Measuring ecosystem degradation through half a century of fish species introductions and extirpations in a large isolated lake

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ABSTRACT

The introduction of exotic species and the extirpation of native species that occurred during the past two centuries have strongly modified the structure of most plant and animal assemblages across the globe. Such a biotic change is particularly marked in isolated environments such as islands or isolated lakes. Most studies reported drastic changes between before and after human disturbances, but the dynamics of change in assemblage structure through the invasion and extirpation processes are rarely reported. Here we measured the aquatic ecosystem degradation through exotic species introduction and native species extirpation experienced by Lake Erhai (China) during the last 50 years using structural, functional and taxonomic distinctness biodiversity indices. Structural diversity (species richness) did not varied monotonically along the temporal gradient, due to an opposite trend between exotic species increase and a concomitant decline of native species richness. Functional diversity displayed unclear ascending trends driven by the introduction of exotic species having distinct functional traits than natives. Taxonomic distinctness indices exhibited an increase of the average taxonomic distinctness (Δ^+), but a decrease of the variation in taxonomic distinctness (Λ^+) through time. Structural, functional and distinctness indices providing complementary information on ecosystem degradation, we here proposed a new multifaceted degradation index integrating these three facets of biodiversity. Such an index provided an accurate representation of the faunistic changes experienced by Lake Erhai and might constitute a comprehensive way to measure ecosystem degradation through exotic fish species introductions and native fish species extirpations.

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1. Introduction

The freshwater biodiversity is currently experiencing an unprecedented worldwide decline (Dudgeon et al., 2006; Olson et al., 2002; Poff, 2014). This decline is particularly marked in lakes that suffer from multiple human disturbances such as habitat fragmentation and loss, hydrologic alteration, climate change, overexploitation and pollution that are responsible from a marked extinction trend (Dudgeon et al., 2006; Sala et al., 2000). In addition to extinctions, human-induced exotic species introductions are also listed as one of the most detrimental anthropogenic activities (Dudgeon et al., 2006; Sala et al., 2000). Exotic species can threaten aquatic biodiversity and influence ecological process (Clarkson et al., 2005; Jeschke et al., 2014; Volta et al., 2013). There is thereby a pressing need to manage the use of biodiversity and resources,

and to conserve and restore ecological processes. This necessitates developing appropriate metrics to measure and manage biological diversity and its changes through extinctions and invasions.

A wide variety of indices are currently available in biodiversity assessment (Gallardo et al., 2011; Lyashevska and Farnsworth, 2012; Purvis and Hector, 2000). These indices can be classified into three major categories: structural/compositional diversity metrics, taxonomic distinctness metrics, and functional diversity metrics (Lyashevska and Farnsworth, 2012). The most commonly used metrics are structural diversity indices, such as richness, Shannon index, Pielou's Eveness, or Simpson index. All these indices take into account species richness and/or evenness, but they are facing criticism for uncertain ecological interpretation, excessive data requirement, insensitiveness to disturbance, and oversimplification (Brosse et al., 2011; von Euler and Svensson, 2001).

Functional diversity is defined as the diversity of functional traits in a community weighted by their abundances (Villéger et al., 2008). Functional diversity indices consider the biological characteristics of the species, i.e., value, range, distribution, and relative

abundance of the functional traits in a community. It was efficiently used to detect functional changes in fish assemblages across Europe due to species introductions and extirpations (Villéger et al., 2014). Functional approaches are nevertheless limited by the necessity to run precise measures on living or well-conserved specimens, which is rarely feasible after the extinction of endemic species (Cordlandwehr et al., 2013). Moreover, the functional approaches are also limited by their inability to detect anthropic disturbances when the extirpated species are replaced by functional similar non-native species (Wellnitz and Poff, 2001).

The taxonomic distinctness indices are a measurement of the taxonomic relatedness of species. They stipulate that for a given species richness, an assemblage including species from different families is more diverse than an assemblage with the same number of species from one family (Warwick and Clarke, 1998). These indices are widely used in biodiversity assessment due to their independence to sampling methods (e.g., sample size and sampling effort) and natural habitat type or complexity (Clarke and Warwick, 1999; Warwick and Clarke, 1998; Xu et al., 2012). Testing the sensitivity of taxonomic distinctness indices in discriminating anthropogenic impacts was the subject of a number of studies, but they yielded inconsistent results. Their sensitivity to human disturbances was shown in some studies (Campbell et al., 2011; Milosevic et al., 2012; Miranda et al., 2005), but not in others (Abellan et al., 2006; Costa et al., 2010; Leira et al., 2009).

Structural, functional, and distinctness indices reveal independent facets of biodiversity, and are hence complementary (Gallardo et al., 2011). Nevertheless, few studies have been devoted to a comprehensive consideration of those facets (Lyashevska and Farnsworth, 2012; Miranda et al., 2005; Strecker et al., 2011). The purpose of the present study is to analyze the response of these three facets through a gradient of disturbance strength in Lake Erhai (Yun-Gui Plateau, South China), an isolated lake system subjected to non-native species introduction and native species extirpation processes across a more than 50 years' time frame (from 1960 to 2014). We hence measured the sensitivity of compositional diversity, taxonomic distinctness, and functional diversity indices to the human mediated changes in fish assemblage composition, and evaluated the usefulness of each index as a metric to measure human disturbance estimator. Finally, we proposed a new multifaceted index integrating these three facets of biodiversity to measure the ecosystem degradation through fish species introductions and extirpations across time.

2. Methods

2.1. Study area

Lake Erhai (25°36′–25°58′ N; 100°06′–100°18′ E; 1973.7 m above the sea level) is the second largest freshwater lake from the Yun-Gui Plateau (Yunnan Province, South China; Fig. 1). It covers a surface area of c.a 249.8 km², for a volume of c.a. 25.3×10^8 m³. It is 42 km long, and has an 8.4 km maximum width. Average depth is 10.5 m and maximum depth 20.9 m. This tectonic rift lake is subjected to a subtropical plateau monsoon climate, with mean annual precipitation of 1060 mm, mean annual air temperature of 15 °C (minimum: 8.5 °C; maximum: 20.1 °C), and mean annual evaporation of 1209 mm (Wang and Dou, 1998). It belongs to the upper Mekong River (Lancang-Jiang in Chinese) basin, and its water discharges into the Yangbi Jiang, an upstream tributary of this basin. Fish exchanges between this lake and the Yangbi-Jiang were blocked by a dam constructed in 1960s.

Lake Erhai, like other lakes on the Yun-Gui plateau, has a depaurate indigenous fish diversity with less than 30 species, in contrast to 60–70 species found in shallow-water lakes of the Yangtze River

floodplain (Chu and Chen, 1989; Li, 1982). Lacking predator fishes and having plenty of unoccupied niches have led to a high degree of species endemism found in this lake. Historically, it harbored only 17 native species, 7 of which are endemic. Most of this native fish assemblage comes from two cyprinid genera: *Schizothorax* (4 species) and *Cyprinus* (5 species) (Du and Li, 2001; Li, 1982; Wu and Wang, 1999). These middle-sized fish species are of economic importance, and are thus exploited by local fisheries.

During the past six decades, Lake Erhai has been experiencing drastic changes in fish assemblages that were due to several human disturbances among which over-harvesting, exotic species introductions for aquaculture and eutrophication are the most obvious (Fei et al., 2012; Lin et al., 2013; Wu and Wang, 1999). Aquaculture activity started from the 1960s. Four domestic Chinese carps, i.e., the black carp (*Mylopharyngodon piceus*), the grass carp (*Ctenopharyngodon idella*), the silver carp (*Hypophthalmichthys molitrix*), and the bighead carp (*Aristichthys nobilis*), and the icefish (*Neosalanx taihuensis*) were purposefully introduced for fish farming. The others exotic fishes were introduced as fellow travelers, such as the topmouth gudgeon (*Pseudorasbora parva*), and gobies (*Rhinogobius giurinus*, and *Rhinogobius cliffordpoei*) (Du and Li, 2001; He et al., 2010; Wu and Wang, 1999). Following the establishment of those non-native species and the concomitant decline or extirpation of native species over the past 50 years, the main harvest species of Lake Erhai shifted from the middle-sized native fishes (*Schizothorax taliensis*, *Cyprinus chilia*, and *Cyprinus megalophthalmus*) to the small-sized exotic fishes (*P. parva*, *R. giurinus*, and *R. cliffordpoei*) (Du and Li, 2001; Tang et al., 2013; Wu and Wang, 1999). Currently, 11 out of the 17 native fish species are included in the China Red List of Threatened Species, with 6 listed as critically endangered.

2.2. Data sets

Historical fish assemblages of Lake Erhai as well as their changes through the last 60 years have been well documented in the literature and our data results from an extensive literature survey on the lake fish fauna since the fifties. The main data sources were Ley et al. (1963), Chu and Chen (1989), Chen et al. (1998), Zhou (2000), Du and Li (2001), Lu and Song (2003), Wang et al. (2006), He et al. (2010), Yuan et al. (2010), and Tang et al. (2013). On the basis of these published literature, we grouped data per decades giving rise to seven time periods: 1950s (1950–1959); 1960s (1960–1969), 1970s (1970–1979), 1980s (1980–1989), 1990s (1990–1999), 2000s (2000–2009), and 2010s (2010–2014). As sampling methods and efforts varied between periods, we did not consider fish abundance; only the presence or absence of the species during each period was considered, giving rise to a data matrix with 7 time periods and 39 fish species (Table 1).

The functional diversity measure in each period was based on a set of 10 biological and ecological traits related to fish morphology, trophy, life history, and habitat (Table 2). Trait assignments were compiled from the literature (scientific papers, books, and gray literature) and Fishbase (Froese and Pauly, 2014). The raw functional matrix contained continuous and categorical variables. Categorical variables were then transformed into binary variables to make all variables numerical.

2.3. Data analysis

Two taxonomic distinctness metrics were computed: the average taxonomic distinctness (Δ^+) and the variation in taxonomic distinctness (Λ^+). Δ^+ is defined as the average path length between all pairs of species through a Linnean hierarchical taxonomic tree; a sample with only multiple species within a single family will have lower taxonomic distinctness than a sample having multiple
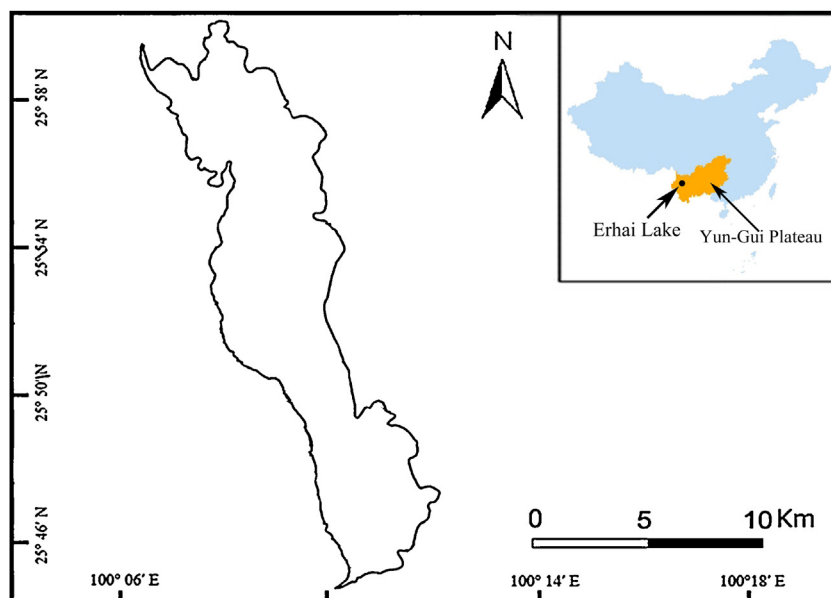
Fig. 1. Geography and location of Lake Erhai in Southwest China.

Table 1
Fish species observed (+) and not observed (−) in Lake Erhai from 1950s to 2010s.

Species	1950s	1960s	1970s	1980s	1990s	2000s	2010s
Schizothorax taliensis[a]	+	+	+	+	−	−	+
Schizothorax yunnanensis[a]	+	+	−	−	−	−	+
Schizothorax lissolabiatus[a]	+	+	−	−	−	−	−
Schizothorax griseus[a]	+	+	−	−	−	−	−
Cyprinus barbatus[a]	+	+	−	−	−	−	−
Cyprinus daliensis[a]	+	+	−	−	−	−	−
Cyprinus megalophthalmus[a]	+	+	+	+	−	−	−
Cyprinus chilia[a]	+	+	+	+	−	−	+
Cyprinus longipeatoralis[a]	+	+	+	+	−	−	+
Poropuntius cogginii[a]	+	+	+	+	−	−	−
Poropuntius exiguus[a]	+	+	−	−	−	−	−
Cyprinus carpio	−	+	+	+	+	+	+
Carassius auratus[a]	+	+	+	+	+	+	+
Mylopharyngodon piceus	−	+	+	+	+	+	+
Ctenopharyngodon idella	−	+	+	+	+	+	+
Hypophthalmichthys molitrix	−	+	+	+	+	+	+
Aristichthys nobilis	−	+	+	+	+	+	+
Megalobrama amblycephala	−	−	+	+	+	+	+
Pseudorasbora parva	−	−	+	+	+	+	+
Rhodeus ocellatus	−	+	+	+	+	+	+
Acheilognathus chankaensis	−	+	+	+	+	+	+
Abbottina rivularis	−	+	+	+	+	+	+
Cyprinus rubrofuscus	−	−	−	−	−	−	+
Hemiculter leucisculus	−	−	−	−	−	+	+
Parabramis pekinensis	−	−	−	−	−	−	+
Misgurnus anguilicaudatus[a]	+	+	+	+	+	+	+
Yunnanilus pleurotaenia[a]	+	+	+	+	+	+	+
Homatula anguilliodes[a]	+	+	+	+	+	+	+
Oryzias sinensis[a]	+	+	+	+	+	+	−
Monopterus albus[a]	+	+	+	+	+	+	+
Micropercops swinhonis	−	+	+	+	+	+	+
Rhinogobius cliffordpopei	−	+	+	+	+	+	+
Rhinogobius giurinus	−	+	+	+	+	+	+
Neosalanx taihuensis	−	−	−	+	+	+	+
Channa argus	−	−	−	−	−	+	+
Gambusia affinis	−	−	−	−	−	−	+
Hypomesus olidus	−	−	−	−	−	−	+
Macropodus ocellatus	−	−	−	−	−	+	+
Pseudobagrus fulvidraco	−	−	−	−	−	−	+

[a] Indicates native species, some extirpated species appears in 2010s due to recent reintroduction.

Table 2
List of the functional traits for fish species from Lake Erhai.

Trait	Type	Units/description
Maximum body length	Continuous	Maximum standard body length (cm)
Body shape	Categorical	Cylindrical, Fusiform, Compressed, Oval, Anguilliform, Dorso-ventraly flattened
Vertical position	Categorical	Littoral habitat/Profundal habitat (pelagic, benthopelagic, demersal)
Trophic guild	Binary	Omnivore, Herbivore, Invertivore, Piscivore, Detritivore, Planktivore
Dietary component	Binary	Plant, Algae, Detritus, Zoobenthos, Zooplankton, Fish/shrimp/egg
Trophic level	Continuous	Trophic position in the food chain
Age at maturation	Continuous	Age at maturation (years)
Length at maturation	Continuous	Length at maturation (cm)
Longevity	Continuous	Maximum potential life span (years)
Growth rate	Continuous	Growth rate (year^{-1})

Table 3
Weights and branch lengths used for calculating average taxonomic distinctness and variation in taxonomic distinctness.

	Taxon	Weight	Branch length
Native	Species	1	20.5
	Genus	1	41
	Subfamily	0.88	59
	Family	1	79.5
	Order	1	100
Exotic	Species	1	21.8
	Genus	1	43.6
	Subfamily	0.59	56.4
	Family	1	78.2
	Order	1	100
Both	Species	1	21.2
	Genus	1	42.4
	Subfamily	0.72	57.6
	Family	1	78.8
	Order	1	100

species from different families. Λ^+ measures variance in pairwise path lengths between each pair of species, reflecting the unevenness of the taxonomic tree for a given sample. The pairwise indices were calculated using the following formulas:

$$\Delta^+ = \frac{\left[\sum\sum_{i<j}w_{ij}\right]}{[S(S-2)/2]}, \quad \Lambda^+ = \frac{\left[\sum\sum_{i<j}(w_{ij} - \Delta^+)^2\right]}{[S(S-1)/2]}$$

where w_{ij} is the weight given to the path length linking species i and j in the hierarchical taxonomic tree, and S is the number of species (Warwick and Clarke, 1995, 1998).

According to Clarke and Warwick's (1999) simple linear scaling, the maximum distance through the tree is set at $\omega = 100$, and the step between each taxonomic level is equal if branch lengths are unweighted. If some groups have defined taxonomic level while others do not, we need to weight the branch lengths. Following Tolimieri and Anderson (2010), the weight is the proportion of species at a given taxonomic level, and the branch length is calculated within the taxonomic tree to that level after weighting. In this case, subfamily was weighted 0.72 because 72% of species were defined at that level. The weights and branch lengths used for calculating taxonomic distinctness are given in Table 3.

Two functional diversity indices were measured to account for functional richness and functional evenness (Villéger et al., 2008). Functional richness was measured using the RaoQ, which is the sum of pairwise distances between species weighted by relative abundance. This index is based on trait-based Euclidean distances between pairs of species. As the results can vary according to the method used to calculate functional richness (Maire et al., 2015), we also measured the functional diversity using a Convex Hull approach (FRic index, Villéger et al., 2008). As RaoQ and FRic indices showed similar trends, only RaoQ results are shown here. FEve describes the regularity of species' abundance distribution in the trait space. Using Euclidean distances between all species pairs to calculate the minimum spanning tree (MST), this index is a sum of MST branch length weighted by relative abundance. The pairwise

indices were calculated following these equations:

$$RaoQ = \sum_{i-1}^{s-1}\sum_{j=i+1}^{s-1}d_{ij}p_ip_j,$$

$$FEve = \left[\sum_{i=1}^{s-1}\min\left(PEW_i, \frac{1}{s-1}\right) - \frac{1}{s-1}\right] / \left(1 - \frac{1}{s-1}\right)$$

where d_{ij} is dissimilarity between species i and j, p_i and p_j are the relative abundance of species i and j, PEW is the partial weighted evenness, and S is the total species richness. Since relative abundance was not available for this study, it was set to $1/S$ for each species. Calculations of the two functional diversity indices were performed in the statistical programming environment R (R development core team, 2008) using the package FD (Labierte and Shipley, 2011).

Richness, Δ^+, Λ^+, RaoQ, and FEve were calculated for native species, exotic species and overall species at each period, respectively. Then, a multifaceted index integrating structural, taxonomical and functional diversity was calculated to evaluate the ecosystem degradation through non-native species introduction and native species extirpation. All the biodiversity indices for 1950s were treated as the reference condition (baseline), and the degradation index in 1950s was 0. Then in a following period, the degradation index was calculated following the equation:

Degradation index

$$= \left[\frac{Schange}{S1950s} + \frac{Fchange}{F1950s} + \frac{(\Delta change/\Delta 1950s) + (\Lambda change/\Lambda change)}{2}\right]/3$$

where *Schange* is the mean value of the percentage of extirpated and introduced species; *S1950s* is the richness in 1950s; *Fchange* is the change of functional diversity relative to that in 1950s; *F1950s* is the functional diversity in 1950s; *Δchange* and *Λchange* are the changes of Δ^+ and Λ^+ relative to that in 1950s; and *Δ1950s* and *Λ1950s* are the Δ^+ and Λ^+ in 1950s.

The relationships among different periods were estimated by cluster analysis on the basis of 5 biodiversity indices for overall species. Euclidean distances were computed for log-transformed continuous data (the 5 biodiversity indices). Subsequently, resemblance matrixes were generated and hierarchical agglomerative cluster dendrograms were created on the basis of group average linkage (UPGMA). SIMPROF test with 1000 permutations was

performed to evaluate the significance of each cluster (Clarke and Gorley, 2006). Non-metric multidimensional scaling (MDS) was used for ordination of temporal samples based on the same similarity and distance matrices as the cluster analysis. These analyses were performed in PRIMER v6.1 statistical software (Clarke and Gorley, 2006).

3. Results

The changes in fish assemblage composition from the 1950s to the 2010s are given in Table 1. Among the entire species pool of 39 fish species, there was no clear temporal trend concerning species richness, but a remarkable increase for higher taxonomic levels, as the historical fish assemblage counted only 8 genera belonging to 3 orders and the current assemblage counts 28 genera belonging to 7 orders (Table 4). Such temporal changes were due to a steep decline of native fish species from 17 in the 1950s to 7 in the 2000s. Across this 50 years' time frame, the extirpation of these ten species in Lake Erhai was accompanied by the loss of 2 genera and one order. Concomitantly to the decline of the native fish fauna, 22 exotic fish species established in the lake with a clear increasing trend across time (Table 4).

The five biodiversity indices depicted distinct temporal variations from the 1950s to the 2010s (Fig. 2). Species richness was the lowest in the 1950s and the highest and in the 2010s, but it fluctuated from the 1960s to the 1990s (Fig. 2A). Those variations led the MDS ordination to identify two groups based on fish species composition, one gathering 1950s and 1990s periods and the other grouping the 5 remaining decades (Fig. 3A). While no monotonic response was found for the entire fish assemblage, the richness of native species showed clear decreasing trends along the temporal gradient. On the contrary, the richness of exotic species continuously increased through times.

Both RaoQ and FEve displayed unclear ascending trends for overall fish species. A steep increase of RaoQ occurred in the 1960s, which then saturated for 30 years before a steep decline in the 2000s (Fig. 2B). As for functional richness, the recent decline of RaoQ drove the assemblage to return to a current functional structure that was close to the initial one, explaining therefore the grouping of 1950s and 2010s decades in the MDS (Fig. 3B). The functional evenness (FEve) displayed a slight increasing trend across time (Fig. 2C), leading the MDS ordination to distinguish between early (1950s and 1960s) and late periods (1970s–2010s) (Fig. 3C). Such an increasing trend nevertheless resulted from strong variations in functional evenness for both exotic and native species.

Δ^+ for overall fish species showed a clear increasing trend along the temporal gradient from the 1950s to the 2000s (Fig. 2D), which separating the early periods (1950s and 1960s) from the late ones (1970s–2010s) (Fig. 3D). Such an increasing trend attributed most to the ascending of exotic species' Δ^+. The overall fish species' Λ^+ displayed a clear decreasing trend across time (Fig. 2E). With a similar decreasing trend, the native species' Λ^+ contributed more to the variations of overall species' Λ^+. Such kinds of variations led the MDS ordination to distinguish three periods with temporal continuity, one exclusively including 1950s, another grouping 1960s–1980s and the last gathering 1990s–2010s (Fig. 3E).

The degradation index displayed a clear increasing trend along the temporal gradient and the subsequent introduction and extirpation processes (Fig. 2F). It also reveals two strong degradations periods, in the 1950–1960s and in the 1980–1990s.

4. Discussion

The overall fish species richness in Lake Erhai showed no monotonic variation from the 1950s to the 2010s, but the decline of native fish species richness and the increase of exotic fish species richness could be used as good indicators to assess the biotic disturbance of species introduction and extirpation (Fig. 2A). Although species richness was widely used in conventional biodiversity assessment to formulate recommendations for conservation because of its simplicity of use and measurement (Cadotte et al., 2011; Devictor et al., 2010; Strecker et al., 2011), it was deemed to ignore much diversity information (Heino et al., 2007; Leira et al., 2009; Magurran, 2004; Wilsey et al., 2005). However, given the particular situation of Lake Erhai with an impoverishment of native fish species and a concomitant introduction of non-natives, the information on anthropogenic disturbances provided by species richness is blurred by the species introduction that compensates species extirpation, thus making species richness an insufficient metric to measure disturbances.

Functional diversity indices (both RaoQ and FEve), although sensitive to anthropogenic changes, displayed an unclear ascending trend along the timeline under species introduction and extirpation (Fig. 2B and C). The particular native fauna of Lake Erhai, which was composed of a few closely related species (specialists) from phylogenetic and ecological points of view (Li, 1982; Wu and Wang, 1999), explains the low historical functional diversity of the fish assemblage. The introduction of non-native species hence increased fish functional diversity in the lake. Despite the continuous introduction of exotic fish species in the last decades, we report a clear decline of the functional diversity (Fig. 2B), probably due to either the introduction of exotic fish species in the 2000s and 2010s that are functionally similar to those introduced earlier in the lake, and the extirpation of native fish species characterized by unique functional characteristics. This was testified by the decline of functional diversity for both native and exotic fish species in the 2010s (Fig. 2B).

Taxonomic distinctness has been widely utilized in detecting different kinds of disturbances like pollution, habitat degradation or river fragmentation (Xu et al., 2011). Nevertheless, to the best of our knowledge, no studies have yet examined the response of taxonomic distinctness indices to biotic disturbances such as non-native species introductions, and native species extirpations. Our study showed a clear increase of Δ^+ and a decrease of Λ^+ under non-native fish species introduction and native fish species extirpation (Fig. 2D and E). The increase of Δ^+ is driven by the introduced species which are phylogenetically distant from the natives. Such a trend was triggered by the low distinctness of the native fish fauna. Indeed, the native fish species of the lake evolved through adaptive radiation under relatively stable physical lacustrine condition, resulting in a highly endemic fauna made of closely related species (Chu and Chen, 1989; Li, 1982). Such a trend has commonly been observed in isolated environments such as islands, endorheic streams or isolated lakes (Blackburn et al., 2008; Seehausen, 2006). Nonetheless, the colonization of exotic distantly-related species from different orders (e.g., *Rhinogobius*, *Channa*, *Neosalanx* from the orders Perciformes and Salmoniformes) contributed to the largest path length. This explains the increase of Δ^+ through time (and hence through exotic species introduction trend). In addition, the decrease of Λ^+ can be afforded to the extirpation of native fishes. Generally, high Λ^+ values are associated to species assemblages that contains species disproportionately coming from different genera (some genera have more species than others), whereas low Λ^+ values are associated to assemblages evenly coming from different genera (different genera have nearly the same number of species) (Zintzen et al., 2011). In Lake Erhai, the loss of some congeneric native species belonging to *Poropuntius*, *Cyprinus*, and *Schizothorax* hence caused a decrease of Λ^+. This was particularly pronounced in 2000s and 2010s indicating a decline of specialists. Taxonomic distinctness hence responded to species introductions and extirpations in a monotonic way. It reflected the variation in

Table 4
Number of taxa at each taxonomic resolution level of fishes in Lake Erhai, for the 7 time periods.

Taxa		1950s	1960s	1970s	1980s	1990s	2000s	2010s	Total
Species	Native	17 (100%)	17 (60.7%)	11 (45.8%)	11 (44.0%)	6 (30.0%)	6 (26.1%)	9 (29.0%)	17
Genus		9	9	9	9	6	6	7	9
Subfamily		7	7	7	7	5	5	5	7
Family		4	4	4	4	4	4	3	4
Order		3	3	3	3	3	3	2	3
Species	Exotic	0 (0%)	11 (39.3%)	13 (54.2%)	14 (56.0%)	14 (70%)	17 (73.9%)	22 (71.0%)	22
Genus		0	10	12	13	13	16	20	20
Subfamily		0	7	9	10	10	13	16	16
Family		0	3	3	4	4	6	9	9
Order		0	2	2	3	3	3	6	6
Species	Both	17	28	24	25	20	23	31	39
Genus		8	18	20	21	18	21	26	28
Subfamily		7	13	14	15	13	15	18	19
Family		4	6	6	7	7	9	11	12
Order		3	4	4	5	5	7	7	7

specialist species, which cannot be detected by compositional or functional diversity indices.

From a general biodiversity management point of view, sustaining high Δ^+ is considered as desirable, and low Δ^+ indicates ecosystem degradation due to human disturbances. This has been confirmed by a number of studies based on different taxa (e.g., nematodes, molluscks, polychaeta, insects, fishes) (Jiang et al., 2014; Leonard et al., 2006; Marchant, 2007; Milosevic et al., 2012; Warwick et al., 2002). However, our study shows that the pristine fish fauna of an isolated Lake had a relatively low Δ^+, and the Δ^+ increased with growing anthropogenic disturbances such as exotic species introductions and native species extirpation. We
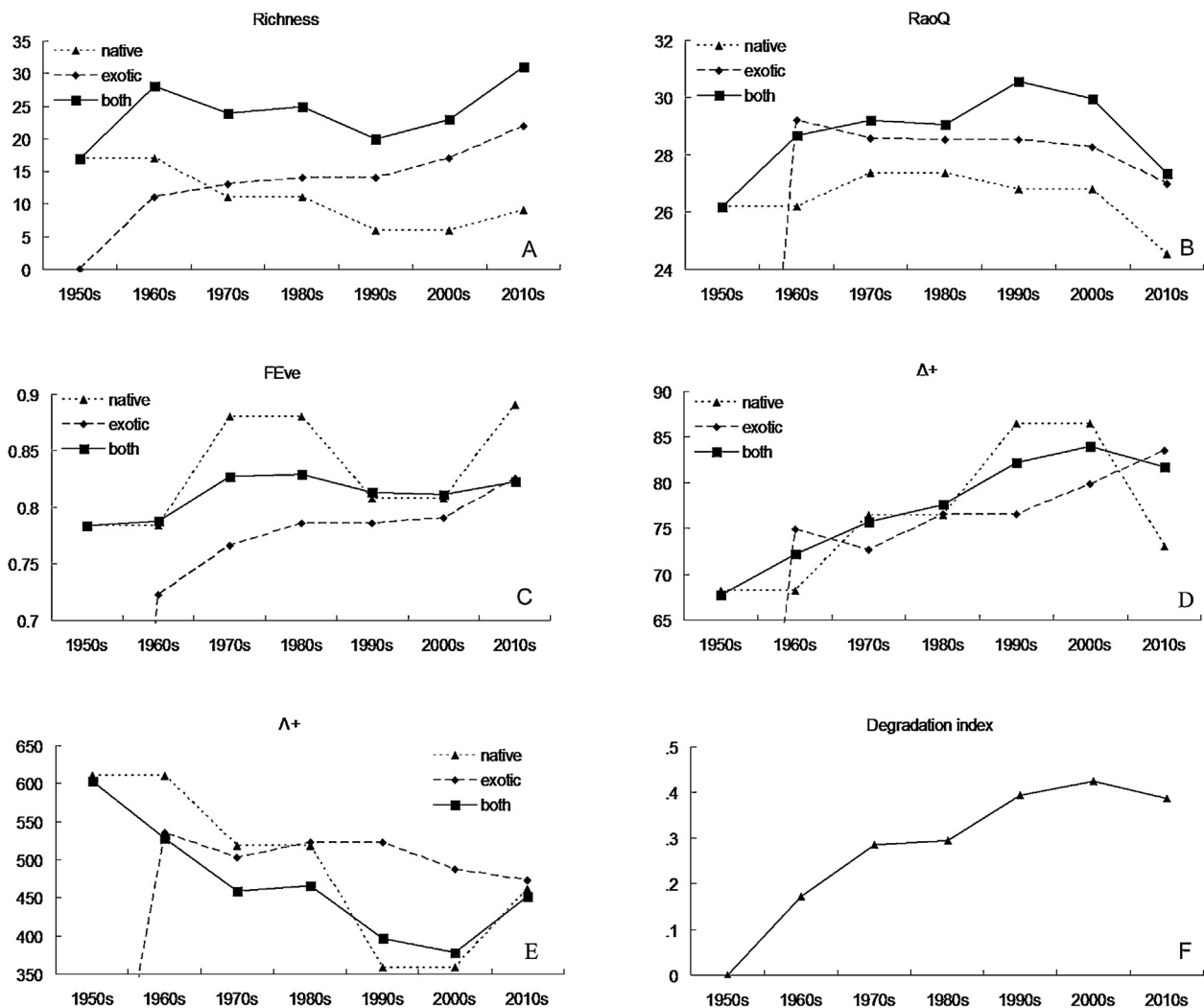

Fig. 2. Temporal variations in measures of different facets of biodiversity indices based on fish fauna datasets during the period of 1950s–2010s. (A) Species richness (Richness); (B) functional richness (RaoQ); (C) functional evenness (FEve); (D) average taxonomic distinctness (Δ^+); (E) variation in taxonomic distinctness (Λ^+); (F) degradation index.
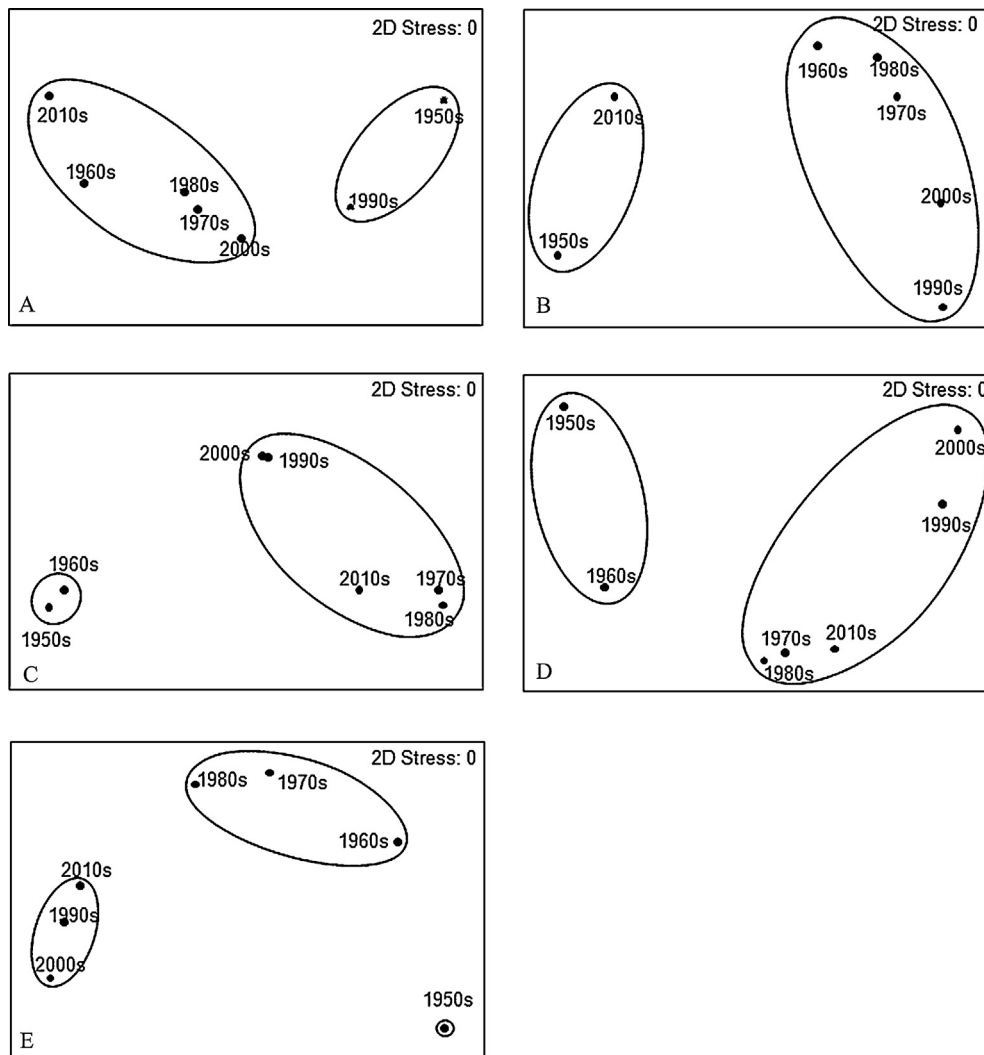
Fig. 3. MDS ordination analyses for temporal variations in patterns of species richness (A), functional richness (B), functional evenness (C), average taxonomic distinctness (D), variation in taxonomic distinctness (E) in Lake Erhai from the 1950s to the 2010s.

hence suggest to sustain a low Δ^+ but a high Λ^+ in Lake Erhai, which characterizes its endemic fauna made of closely related species.

Meanwhile, despite being blurred by the opposite effect of species introduction and extirpation, structural diversity and functional diversity indices provided important information regarding ecosystem condition. From a conservation point of view, functional diversity should be conserved as well as structural diversity (Gallardo et al., 2011), making desirable to consider altogether structural, functional and distinctness approaches in ecological assessment metrics. For instance, a particular attention should also be paid to taxonomy in isolated environments that host endemics. Indeed, the local extirpation of endemic species caused a definitive loss of biodiversity. In the same way, the distinctiveness metrics reflects the roles of historical (dispersal limitation, environmental filtering) and biotic (limiting similarity) forces that shaped the local fauna (Webb et al., 2002; Cavender-Bares et al., 2009). Changes in distinctiveness hence reflect to which extent anthropogenic disturbances modified evolutionary patterns. Bypassing evolutionary filters might change the strength of biotic interactions that at least in part structure the assemblage through limiting similarity processes, and can hence have long-term consequences on ecosystem structure and function (Abellan et al., 2006; Helmus et al., 2010).

Our degradation index reveals a harsh initial decline of the fish fauna in the 1950s–1960s, due to the massive introductions of non-native species (Fig. 2A) having distinct functional attributes and distinct evolutionary history than natives (Fig. 2B, D and E). A second decline occurred in the 1980s–1990s with the extirpation of a few native species (Fig. 2A) with close taxonomic and functional relatedness with the remaining natives (Fig. 2B, D and E). Our degradation index hence integrated the three facets of biodiversity to provide a comprehensive measure of ecosystem degradation. It displayed a clear increasing temporal response to the species introductions and extirpations, demonstrating therefore the interest to consider the three complementary facets of biodiversity. This makes it applicable to particular environments, such as islands or isolated lakes characterized by species assemblages made of a few phylogenetically close native species. As structural and functional metrics are usually sensitive to ecosystem degradation in more classical ecosystems (Villéger et al., 2010), we believe our multifaceted index can be used over a broad range of ecosystems and could hence constitute a promising tool to measure ecosystem degradation, that generate changes in species compositions through species introductions and extirpations. We hence appeal forthcoming studies to test our index on others ecosystems experiencing various disturbances that can generate species introductions and extirpations.

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