

1 **From meta-system theory to the sustainable management of rivers in the**
2 **Anthropocene**

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40 **Running head:** A meta-system approach for river management

41

42 **Abstract**

43 Ecological processes occurring at the regional scale, such as the dispersal of organisms,
44 and spatial flows of material and energy are fundamental for maintaining biodiversity
45 and ecosystem functioning in river networks, yet they remain largely overlooked in
46 most river management practices and underlying policies. We propose a meta-system
47 approach where regional processes acting at different levels of ecological organization –
48 populations, communities and ecosystems – can be integrated into conventional
49 conservation, restoration and biomonitoring of rivers. We recommend a series of
50 measurements and indicators that could be assimilated into the implementation of
51 relevant biodiversity and environmental policies. We highlight the need for alternative
52 management strategies that can guide practitioners towards applying recent advances in
53 ecology to preserve and restore river ecosystems and the ecosystem services they
54 provide in the context of increasing alteration of river network connectivity worldwide.

55

56 **In a nutshell:**

- 57
- 58 • Rivers are hotspots of biodiversity and provide essential ecosystem functions
and services but are heavily threatened globally
 - 59 • Our understanding on how rivers are organized across spatial scales has
60 progressed considerably over the past decades, proving that regional-scale

61 processes are vital for preserving population, community and ecosystem
62 dynamics

- 63 • However, most existing river conservation, restoration and biomonitoring
64 practices focus on local-scale approaches and measures
- 65 • We suggest additional metrics and assessment approaches that better incorporate
66 regional processes to guide the management of river networks in the
67 Anthropocene

68

69 River ecosystems sustain disproportionate levels of biodiversity at landscape, regional
70 and continental scales (Reid *et al.* 2019). They contribute substantially to global
71 biogeochemical cycles through release of carbon dioxide to the atmosphere and
72 transport of carbon and nutrients from continents to oceans (Raymond *et al.* 2013).
73 Rivers also provide key ecosystem services, including provision of drinking water, food
74 production, and climate and water regulation, which are critical to sustaining human
75 well-being (Reid *et al.* 2019). However, in the current Anthropocene era (Panel 1),
76 rivers worldwide are largely impaired by human activities, being among the most
77 threatened ecosystems on Earth (Dudgeon *et al.* 2019). This global trend necessitates
78 better management and environmental legislation to guarantee the biodiversity and
79 functional integrity of river ecosystems.

80 Most river management practices – independently of the spatial scale at which
81 they are implemented – are based on local assessments, as a legacy of the niche
82 paradigm that has prevailed in ecology for decades (Panel 1; Heino 2013). In contrast,
83 scientific understanding of how biodiversity, ecosystem functions and services are
84 organized across river networks has progressed substantially with the emerging meta-
85 system theory (Gounand *et al.* 2018). This framework acknowledges that both local (ie
86 niche selection and biotic interactions at a river reach) and regional (ie dispersal of
87 organisms and spatial flows of material and energy across the river network)
88 mechanisms interact to shape the spatial and temporal organization of populations and
89 communities, and drive ecosystem processes and services. The meta-system framework
90 is particularly relevant for river networks due to their dendritic topology (Panel 1) and
91 the predominantly unidirectional flow of water, which constrain the exchange of matter
92 and organisms at larger spatial scales (Tonkin *et al.* 2018). Current river management

93 practices and underlying policies often fail to incorporate important regional processes.
94 Therefore, our ability to conserve and restore river biodiversity and ecosystem functions
95 efficiently is critically hindered (Erős *et al.* 2018).

96 Management practices focused on the local scale alone will become increasingly
97 unlikely to achieve desired ecological outcomes. Globally, humans modify catchments
98 through land use changes, flow regulation by dams, water diversion and extraction of
99 surface and ground water, pollution and the introduction of invasive species (Dudgeon
100 2019). Fragmentation by dams is the major driver of connectivity loss (Grill *et al.* 2019)
101 and is exacerbated by climate change, which increases the intensity and frequency of
102 droughts and subsequent drying of river networks (Döll and Schmied 2012). Where
103 human densities are high, the flow regimes of streams and rivers have been so greatly
104 altered that ‘novel’ ecosystems exist (Datry *et al.* 2018). Despite having local impacts,
105 most of the threats of the Anthropocene act at the regional or global scale (Dudgeon
106 2019). Overall, the increasing pressure of multiple threats calls for a better integration
107 of scale-dependent approaches to guide water management and conservation policies in
108 a changing world.

109 Here, we aim at translating the meta-system theory into management and policy
110 recommendations for rivers. First, we present the meta-system framework and its
111 relevance for these ecosystems, particularly with respect to decreased connectivity
112 resulting from human-induced fragmentation. Second, we show why this framework
113 can inform river management to effectively achieve environmental and conservation
114 targets. Third, we identify specific policy implications, and provide guidance on how a
115 meta-system approach could be implemented.

116 **The meta-system theory and its relevance in river networks**

117 The meta-system theory states that local- and regional-scale processes interact to
118 influence the dynamics of environmental conditions and biota in a given landscape
119 (Gounand *et al.* 2018 Figure 1). Regional-scale processes determine fluxes of
120 individuals, species or material and energy among local populations, communities and
121 ecosystems, respectively, whereas local-scale dynamics represent interactions with
122 abiotic conditions and other species (Hanski 1998; Leibold *et al.* 2004; Gounand *et al.*
123 2018). Sets of local populations, communities and ecosystems linked by regional fluxes
124 form, respectively, metapopulations, metacommunities and meta-ecosystems (Panel 1,

125 Figure 1). In river networks, dispersal of organisms can be constrained by the dendritic
126 topology, flow regime, physical barriers and the dispersal capability of the organisms,
127 leading to spatial variation of populations and communities (Brown *et al.* 2011). Matter
128 and energy vary spatially, as sources of terrestrial inputs are differentiated across sub-
129 catchments (Creed *et al.* 2015) and upstream-to-downstream physical linkage dominates
130 transport with en-route biogeochemical modulation. Such spatial dynamics in the flows
131 of matter and organisms at the regional sub-catchment scale can determine riverine
132 ecosystem functioning at the local reach scale. The meta-system theory upgrades the
133 perspectives of metapopulation and metacommunity ecology in river ecosystems
134 focused on spatial flows of organisms by incorporating those of resources, material and
135 energy (Gounand *et al.* 2018). It offers a framework to better understand the spatial
136 coupling of biodiversity dynamics and ecosystem functioning, eventually contributing
137 to ecosystem services (Gounand *et al.* 2018), and it reinforces previous research on
138 ecological processes across spatial scales in river networks (Fausch *et al.* 2002; Brown
139 *et al.* 2011; McCluney *et al.* 2014). By explicitly distinguishing the different levels of
140 ecological organization, it also provides a powerful framework for the implementation
141 of current biodiversity and environmental policies.

142 The relevance of the meta-system framework for improving river management
143 can be illustrated through fragmented river networks. Fragmentation, by weirs, dams or
144 drying, not only alters the local environment and biota (eg Datry *et al.* 2014), but also
145 disrupts the flux of water, resources and organisms (Gounand *et al.* 2018; Grill *et al.*
146 2019). The effects of fragmentation cascade across organizational levels, from
147 populations to ecosystems, and eventually to socio-ecological systems, negatively
148 affecting the provision of ecosystem services (Figure 2). Fragmentation can isolate local
149 populations and reduce gene flow within a metapopulation, jeopardizing their long-term
150 persistence due to genetic drift and inbreeding (Fitzpatrick and Reid 2019). Ultimately,
151 this can lead to decreased species ranges and eventually to local or regional extinctions
152 (Hanski 1998). Responses to fragmentation of metapopulations cascade to altered
153 metacommunity dynamics. Reduced dispersal among isolated local communities can
154 lead to shifts in community composition, biodiversity patterns and biological
155 interactions at local and regional scales (Jaeger *et al.* 2014), leading to changes in
156 ecosystem functions (Gounand *et al.* 2018). Fragmentation can also have direct effects
157 on fluxes of material (Figure 2). For example, drying resulting from water over-

158 abstraction, dam construction, or climate change can alter the storage and transport of
159 coarse organic matter and nutrients in the network, as they are retained at sites without
160 flow before subsequent massive releases at flow resumption (Datry *et al.* 2018).
161 Fragmentation may ultimately impact ecosystem service provision at the river basin
162 scale by altering service-providing, service-connecting and service-benefiting areas
163 (Datry *et al.* 2017; Panel 1; Figure 2). Thus, understanding regional processes occurring
164 at each level of organization (ie metapopulation, metacommunity and meta-ecosystem)
165 can be crucial in guiding effective river conservation, monitoring and restoration.

166 **The meta-system theory for integrating regional-scale processes in river** 167 **conservation, restoration and monitoring**

168 The meta-system theory can help managers to better predict how populations respond to
169 anthropogenic stressors at the regional scale and to design conservation plans
170 accordingly (Schiesari *et al.* 2019). When a population follows source-sink dynamics,
171 the regional persistence of the species mainly depends on key ‘source’ populations that
172 contribute via dispersal to ‘sink’ populations (Hanski 1998). Identifying where these
173 key populations and their main dispersal routes are located is crucial to ensure adequate
174 species conservation. Studies on salmonid fishes show that fragmentation by large
175 reservoir dams, hatchery introductions and deterioration of habitat quality can
176 substantially alter metapopulation structure, and that optimal management strategies
177 should be based on maintaining habitat quality and connectivity of key ‘source’
178 populations (Fullerton *et al.* 2016). In very fragmented metapopulations, local
179 populations decline, and the risk of extinction is higher than in large and connected
180 metapopulations (Fitzpatrick and Reid 2019). For example, historically connected
181 metapopulations of the endangered Iberian cyprinid fish *Iberochondrostoma almakai*
182 now suffer from fragmentation as a result of river drying and are subjected to strong
183 genetic drift (Sousa *et al.* 2010). Protecting local habitats alone would not be effective,
184 and conservation strategies should target increasing gene flow (Sousa *et al.* 2010). On
185 the contrary, historically isolated populations require careful management practices to
186 maintain isolation-driven evolutionary processes at the landscape scale (Rahel and
187 McLaughlin 2018). Information about population sizes, dispersal capability and
188 physical distance among populations is necessary to distinguish different
189 metapopulation structures in landscapes, which require different management strategies
190 and priorities (Fullerton *et al.* 2016).

191 Regional-scale thinking is also critical for understanding the spread of invasive
192 species (Strecker and Brittain 2017). In river networks, however, their management is
193 still poorly developed and can be controversial (Chen and Olden 2017). For example,
194 artificial barriers alter natural metapopulation dynamics but also can limit the spread of
195 invasive fish (Rahel and McLaughlin 2018). In contrast, altering naturally intermittent
196 flow regimes of river networks by artificially producing perennial flows can promote
197 new invasions of alien species (Ruhí *et al.* 2019). Identifying the respective role of local
198 and regional processes in the dynamics of invasive species in relation to native ones is
199 fundamental to avoid undesired conservation and management effects (Rahel and
200 McLaughlin 2018).

201 Considering metapopulation structure can improve the prediction of species
202 range shifts in response to climate change, as dispersal capability can determine whether
203 species will be able to reach new suitable regions and habitats (Markovic *et al.* 2014).
204 However, most assessments based on species distribution modeling only consider the
205 potential effects of climate change on local conditions (ie niche-based modeling). If the
206 target is developing more resilient large-scale conservation strategies, the evaluation of
207 species' vulnerability and extinction risk needs to incorporate dispersal-related
208 processes and indeed the effects of projected river network fragmentation on biota
209 (Markovic *et al.* 2017).

210 At the community level, information on the metacommunity structure can be
211 powerful in guiding effective restoration and biomonitoring practices. Currently, most
212 restoration projects may fail in achieving biodiversity and/or ecological quality targets
213 because they are typically limited to the local scale (Tonkin *et al.* 2014). For example,
214 the reduced regional pool of colonizers could hamper achieving expected restoration
215 targets in highly-degraded catchments, where unimpacted sites (ie natural recolonization
216 sources) are very isolated due to fragmentation (Tonkin *et al.* 2014; Swan and Brown
217 2017). Similarly, biomonitoring methods to evaluate river health or ecological status
218 may fail at detecting anthropogenic impacts, mainly as a result of dispersal limitation
219 (Heino 2013). Most biomonitoring methods assume that local communities entirely
220 respond to local environmental conditions and that all species can eventually reach all
221 sites (Cid *et al.* 2020). However, fragmentation can prevent species from reaching their
222 optimal habitats and isolated sites may present lower richness and bioassessment scores

223 despite having good habitat quality (Heino 2013). In naturally intermittent river
224 networks, drying can generate high habitat heterogeneity in terms of wet and dry
225 habitats and might promote species richness, but it can also increase fragmentation and
226 prevent some species from colonizing a site, thereby reducing local species richness
227 (Datry *et al.* 2014). Applications of the basic tenets of metacommunity ecology in
228 biomonitoring and restoration practices can inform on the relative influence of local and
229 regional processes on local community composition (Cid *et al.* 2020).

230 Metacommunity ecology uses a range of scale-sensitive biodiversity measures
231 that are dismissed in local biodiversity assessments based on alpha diversity (Panel 1).
232 For example, beta diversity (Panel 1) and its components can be useful to identify and
233 preserve those sites contributing the most to maintaining regional diversity (Panel 1;
234 Ruhí *et al.* 2017). Thus, expanding the metrics used in routine assessments can provide
235 essential information to evaluate the structure and functioning of metacommunities and
236 improve their conservation (Simons *et al.* 2019).

237 Species in a metacommunity interact at the local and regional scales (Hagen *et al.*
238 *al.* 2012), and biotic interactions can be altered by changes in hydrologic connectivity
239 across the river network. For example, fragmentation by dams can isolate freshwater
240 mussel metapopulations from their host fish, on which they depend for completing their
241 life cycle and disperse across the network (Ferreira-Rodríguez *et al.* 2019).
242 Fragmentation by drying can simplify food webs following top predator loss, having
243 direct effects on ecosystem processes (Hagen *et al.* 2012). Identifying key biotic
244 interactions across the meta-system will help achieve biodiversity targets closely linked
245 with ecosystem functioning (Hagen *et al.* 2012).

246 By modifying the flow of water, sediments and organisms, fragmentation affects
247 the fluxes of matter (ie minerals, carbon and nutrients) across river networks. For
248 example, current dam removal efforts benefit sediment transportation, counteract
249 coastal erosion, and also restore upstream movement of migratory fish, thereby allowing
250 transport of marine nutrients to isolated headwaters (Bellmore *et al.* 2019).
251 Fragmentation can also lead to sub-optimal ecosystem processes both locally and
252 regionally if resources accumulate but organisms processing those are lacking and vice-
253 versa (Gounand *et al.* 2018). This might occur when natural drying of stream channels
254 in intermittent rivers stops the transport of organic matter from upstream and thus limits

255 ecosystem functioning downstream (Datry *et al.* 2018). Identifying when and where
256 various kinds of matter (and energy) are processed and transported is essential for the
257 maintenance of ecosystem functioning and services (Datry *et al.* 2017).

258 **Policy implications and management opportunities**

259 Biodiversity and environmental conservation are governed through several interlinked
260 goals and agreements at the international and national levels. Global objectives, such as
261 those stated in the Aichi Biodiversity Targets and the Sustainable Development Goals
262 aiming for a more sustainable world, are reflected in international and national
263 strategies and policies (Figure 3, Table 1). These policies are articulated and enforced
264 through guidance documents, which include common implementation methodologies
265 describing how to obtain indicator metrics for tracking the achievement of
266 environmental and conservation targets (Table 1). Here, we present different options to
267 integrate regional-scale processes into the current local-scale management of river
268 networks, focusing on biodiversity conservation, biomonitoring and restoration. We
269 propose a series of alternative metrics and indicators (Table 1) that could complement
270 such methodologies and sharpen strategies to guide efforts in reversing current trends of
271 freshwater biodiversity loss and ecosystem degradation due to river fragmentation.

272 ***Metapopulation and metacommunity perspectives for biodiversity conservation***

273 Conservation policies such as the European Union Habitats Directive or the US
274 Endangered Species Act, collect information on the conservation status of species from
275 population estimates, most of them only accounting for species population size and
276 habitat quality (Table 1). Under a meta-system approach, methods and indicators able to
277 assess metapopulation structure should be incorporated. This includes molecular tools
278 and methods for obtaining genetic diversity metrics to infer connectivity within a
279 delimited spatial area (eg catchment or sub-catchment) and/or direct measures of
280 dispersal (Table 1) using mark and recapture or genetic methods (Fullerton *et al.* 2016).
281 However, empirical data on metapopulations are not always available for managers, and
282 monitoring efforts and open data sharing should be promoted. Such information could
283 be integrated in individual-based models and thereby contribute to identify critical
284 thresholds (Dudley 2018).

285 Responses for mitigating the effects of altered river network connectivity on
286 biodiversity can be varied (Fuller *et al.* 2016). In general, when freshwater
287 metapopulations are suffering from lack of gene flow, conservation actions should
288 promote connectivity. This can be done by removing artificial barriers, installing fish
289 passages, or implementing environmental flows (Poff *et al.* 2010). Despite important
290 efforts to shift environmental flow management from local to regional scale (eg
291 Stewardson and Guarino 2018), most dam management practices still focus on restoring
292 flow regimes at the immediate downstream river segments. Instead, coordinated dam
293 management across the river network provides an opportunity to increase connectivity
294 and maintain meta-system dynamics (McCluney *et al.* 2014; Chen and Olden 2017). In a
295 meta-system context, environmental flow management should target the conservation
296 and restoration of variation in regional ecological features (eg by using the metrics
297 listed in Table 1). If increasing connectivity is not feasible through restoration, or if
298 populations are too isolated to allow dispersal of individuals after improving
299 connectivity, conservation measures could be directed to protect local habitats and
300 conducting assisted colonization (Lawler and Olden 2011).

301 Protected areas are major assets for current conservation policies. However, they
302 rarely capture the complex spatial structure of river networks, making conservation of
303 riverine biodiversity challenging (Carrizo *et al.* 2017; Acreman *et al.* 2020). Under a
304 meta-system approach, protected areas within a catchment should be designed to ensure
305 the conservation of key sites across the network that allow metapopulations and
306 metacommunities to persist. This could be achieved using prioritization methods in
307 conservation planning that include the analysis of connectivity and spatial congruence
308 of multiple species (Albert *et al.* 2017). For example, in river networks experiencing
309 fragmentation through drying, the selection of pivotal refugia acting as sources for
310 dispersal are key to ensure the protection of network-wide biodiversity (Hermoso *et al.*
311 2013). Sites to be protected and/or restored across the network can be selected using
312 information on populations' genetic diversity and on communities' beta diversity
313 components (Table 1; Ruhí *et al.* 2017; Paz-Vinas *et al.* 2018).

314 ***Metacommunity-based biomonitoring and restoration for river basin management***

315 Most legislation protecting surface waters relies on local reach-scale evaluations of
316 ecological status (Heino 2013). For example, despite the management unit of the

317 European Union Water Framework Directive and the US Clean Water Act is the river
318 basin, they prescribe evaluation of different river reaches individually, based on the
319 structural and/or functional properties of ecological assemblages. However, neither of
320 the two policies explicitly encourages biological assessments at multiple spatial scales.

321 River biomonitoring methods are based on comparing the biotic community of a
322 focal site with a reference value obtained from a group of unimpacted or least impacted
323 sites (Cid *et al.* 2020). Using these unimpacted sites, the expected biological community
324 at a site is predicted based on local environmental conditions (Heino 2013; Cid *et al.*
325 2020). To consider regional processes in metacommunity dynamics, water managers
326 could integrate proxies for dispersal based on spatial connectivity (eg fragmentation
327 caused by dams, drying, and topographical barriers) and dispersal-related species traits
328 into biomonitoring methods (Cid *et al.* 2020).

329 To better consider current and predicted levels of fragmentation, monitoring
330 sites within a river network may have to be redesigned. For example, while large dams
331 are usually considered when selecting monitoring sites, fragmentation by small barriers
332 and potential drying events have traditionally been overlooked (Erős *et al.* 2018).
333 Assessing fragmentation within a river network and its potential interactive or additive
334 effect(s) with other anthropogenic stressors will contribute to better predictions of
335 ecological integrity using bioindicators.

336 Under a meta-system approach, restoration practices should include information
337 on the regional species pool and the capability of species to reach restored habitats. Key
338 sites acting as sources of colonizers should be identified, and their connectivity with
339 restored river reaches should be evaluated (Heino *et al.* 2017). This is especially
340 relevant when fragmentation is due to drying, as source sites within the regional species
341 pool are typically located in dry season refugia (Datry *et al.* 2014). To assess whether
342 improvements in local diversity have positive effects on regional biodiversity, managers
343 could incorporate indices such as taxonomic and functional beta, zeta and gamma
344 diversity (Panel 1, Table 1) (Simons *et al.* 2019).

345 ***Towards a more holistic ecosystem-based management in rivers***

346 At the ecosystem level, the need for spatially explicit examinations of biogeochemical,
347 hydromorphological and ecological patterns and processes has been recognized for

348 science and management (Gounand *et al.* 2018; Mc Cluney *et al.* 2014). There are
349 already some prioritization tools available to integrate spatial dynamics into
350 conservation planning (e.g. Hermoso *et al.* 2013; 2018), and most policies and related
351 guidance documents promote adaptive management incorporating cross-ecosystem
352 processes and scale-dependency. However, the implementation of these tools and
353 principles is still rare (Acreman *et al.* 2020). Research and capacity-building on how to
354 overcome these barriers for more effective integration of the state-of-the-art ecological
355 theory to environmental management is needed. Monitoring programs should include
356 measures of ecosystem processes across the river network, such as decomposition of
357 leaf litter and ecosystem metabolism (Young *et al.* 2008), or measures of food web
358 structure (Otto *et al.* 2018), which could help to identify hotspots of functioning
359 (McClain *et al.* 2003). These measures could be integrated systematically in
360 conservation planning. As different biodiversity facets, ecosystem processes and
361 services may vary in their degree of spatial congruence across the river
362 network, prioritization methods that integrate these variables simultaneously could be
363 used to maximize their protection in a holistic way (Hermoso *et al.* 2018; Erős and
364 Bányai 2020).

365 **Conclusions**

366 The meta-system theory is a powerful framework to understand the dynamics of
367 populations, communities and ecosystems, and guide the conservation, biomonitoring
368 and restoration of increasingly fragmented river networks. Yet, the applications of this
369 approach are just emerging, and many methodological and empirical developments are
370 urgently needed to integrate it into environmental legislation and policies. Guidance
371 based on meta-system theory could strengthen the quality of legislation, build
372 understanding of causes and effects across spatial scales, and make significant steps
373 towards sustainable, adaptive management of rivers in the Anthropocene. The relevance
374 of this framework will be even greater in the near future. This is because climate change
375 and increased water needs for human activities are exacerbating the occurrence and
376 magnitude of extreme events, such as floods and droughts, thereby rapidly altering river
377 connectivity and producing unprecedented river network fragmentation.

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535 **Figure captions:**

536 **Figure 1:** Schematic representation of metapopulations, metacommunities and meta-
537 ecosystems in a drying river network. Local populations, communities and ecosystems
538 (green rectangles) are connected by gene flow, dispersal of individuals, and flow of
539 resources across the landscape, respectively (arrows). Photo credit: N. Bonada.

540 **Figure 2:** Conceptual diagram of the cascading effects of the alteration of river network
541 connectivity across the different levels of the meta-system (ie metapopulation,
542 metacommunity and meta-ecosystem) and socioecological system (ie ecosystem
543 services). Note that for ecosystem services, blue and red arrows represent the flow
544 between service-providing and service-benefiting areas (Panel 1).

545 **Figure 3:** The current loss of river network connectivity worldwide will be exacerbated
546 by climate change and affect the associated socio-ecological system. Legislation and
547 regulations at all levels should adapt to these changes: international policies include the
548 Aichi Biodiversity Targets or Sustainable Development Goals; related regional policies
549 (here, examples from Europe) reflect these global agreements, which form the basis to
550 national level regulations for water, nature conservation, or spatial planning.

551

Alpha diversity: The diversity within a specific ecosystem or area (the local species richness) usually expressed as the number of species present (Whittaker 1972).

Anthropocene: A new human-dominated geological epoch, beginning between 1610 and 1964 according to different lines of evidence (Lewis and Maslin 2015).

Beta diversity: A quantification of the number of different communities in a region measured as extent of change (Whittaker 1972).

Dendritic structure (in river networks): Rivers and streams follow a geometric pattern of arborescent bifurcation originating from one node and extending out in one direction, forming a hierarchical network of nodes and branches (Heino 2013).

Dispersal: Movement of individuals from one locality to another (Leibold *et al.* 2004).

Niche: Range of resource availability and physical conditions that a given species can tolerate to survive at a locality (Leibold *et al.* 2004).

Metapopulation: A set of local populations of a single species that are linked by dispersal (Hanski 1998).

Metacommunity: A set of local communities that are linked by dispersal of multiple potentially interacting species (Leibold *et al.* 2004).

Meta-ecosystem: A set of ecosystems connected by spatial flows of energy, material and organisms across ecosystem boundaries (Gounand *et al.* 2018).

Regional diversity (gamma diversity): The total diversity within the entire landscape, ie regional species pool (Whittaker 1972).

Service-providing areas: The spatial units that are the sources of ecosystem services in a given landscape (Syrbe and Walz 2012).

Service-connecting areas: The spatial units where the benefits from ecosystem services are required in a given landscape (Syrbe and Walz 2012).

Service-benefiting areas: The spatial units that are connecting providing and benefiting areas in a given landscape (Syrbe and Walz 2012).

Zeta diversity: The number of species shared by multiple communities (Simons *et al.* 2019)

555 **Table 1** Current metrics and indicators used in core environmental and biodiversity policies. Also shown are additional ones that could be
 556 implemented in a meta-system approach.

Management action and organizational level of application	Policies	Current metrics/indicators	Additional metrics/indicators
Conservation/ restoration, (meta) population	European Biodiversity Strategy and Habitats Directive	Species range* (km) Species occupancy area* (km ²) Species population size* (grid, individuals)	Genetic diversity Gene flow Inbreeding Hybridization
	US Endangered Species Act	Species age structure Species habitat area and quality	Species effective dispersal Number and location of metapopulation key habitats (eg refugia, dispersal routes)
	Australia Environment Protection and Biodiversity Conservation Act		Area and quality of metapopulation key habitats Connectivity between key habitats (eg dendritic connectivity index)
Biomonitoring/restoration, (meta) community	European Water Framework Directive	Local (alpha) taxonomic richness and diversity of different taxonomic groups (ie macroinvertebrates, fish, diatoms, macrophytes, riparian plants)** Species environmental tolerance** Number and richness of alien species** Riparian vegetation cover** Morphology of the riverbed and riverbanks**	Gamma species diversity Beta and zeta species diversity
	US Clean Water Act		Species dispersal capability (eg using organisms' traits as a proxy for dispersal)
	Australia Water Act		Species effective dispersal Metacommunity key habitats area and quality (ie refugia, dispersal routes) Connectivity between key habitats (eg dendritic connectivity index)

Management action and organizational level of application	Policies	Current metrics/indicators	Additional metrics/indicators
Ecosystem-based management/restoration, (meta) ecosystem and ecosystem services	European Biodiversity Strategy ***	Nutrient load and retention Sediment transport and retention Carbon storage, processing and transport Fish production (catch by fishermen) Wood produced by riparian forest N° bathing areas and quality Fishing reserves Most of the indicators listed above within other categories (eg riparian vegetation cover)	Leaf litter decomposition Ecosystem metabolism Food web structure Riparian stocks (eg using remote sensing) Number and location of hotspots of functioning (eg organic matter and nutrient processing) Number and location of service-providing, service-connecting and service-benefiting areas

557

558 *These metrics are reported at the national level and, usually, for protected areas. The conservation status is assessed using reference values.

559 **These measurements are the basis for the development of biological and hydromorphological quality metrics under the main water policies
560 such as the Water Framework Directive. They are developed at the national level.

561 *** One of the main targets is the mapping and assessment of ecosystem services, which uses indicators from several sources.