freshwater ecosystems to land degradation, thus informing future conservation and management efforts (Foster et al., 2003; Hilderbrand, Utz, Stranko, & Raesly, 2010). Here we provide the first test for threshold responses of freshwater fish communities to land use conversion for regions across the world. By examining a database with many hundreds of fish species from thousands of streams and rivers located in eight different regions (countries) and four continents, we characterize fish community composition changes along diverse gradients of urbanization and agricultural land use, and identity threshold values beyond which
rapid alterations in species composition exists. An analysis of multivariate aggregation of taxon-specific abundance responses is performed to better reflect the complexity of fish assemblage responses to land use development. We compare community composition thresholds to those describing univariate responses in fish species richness to land use conversion, to elucidate whether observed nonlinear changes are a result of species turnover or the loss of species. Lastly, we investigate multidecadal land use trends for the United States to evaluate whether past land use practices (i.e., land use legacies) relate to current threshold responses of fish communities. Our expectations are as follows: lower and more geographically consistency threshold responses of fish community composition to increasing urban land compared to agricultural land; lower threshold values for community compositional change compared to responses in fish species richness; and river basins with greater rates of past urbanization and agricultural conversion demonstrate higher current-day threshold values because more sensitive fish species have already been lost or reduced in abundance. By addressing these specific objectives, our study seeks to investigate the potential universality by which freshwater fish communities have fundamentally changed to increasing intensity and spatial extent of land practices across biogeographic regions reflecting temperate, subtropical, and boreal climates.

2 | MATERIALS AND METHODS

2.1 | Fish community data

We compiled a comprehensive fish database of >18,500 survey sites from streams and rivers in eight regions: Australia (southeastern Queensland, SEQ), Belgium (Flanders), France, New Zealand, South Korea, Sweden, United Kingdom (England), and the contiguous United States (Figure 1). Fish community surveys were performed by natural resource and environmental agencies, federal government agencies, and university researchers (Table S1), and in all cases were designed to ensure an accurate characterization of species occurrence and abundance for the entire fish assemblage at each locale. The large majority of surveys were part of regional- or national-scale monitoring efforts; consequently, the compiled dataset is considered synoptic in scope and broadly representative of diverse riverine habitats. Fish sampling methods for all sources included standardized backpack or boat electrofishing, and in more rare occasions involved kick nets, cast nets, and seine-netting of defined length. However, sampling methods showed generally marked consistency within each region, and were selected specifically to be the most effective given the targeted habitat (more details provided in the Supporting Information). To ensure comparability across fish communities, relative fish abundance was computed to reduce the effects of different,
but always comprehensive, sampling efforts among sites. As low presence limits ability for model developments and validations, we excluded species with less than five occurrences in each region from further analysis according to Wagenhoff, Clapcott, Lau, Lewis, and Young (2017). We subsampled the dataset to include only a maximum of three sites (Tables S1 and S2; Figures S1 and S2) in each subwatershed (i.e., HydroBASINS level-12) in which the year of the survey was closest to (but not after) 2010 representing the timing of land use survey (see details below). This subsampling approach minimized mismatches between the timing of fish and land use surveys and avoided unbalanced spatial coverage of data (Tables S1). The final community database included 583 fish species occurring in 13,069 sites (Figure 1; Table S1). The survey sites contained a median of six (range: 1–51) species and 2.1% (range: 0.4%–5.4%) relative abundance per site (Table S3; Figure S3).

2.2 Land use and environmental data

Numerous studies report that land use estimated at the subwatershed scale often better predicts biotic condition of rivers when compared to larger, catchment scales (e.g., Schiff & Benoit, 2007; Sheldon et al., 2012). Therefore, we delineated the contributing watershed for each site according to level-12 subwatersheds from HydroBASINS, and the subwatershed area averaged 149.4 ± 54.4 km² (±SD; Table S4; Figure S4). HydroBASINS layers were derived from World Wildlife Fund’s HydroSHEDS data (15 arc-seconds [-500 m] resolution; Lehner & Grill, 2013), providing standardized hydroenvironmental information across the world. For each site, we calculated the percent area of the contributing subwatershed in urban (summed across urban, built-up, and developed land categories) and agricultural land (summed across crop and agricultural land categories), according to statistically downscaled land use classes at 1 km pixel resolution from the MODIS Land Cover Type Product referenced to 2010 (Li et al., 2017). Urban and agricultural surface area ranged from 0% to 100% of the subwatershed, with a mean of 3.1% (SD 10.9%) urban and 34.5% (SD 37.1%) agriculture across the survey sites (Figure 1; Table S4). Correlations between percent urban and percent agricultural land was generally low across all sites for each region (Pearson correlation coefficients: Australia [SEQ] r = −.23, Belgium [Flanders] r = −.74, France r = −.37, New Zealand r = .07, South Korea r = −.01, Sweden r = .31, United Kingdom [England] r = −10, United States r = −.09).

Using HydroBASINS, we also calculated the following environmental variables for each site: long-term (1950–2000) average annual air temperature (°C) according to WorldClim (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005), average elevation within subwatershed (m), modeled long-term average annual “naturalized” discharge (m³/s) according to the global integrated water model WaterGap v2.2 (Döll, Kaspar, & Lehner, 2003), and degree of flow regulation (%) calculated as the percent of the total annual discharge volume of the reach that can be withheld by all upstream reservoirs according to HydroSHEDS and Global Reservoir and Dam Database (https://www.hydrosheds.org/page/hydroatlas; Linke et al., 2019). The sites varied in long-term average annual air temperature (9.6 ± 4.0°C), average elevation within subwatershed (453.0 ± 491.0 m), modeled long-term average annual “naturalized” discharge (38.0 ± 54.4 m³/s), and degree of flow regulation at the subwatershed scale (15.4 ± 162.5%); thus representing a broad range of riverine types and sizes in temperate, subtropical, and boreal climate zones (Figure 1; Table S4; Figure S4). These variables represent well-known surrogates for habitat size and productivity that are predictive of fish community composition (Jackson, Peres-Neto, & Olden, 2001) and commonly covary with land use patterns (Kominoski et al., 2018; Moore & Olden, 2017; Radiger et al., 2016).

2.3 Historical land use change in the United States

Trends in land use were quantified for the conterminous United States at 250 m resolution between 1950 and 2005 according to the National Land Cover Dataset (Sohl et al., 2014, 2016). These modeling efforts focused on forecasting anthropogenic land use classes associated with urbanization and agricultural practices using spatially explicit data available for the modeled time period. First, percent urban (urban, built-up, and/or developed lands categories) and agricultural (crop and/or agricultural lands categories) areal coverage were calculated at 5-year intervals (i.e., 1950, 1955, 1960, ... and 2005) for each site at the subwatershed scale containing fish survey sites (n = 5,686 subwatersheds). Second, land use cover for each of the 13 subbasins (according to HydroBASINS level-3: Figure S5) containing at least 50 fish survey sites was calculated as the average, area-weighted land use percent across all subwatersheds. Third, trends in land use for each subbasin was estimated by regressing percent urban and percent agriculture (separately) against year (i.e., 1950, 1955, 1960, ... and 2005) using general linear modeling (GLM). The model slope (β1) was used as a measure of the rate of past land use change for each sub-basin, where positive values indicate an increase and negative values indicate a decrease in either urban or agriculture coverage over time. By examining land use change over half a century this analysis reflects a contemporary period of significant environmental alteration over which fish communities have demonstrated marked change (e.g., Kominoski et al., 2018; Martinuzzi et al., 2014).

2.4 Quantifying land use thresholds in fish community composition

Gradient forest (GF) was used to test for threshold responses of fish composition change to percent urban and percent agricultural land use in each region. GF is a highly flexible, nonparametric and nonlinear method for exploring the magnitude and pattern of change in species composition along environmental gradients (Ellis, Smith, & Pitcher, 2012; Pitcher et al., 2012; Stephenson et al., 2018), while simultaneously accounting for other potential explanatory variables in a multivariate manner. GF is an ensemble of random forest (RF) models (Breiman, 2001), where each regression tree uses a recursive
Species richness

influence of multicollinearity (Ellis et al., 2012; Roubeix et al., 2017).
strained permutations with correlation threshold of 0.5 to reduce the
generated 1,000 trees for each RF model and used default con
occurs in relation to increasing urban and agricultural land use. We
where the first substantial change in fish community composition
ized ratio of split density identified
peak value that exceeded the 95% confidence interval of all standard
ing the highest manifestation of a threshold (Pitcher et al., 2012). All
curve were identified using the R package “pracma” (Borchers, 2019).
tified the most influential (first) split value (when existing) for percent
urban and percent agriculture for each ensemble tree of the RF, thus
providing an estimate where the greatest substantial change in fish
richness occurs in relation to each land use gradient. The average val-
ues of the first splits for percent urban and percent agriculture accord-
ing to the 5,000-tree RF model were considered the most supportive
land use threshold for fish species richness.

2.6 Influence of land use legacies on fish community composition in the United States

We quantified associations between past trends in urban and ag-
icultural conversion and current threshold responses of fish com-
munities to land use change. First, we developed GF models (same
model structure as above) for each subbasin of the United States to
estimate thresholds values of urban and agricultural land at which
fish community composition changes (Figures S6 and S7). Second,
we examined the relationship between the rate of past land use
change for each subbasin (see Section 2.3) and GF-estimated com-

All statistical and spatial analyses were undertaken in R ver-
-3.5.1 (R Core Team, 2016) and included the packages “mgcv”
(Wood, 2017), “nlme” (Pinheiro et al., 2017), and a number of addi-
tional data manipulation functions.

3 RESULTS

Fish communities demonstrated clear evidence for threshold or
abrupt nonlinear responses to increasing land use alteration across
the world (Table 1). Estimates of threshold values along the gradient

<table>
<thead>
<tr>
<th>Community composition</th>
<th>Species richness</th>
</tr>
</thead>
<tbody>
<tr>
<td>% urban</td>
<td>% agriculture</td>
</tr>
<tr>
<td>Australia (SEQ)</td>
<td>10.9</td>
</tr>
<tr>
<td>Belgium (Flanders)</td>
<td>11.7</td>
</tr>
<tr>
<td>France</td>
<td>11.3</td>
</tr>
<tr>
<td>New Zealand</td>
<td>4.1</td>
</tr>
<tr>
<td>South Korea</td>
<td>4.4</td>
</tr>
<tr>
<td>Sweden</td>
<td>1.8</td>
</tr>
<tr>
<td>United Kingdom (England)</td>
<td>3.7</td>
</tr>
<tr>
<td>United States</td>
<td>10.9</td>
</tr>
</tbody>
</table>

Abbreviation: SEQ, southeastern Queensland.
of agricultural conversion (2%–37%) were much more variable between regions compared to subwatershed urbanization (1%–12%). Fish community composition in Sweden demonstrated the highest sensitivity to urban land development (threshold = 1.8%), whereas the lowest sensitivity was evident in France (11.3%) and Belgium (Flanders; 11.7%; Figure 2). Thresholds of community composition change in response to subwatershed agriculture were the lowest for New Zealand (2.5%) and South Korea (3.9%), and highest for the United States (31.1%) and United Kingdom (England: 36.4%; Figure 3). With the exception of New Zealand, threshold estimates of fish composition change were comparable or lower for subwatershed in urban versus agricultural use (Table 1). The relative contributions of urban and agricultural land use variables were consistently high in the GF models (Figure 4).

Threshold responses of fish species richness in response to subwatershed urbanization and agriculture were often higher or comparable to threshold values identified for fish community composition (Table 1). Across regions, geographic variability in threshold responses of species richness ranged between 2%–19% and 12%–73% in the subwatershed urbanization and agriculture, respectively. The largest differences were observed for South Korea where richness thresholds were 2.5 times as large as the community composition threshold for percent subwatershed urbanization. Similarly, with respect to agricultural land use, richness thresholds exceeded community composition thresholds by 8–9 times for Belgium (Flanders), New Zealand, and South Korea. The one exception was the United States, where community composition and richness thresholds were similar for urban and agricultural land use (Table 1).

**FIGURE 2** Compositional change in fish assemblages across an urbanization gradient as revealed by a gradient forest analysis. In each plot, gray bars indicate the binned raw importance of splits from random forest models; the black line is the raw importance density computed by kernel density estimation of split points weighted by importance; the red line is the density the observed percent urban values; the blue line is the estimated importance or magnitude of compositional turnover change at any given percent urban value (calculated as the ratio of the density of split importance to the density of data values along the percent urban gradient); and the horizontal dashed line indicates where the aforementioned ratio is 1. Evidence for threshold responses occur when the standardized ratio of density >1, indicating relatively large compositional change at a value of percent urban land use. 
The extent of subbasin urban land use has shown consistent increases over the last half century in the United States (GLM slope $\beta_1$: mean = 0.05, range 0.01–0.15; Figure 5a), whereas agricultural land use demonstrated more variable trends over this same time period (GLM slope $\beta_1$: mean = −0.06, range −0.01 to 0.02; Figure 5b). Subbasins with the highest levels of current urban and agricultural land tend to show the greatest rates of past land conversion. Current threshold responses of fish community composition demonstrated strong associations with legacies of past land use change. Thresholds were greater for subbasins experiencing faster rates of land conversion to either urban, albeit with considerable variation (GAM adj. $R^2 = .16$, $p < .001$; Figure 5c) or agricultural use (GAM adj. $R^2 = .13$, $p = .02$; Figure 5d).

**FIGURE 3** Compositional change in fish assemblages across an agricultural gradient as revealed by a gradient forest analysis. In each plot, gray bars indicate the binned raw importance of splits from random forest models; the black line is the raw importance density computed by kernel density estimation of split points weighted by importance; the red line is the density of the observed percent agriculture values; the blue line is the estimated importance or magnitude of compositional turnover change at any given percent agriculture value (calculated as the ratio of the density of split importance to the density of data values along the percent agriculture gradient); and the horizontal dashed line indicates where the aforementioned ratio is 1. Evidence for threshold responses occur when the standardized ratio of density >1, indicating relatively large compositional change at a value of percent agricultural land use.
Figure 4: Overall $R^2$ weighted importance of subwatershed urban land use (%), agricultural land use (%), subwatershed area (km$^2$), average elevation within subwatershed (m), long-term average annual air temperature (°C), modeled long-term average annual "naturalized" discharge (m$^3$/s), degree of flow regulation (%), and HydroBASINS level-3 subbasin identity in the gradient forest model for each region.
regions of the world, marked changes in fish community composition were found in streams and rivers characterized by subwatershed urbanization ranging between 1% and 12% and agriculture ranging between 2% and 37%. We demonstrated that fish community compositional thresholds typically occurred at lower levels of subwatershed urbanization and agriculture when compared to species richness thresholds. This supports the notion that aggregating taxon-specific responses may better reflect the complexity of assemblage responses to land use development (Socolar, Gilroy, Kunin, & Edwards, 2016), especially in freshwater ecosystems (King & Baker, 2010). We further provide evidence for associations between land use legacies and current threshold responses of fish community composition, thus indicating that the ghost of land use past may play an important role in moderating the sensitivity of present-day fish communities.

Fish communities demonstrated marked changes in species composition at levels of subwatershed urbanization and agriculture much lower than that seen for changes in species richness. These results suggest that constancy in local species richness (alpha diversity) can mask dramatic compositional turnover in species communities (beta-diversity) across gradients of land use change (McGill, Domelas, Gotelli, & Magurran, 2015; Socolar et al., 2016). Here threshold responses of fish community composition are driven by differential sensitivity of species to land use change, caused by marked changes in abundance but not necessarily associated with local species extirpation leading to reduced alpha diversity (Clavel, Julliard, & Devictor, 2011; Moore & Olden, 2017; Mori, Furukawa, & Sasaki, 2013). These shifts in community structure result from sensitive specialist, often native fish species being lost or reduced rapidly from river systems experiencing low land use change, whereas more tolerant generalists, often nonnative species colonize or thrive under these degraded conditions (Dala-Corte et al., 2016; Walsh et al., 2005). Indeed, this gradual homogenization of biological communities in response to land use conversion is prevalent across the world (Olden, Comte, & Giam, 2018). Interestingly, similar threshold values existed for community composition and richness in the United States, a country experiencing high magnitudes of fish faunal homogenization and thus where the majority of highly sensitive species have already been lost (Villéger, Blanchet, Beauchard, Oberdorff, & Brosse, 2011). In summary, our results support the growing notion that human activities do not randomly reshuffle biodiversity; instead communities have reassembled according to varying rates of species losses and gains (Dornelas et al., 2014), and that these changes may manifest as abrupt threshold responses to environmental degradation.

Threshold changes of fish community composition to land use varied geographically but were generally more consistent across countries in relation to subwatershed urbanization versus agricultural use.
The urban stream syndrome highlights broad commonalities in community responses to impervious surfaces in urbanized watersheds (Booth et al., 2016), despite regional differences in the magnitude of loss of fish and other aquatic organisms (e.g., Brown et al., 2009; Utz, Hilderbrand, & Boward, 2009; Utz et al., 2010). By contrast, agricultural practices often entail a more diverse array of perturbations on the landscape, ranging from habitat modification due to different varieties of crops and variable application of fertilizers and pesticides, and therefore effects on biota may similarly vary (Watson, Luck, Spooner, & Watson, 2014). We found that fish community change was much more variable in relation to agriculture intensity; a pattern supported by regional-based studies (e.g., Feld, 2013). Geographic variability in threshold responses of fish communities is likely related to differences in the magnitude and rate of land use change. For example, in regions where agricultural land use conversion has a long history, impacts on riverine systems are generally more severe (Weijters, Janse, Alkemade, & Verhoeven, 2009). In support of this, we found threshold values for fish community composition change were quite larger for England (but not France) with a considerably greater period of significant land use (Ellis et al., 2013) compared to other regions examined in this study.

Our results suggest strong consistencies in the legacy effects of past land use change on riverine fish biodiversity (Harding et al., 1998; Wenger, Peterson, Freeman, Freeman, & Homans, 2008), despite inherent difficulties to detect signals of community change subjected to the incremental land use changes over time (Hughes, Linares, Dakos, van de Leemput, & van Nes, 2013). Threshold responses in fish composition across the United States were strongly associated to past trends in land use conversion, whereby river basins exhibiting more extreme urbanization and agricultural rates over the last half century demonstrated higher threshold values beyond which marked compositional change occurred. This finding suggests that more sensitive and/or specialist species have already been lost or reduced in population abundance in locations experiencing a longer history of land use change (Watson, Luck, Spooner, & Watson, 2014), resulting in communities characterized by relatively more tolerant and generalists (e.g., non-native) species (Blanchet et al., 2009; Essl et al., 2015). Such species often have non-native origins (Moore & Olden, 2017).

Abrupt shifts in the composition of fish communities are the result of species-level responses to land conversion (Rhodes et al., 2008; Zhang et al., 2019). We found that fish communities in disparate biogeographic regions of the world showed marked consistency in patterns of species turnover that occurred at comparable or lower threshold levels of urbanization (1–10 times lower; Table 1) compared to agricultural land use. One exception to this association was New Zealand, where fish community composition shifted rapidly to much lower threshold levels of agricultural (>1.5 times) compared to urban land use. Agricultural intensification is a well-recognized cause of substantial loss of freshwater fish diversity in New Zealand (Joy, Foote, McNie, & Piria, 2019). This is driven, in part, by the fact that the native fish fauna is unique from other regions/countries in lacking both planktivorous and herbivorous species, and thus is particularly prone to agricultural-induced alteration to habitat quality and primary productivity. Meanwhile, New Zealand generally has the shortest legacy of widespread agricultural land conversion among nearly all study regions (Ellis et al., 2013).

Despite providing large-scale evidence for fish community thresholds to land use change, several limitations must be acknowledged. First, the integration of disparate datasets from multiple sources offers powerful opportunities to conduct macroecological investigations, yet it necessarily introduces challenges of sampling bias. We minimized potential biases through careful geographical, environmental, and temporal filtering of fish composition data (see Supporting Information), yet residual inconsistencies among datasets may still exist. Second, the mechanisms by which urban and agricultural land use practices affect fish communities are inherently complex, ranging from modified discharge and hydrological connectivity, degraded physical habitat, deteriorated water quality, and compromised pathways of cross-ecosystem energy and matter exchange (Allan, 2004; Martinuzzi et al., 2014; Radinger et al., 2016). Our study sought to test for the existence, but not likely cause, of threshold responses of fish communities to land use change. Third, fish species possess biological traits that make them more or less susceptible to changing land use conditions; for example, tolerant species are often generalists with wide environmental requirements, broad diets, and high dispersal abilities, whereas sensitive species tend to display the opposite. Therefore, geographic variability in estimates of threshold values reported here is likely influenced by differences in the taxonomic, and hence functional composition, of the regional species pools. We see considerable value in deploying traits-based approaches to reveal insights into the possible mechanisms responsible for spatially varying thresholds (Olden et al., 2010).

Threshold responses of community composition, such as those identified by our study, can be used to help prioritize management and conservation strategies in regions facing substantial changes in land use (Luck, 2005). Determining the identity and value of thresholds is key to understand changes in ecological processes (e.g., shifts in ecosystem state) and to determine conservation actions that seek to ensure that such thresholds are not exceeded (Hughes, Carpenter, Rockström, Scheffer, & Walker, 2013; Lindenmayer & Luck, 2005). For example, the identification of ecological impact thresholds allows for planning and proactive management of communities before rapid compositional changes are realized and prior to a point where a system loses vital ecosystem functions (Hilderbrand et al., 2010; Moore & Olden, 2017). Similarly, ecological thresholds can be used to prioritize restoration and assess recovery in systems where particular stressors have been reduced or eliminated (Clements, Vieira, & Sonderegger, 2010). Together, threshold values such as those reported here support the design of adaptive conservation goals seeking to protect or restore freshwater fish biodiversity facing
continued changes in land use. Our study illustrates the need for a globally coordinated effort to prioritize country-specific management and policy initiatives that seek to prevent or minimize the impacts of land use change in freshwater ecosystems (Gonzalez et al., 2016; Januchowski-Hartley et al., 2016; Martinuzzi et al., 2014). This is particularly necessary to address current national policy goals and targets such as post-2020 biodiversity goals associated with the Convention on Biological Diversity and the Sustainable Development Goals.

ACKNOWLEDGEMENTS
We acknowledge the contribution of all the researchers who collected, maintained, and shared the large datasets that our study is founded upon; these individuals recognized the importance of data sharing to tackle macro-ecological challenges in freshwater ecology. K.C. was supported by the China Scholarship Council (grant no. 201806855012) and Nanjing Agricultural University, and J.D.O. was supported by the H. Mason Keeler Endowed Professorship from the School of Aquatic and Fishery Sciences, University of Washington. We thank Ryan Hill (Pacific Ecological Systems Division, US EPA) for R scripts suggestions, Lise Comte for help with data cleaning, and we thank the following individuals recognized the importance of data collected, maintained, and shared the large datasets that our study is founded upon. These individuals recognized the importance of data sharing to tackle macro-ecological challenges in freshwater ecology. K.C. was supported by the China Scholarship Council (grant no. 201806855012) and Nanjing Agricultural University, and J.D.O. was supported by the H. Mason Keeler Endowed Professorship from the School of Aquatic and Fishery Sciences, University of Washington. We thank Ryan Hill (Pacific Ecological Systems Division, US EPA) for R scripts suggestions, Lise Comte for help with data cleaning, and three anonymous reviewers whose feedback greatly improved the final paper.

AUTHOR CONTRIBUTION
J.D.O. conceived and designed the study, K.C. performed the analysis and prepared figures and/or tables, and K.C. and J.D.O. jointly wrote and edited the paper.

DATA AVAILABILITY STATEMENT
The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID
Julian D. Olden https://orcid.org/0000-0003-2143-1187

REFERENCES


