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Critical catchments for freshwater biodiversity conservation in Europe: identification, prioritisation and gap analysis

Savrina F. Carrizo*[,1], Szabolcs Lengyel[2], Felícia Kapusi[3], Márton Szabolcs[2,3], Hans D. Kasperidus[4], Mathias Scholz[4], Danijela Markovic[5], Jörg Freyhof[6], Núria Cid[7], Ana C. Cardoso[7] and William Darwall[1]

[1]Freshwater Biodiversity Unit, IUCN Global Species Programme, The David Attenborough Building, Pembroke Street, Cambridge CB2 3QZ, UK; [2]Department of Tisza Research, Danube Research Institute, Centre for Ecological Research, Hungarian Academy of Sciences, Bem tér 18/c, 4026 Debrecen, Hungary; [3]Pál Juhász-Nagy Doctoral School, University of Debrecen, Egyetem tér 1, 4032 Debrecen, Hungary; [4]Department Conservation Biology, UFZ – Helmholtz Centre for Environmental Research, Permoserstraße 15, 04318 Leipzig, Germany; [5]Osnabrück University of Applied Sciences, Caprivistraße 30 A, 49076 Osnabrück, Germany; [6]Leibniz Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587 Berlin, Germany; and [7]European Commission, Joint Research Centre (JRC), Directorate D – Sustainable Resources, Water and Marine Resources Unit, Via Enrico Fermi 2749, 21027 Ispra, VA, Italy

Summary

1. The conservation of freshwater ecosystems has lagged behind that of marine and terrestrial ecosystems and often requires the integration of large-scale approaches and transboundary considerations. This study aims to set the foundations of a spatial conservation strategy by identifying the most important catchments for the conservation of freshwater biodiversity in Europe.

2. Using data on 1296 species of fish, mollusc, odonate and aquatic plant, and the key biodiversity area criteria (species Red List status, range restriction and uniqueness of species assemblages), we identified a network of Critical Catchments for the conservation of freshwater biodiversity. Applying spatial prioritisation, we show how the prioritised network differs from the ideal case of protecting all Critical Catchments and how it changes when protected areas are included, and we also identify gaps between the prioritised network and existing protected areas.

3. Critical Catchments (n = 8423) covered 45% of the area of Europe, with 766 qualifying (‘trigger’) species located primarily in southern Europe. The prioritised network, limited to 17% of the area of Europe, comprised 3492 catchments mostly in southern and eastern Europe and species targets were met for at least 96% of the trigger species.

4. We found the majority of Critical Catchments to be inadequately covered by protected areas. However, our prioritised network presents a possible solution to augment protected areas to meet policy targets while also achieving good species coverage.

5. *Policy implications*. While Critical Catchments cover almost half of Europe, priority catchments are mostly in southern and eastern Europe where the current level of protection is not sufficient. This study presents a foundation for a Europe-wide systematic conservation plan to ensure the persistence of freshwater biodiversity. Our study provides a powerful new tool for optimising investment on the conservation of freshwater biodiversity and for meeting targets set forth in international biodiversity policies, conventions and strategies.

Key-words: alliance for zero extinction, dragonfly, fishing and fishery, key biodiversity area, Marxan, reserve design, snail, mussel and clam, systematic conservation planning, threatened species, watershed management and restoration

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*Correspondence author. E-mail: savrinacarrizo@gmail.com

Introduction

Freshwater ecosystems cover less than 1% of the Earth's surface and are among the most diverse and threatened systems in the world (Strayer & Dudgeon 2010). Freshwater species and habitats are of high value to people's livelihoods as a food resource and serve important functions such as water purification and flood regulation yet have not been afforded the conservation focus required (Darwall *et al.* 2011). More than 29% of the 25 872 freshwater species assessed for the IUCN Red List of Threatened Species™ ('Red List') are globally threatened with extinction (IUCN, 2015). The overriding threat to freshwater biodiversity is habitat loss and degradation (Allan 2004; Darwall *et al.* 2011). Consequently, site-based approaches such as protected areas are an important tool for freshwater conservation. However, protected areas have been rarely designated for the purpose of conserving freshwater biodiversity (Abell, Allan & Lehner 2007). For example, rivers are commonly used to delineate the borders of a protected area rather than being the targets of conservation themselves (Abell, Allan & Lehner 2007). Even within protected areas, freshwater habitats often Critical Catchments to pollution and other threats propagated from outside the protected area, and migratory fish are rarely guaranteed passage or protection (Dudgeon *et al.* 2006).

Identification of globally significant areas for the persistence of biodiversity, known as key biodiversity areas (KBAs) is an important and well-regarded conservation tool. KBAs can help guide the improvement and expansion of protected area networks (Rodrigues *et al.* 2004; Langhammer *et al.* 2007) as they can serve as 'shadow lists' for site designation (IUCN, 2016). KBAs are also used to address the Aichi Biodiversity Targets 2, 4, 11, 12, 14 and 20 (IUCN & BirdLife International, 2013) and the corresponding European Union Biodiversity Strategy targets (EC, 2011). KBAs also inform public and private sector environmental policies via online data bases such as the Integrated Biodiversity Assessment Tool (IUCN, 2016). The IUCN-led global consultative process to consolidate a standard for identifying KBAs (IUCN, 2016) has raised the profile of this important tool.

Although some freshwater KBAs have been identified (Silvano *et al.* 2007; Holland, Darwall & Smith 2012; Darwall *et al.* 2014), comprehensive and standardised knowledge about the spatial distribution of the most important areas for freshwater biodiversity is lacking. Furthermore, Alliance for Zero Extinction (AZE) sites, that contain the last or only populations of globally threatened species (Ricketts *et al.* 2005), are an important subset of KBAs and are in urgent need of identification for freshwaters. In Europe, only one freshwater AZE site has been identified to date for the amphibian *Calotriton arnoldi* in Spain (Carranza & Amat 2005).

Our first objective was to identify the freshwater catchments that contain sites likely to qualify as freshwater KBAs. These catchments, hereafter called 'Critical Catchments', represent the broader ecological context within which freshwater KBAs are located (Darwall & Vie 2005) and should ideally be the primary targets for further conservation actions. Our second objective was to identify a subset of Critical Catchments that adequately covers threatened species, range-restricted species and unique assemblages of species at the lowest possible cost and which also considers the existing protected area network. Given the constraints of competing land uses and limited funds for conservation, spatial prioritisation is thus a necessary step towards a pragmatic strategy (Juffe-Bignoli *et al.* 2016). Spatial prioritisation has been applied extensively in terrestrial and marine realms (Carwardine *et al.* 2008b; Klein *et al.* 2008), but at relatively small geographical and taxonomic scales for freshwater systems (Abell, Allan & Lehner 2007; Linke, Turak & Nel 2011). Here we use data from geographical Europe and follow recommendations by IUCN (2014, p. 62) to spatially prioritise the Critical Catchments. Our final objective was to identify gaps in the spatial overlap between the Critical Catchments and the current network of protected areas. Our approach ensures methodological consistency with previous freshwater assessments and provides input to the global KBA standard (IUCN, 2016) and to stakeholder workshops where KBAs within Critical Catchments will subsequently be identified and validated in line with the global KBA standard.

Materials and methods

STUDY AREA AND DATA

We used distribution data on 1296 species of freshwater fish ($n = 511$), molluscs ($n = 617$), odonates ($n = 73$) and plants ($n = 95$), each of which was globally assessed according to the IUCN Red List process (IUCN, 2013). Species taxonomy, nomenclature and threat categories used in this paper follow the Red List. Critically endangered (CR), endangered (EN) and vulnerable (VU) species are considered jointly as threatened species. We also included species in all other Red List categories, data deficient (DD), least concern (LC) and near threatened (NT) species but excluded all extinct (EX) and extinct in the wild (EW) species from the analysis. We also filtered species occurrences based on their degree of certainty and origin (see Data S1, Supporting Information).

Species occurrence data were mapped to catchment units of HydroBASINS (Lehner & Grill 2013), a global standardised hydrological data base. Of the 12 hierarchical levels of HydroBASINS, we used level 8, where our study area (Fig. 1; 10 128 044 km^2) comprises 18 816 catchments or planning units (mean area 538·3 ± SD 649·45 km^2).

We obtained data on existing protected areas both from the European Union's Natura 2000 system of protected areas (www.eea.europa.eu, December 2012, data on all sites) and the World Database on Protected Areas (WDPA, www.wdpa.org, July 2013; IUCN categories I–IV).

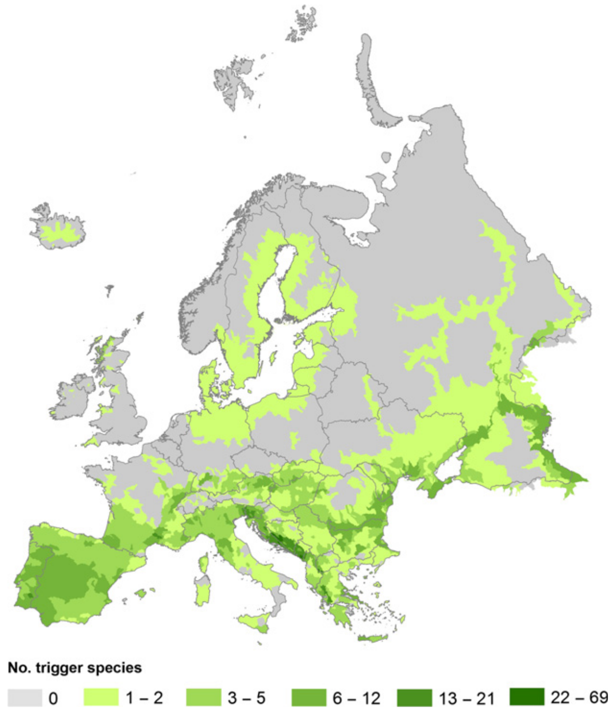

Fig. 1. Critical Catchments for fishes, molluscs, odonates and aquatic plants, with catchments shaded by the number of distinct trigger species. [Colour figure can be viewed at wileyonlinelibrary.com]

IDENTIFICATION OF CRITICAL CATCHMENTS

In the first step, we identified Critical Catchments based on three criteria and corresponding thresholds (see below) examined in detail in Holland, Darwall & Smith (2012). We applied the criteria to the species in each catchment and if at least one criterion was met, the catchment qualified as a Critical Catchment. Species satisfying the criteria are called 'trigger species' hereafter.

Criterion 1: A catchment is known or thought to hold one or more globally threatened species.
Threshold: The presence of one or more threatened species will trigger the site as a Critical Catchment. Critical Catchments thus included all potential AZE sites (Ricketts *et al.* 2005).

Criterion 2: A catchment is known or thought to hold one or more species with restricted ranges.

Threshold: A range smaller than 20 000 km^2 was considered restricted for fishes, plants and molluscs, and a threshold of 50 000 km^2 was applied to odonates, where most species have high dispersal ability and large ranges.

Criterion 3: A catchment is known or thought to hold a significant proportion of species that are confined to an appropriate biogeographic unit.

Threshold: At least 25% of the species from a specific taxonomic group within the catchment are restricted (endemic) to the biogeographic region in which the catchment is located. The freshwater ecoregion (Abell *et al.* 2008) is used as the biogeographic unit because, unlike many other delineations, it is defined in large part by catchment boundaries. This Criterion complements the species-based Criteria 1 and 2 and considers biogeographically unique assemblages. Such areas usually have high proportions of endemic species, whose confinement to certain ecoregions often predisposes them to become vulnerable to extinction.

PRIORITISATION OF CRITICAL CATCHMENTS

In the second step, we prioritised all catchments that qualified as Critical Catchments based on Criteria 1–3 above, first with no consideration of protected areas (Scenario 1), then with protected areas considered (Scenario 2). In addition, we also prioritised all catchments in Europe regardless of whether they qualified as Critical Catchments or whether they contained protected areas to provide a baseline for comparison (Scenario 3). We used Marxan (version 2.4.3, Ball, Possingham & Watts 2009) to identify the optimal network that meets the species targets specified at the lowest possible cost and to prioritise catchments based on their irreplaceability. We used catchment area (km^2) as a proxy for cost (Moilanen, Wilson & Possingham 2008), and we set the maximum total cost as 17% of the area of Europe. This value was based on Aichi Target 11 which specifies that 17% of terrestrial and inland water areas are to be protected by 2020 (http://www.cbd.int/sp/targets/).

In each of the three scenarios, we defined more stringent targets based on species representation. We set up Marxan to cover 100% of the occurrences of CR species, at least 75% of the occurrences of EN species and at least 50% of the occurrences of VU species. For all other species, two occurrences were specified as targets. These targets were based on those tested for freshwater KBAs by Holland, Darwall & Smith (2012). To ensure that targets for threatened species were met, we used a species penalty factor of 1 000 000 for CR, 1000 for EN and 10 for VU species. The 1% of Critical Catchments ($n = 99$) that qualified under Criterion 3 were included *a priori* ('locked in') in each scenario.

In Scenario 1, no information on protected areas was used and only catchments qualifying under Criterion 3 were locked in. In Scenario 2, we followed a pragmatic approach to conservation and included catchments adequately covered by protected areas and AZE sites. We considered Critical Catchments adequately protected if at least 70% of their area was protected (Holland, Darwall & Smith 2012). The 70% threshold was based on previous estimates suggesting that if disturbance in a catchment exceeds 30% of the catchment area, there is often a notable decline in the quality of a river system (Allan 2004). We also locked in catchments with AZE sites as their loss would likely lead to the extinction of AZE species. In total, in Scenario 2, we locked in 7% of Critical Catchments ($n = 587$ catchments either qualifying under Criterion 3 or protected in at least 70% of the area or containing AZEs), while any of the remaining 93% of Critical Catchments could be selected in the prioritisation.

Finally, in Scenario 3, we prioritised all catchments in Europe and locked in only Criterion 3 catchments ($n = 99$), while all other catchments could be selected. This prioritisation ensured the full use of complementarity, one of the key principles of spatial prioritisation, and provided a reference to compare with results from Scenarios 1 and 2. If such a comparison demonstrates little difference between scenarios, then prioritisation can reasonably progress from a subset of catchments, as recommended in cases when there are data gaps, which is often the case in large-scale prioritisations. In contrast, if there are substantial differences, such an approach would not be recommended.

Each Marxan run started with a random 10% of the selectable catchments and progressed with the main parameters of the simulated annealing algorithm set at their default values as recommended in Ardron, Possingham & Klein (2010). We ran each scenario 1000 times and used the number of times a catchment was selected in the optimal network (selection frequency) as a measure of its irreplaceability. We considered catchments selected in each of the 1000 runs as 'irreplaceable'.

Our catchment data base did not have a fully resolved topology of the hydrological relationships among catchments, which prevented us from using hydrological connectivity in the prioritisation. However, some basic level of connectivity can be controlled in Marxan by the Boundary Length Modifier (BLM). This parameter controls the length of the boundaries of the selected network relative to the area selected for protection, with higher values leading to more clumped, less fragmented networks. To find an optimal BLM, we ran each scenario by varying the BLM at six levels (0·001, 0·01, 0·1, 1, 10 and 25). We then compared the total boundary length relative to the area protected and evaluated the results at each BLM level as recommended in Stewart & Possingham (2005). We found that a BLM of 10 was a suitable compromise between fragmentation, geographical representation and coverage of threatened species, and this value was used in all prioritisations.

Finally, we mapped two Marxan outputs, the minimum-cost network that best met the pre-defined targets for each scenario, and catchment irreplaceability measured by selection frequency. Furthermore, we present the number and proportion of threatened species for which targets were met for each scenario.

GAP ANALYSES

We first conducted a gap analysis between all Critical Catchments and the protected area network represented by the union of polygons from the WDPA and Natura 2000 data bases. Following Rodrigues *et al.* (2004), if protected areas overlapped any part of a Critical Catchment, it was considered to be 'covered' and did not constitute a 'gap'. This approach is a theoretical best case scenario since any arbitrary threshold of coverage is not necessarily an accurate representation of effective protection. We then summarised the geographic distribution and proportion of coverage of Critical Catchments, AZEs catchments and CR trigger species. We similarly examined coverage by Ramsar sites.

Second, using the same method as above, we identified gaps in spatial overlap between either the full or the prioritised Critical Catchment networks and the Natura 2000 protected areas. We then identified the Critical Catchments, AZE catchments, CR/EN trigger species and, in particular, the irreplaceable Critical Catchments not covered by Natura 2000 areas. We highlight these gaps as potential targets for the expansion of Natura 2000 areas and for conservation initiatives other than Natura 2000. All data preparation and analyses were conducted using R version 2.15.2/3 (R Core Team, 2012), ArcGIS 10 and MS Access 2010.

Results

IDENTIFICATION OF CRITICAL CATCHMENTS

A total of 8423 Critical Catchments were identified covering 4 578 193 km^2 or 45% of Europe (Fig. 1). These catchments are mainly located in southern Europe and were triggered by 766 distinct species (Table 1). The catchment with the maximum number of trigger species ($n = 69$) was Lake Ohrid (western Balkans). The number of distinct species and catchments across criteria and taxon groups is shown in Table 1 (see Fig. S1 for Critical Catchments per taxon group).

Table 1. Number of trigger species and number of triggered catchments for threatened species (C1), restricted range species (C2), and ecoregion-restricted communities (C3) and all criteria (C1–C3) for each taxon group

	Number of trigger species				Number of triggered catchments			
	C1–C3	C1	C2	C3	C1–C3	C1	C2	C3
Fishes	260	186	218	18	7547	7320	856	99
Molluscs	479	349	465	53	2724	2269	1621	1
Odonates	7	6	5	0	642	632	119	0
Plants	20	15	12	0	988	979	85	0
Total	766	556	700	71	8423	8144	2207	99

The total for catchments is the number of *distinct* catchments and is thus not the sum of the rows.

Ninety-seven per cent of Critical Catchments qualified under Criterion 1 and 26% qualified under Criterion 2 with all four taxon groups contributing trigger species. Only fishes and molluscs triggered Criterion 3 (Table 1), with all 99 Critical Catchments located in three ecoregions (Iceland – Jan Mayen, Northern British Isles and Southeast Adriatic Drainages). Molluscs only triggered Criterion 3 within the Southeast Adriatic Drainages ecoregion, while fishes triggered Criterion 3 within each of the three ecoregions.

Sixty-five AZE catchments were identified (see Fig. S2). Fishes, molluscs and plants comprised the AZE species. There were 73 CR AZE species and 44 EN AZE species. The AZE catchment with most AZE species ($n = 26$) was Lake Ohrid. The majority of AZE catchments contained only one AZE species (see Table S1).

PRIORITISATION OF CRITICAL CATCHMENTS

Our spatial prioritisation identified the 17% of the area of Europe that was most important for preventing the loss of freshwater biodiversity (Fig. 2). In comparison to the full set of Critical Catchments (Fig. 1), the priority catchments selected in the three scenarios (Fig. 2) were mostly in southern and eastern Europe. Critical Catchments missing from the prioritised networks were those containing one or two trigger species in north-western or north-eastern Europe. The prioritisation selected 3401 Critical Catchments in Scenario 1, 3492 in Scenario 2 and 3776 in Scenario 3, corresponding to 40%, 41% and 45% of the total number of Critical Catchments ($n = 8423$), respectively. Sixty-five per cent of Critical Catchments selected ($n = 2719$) were shared by Scenarios 1 and 2, and 682 of

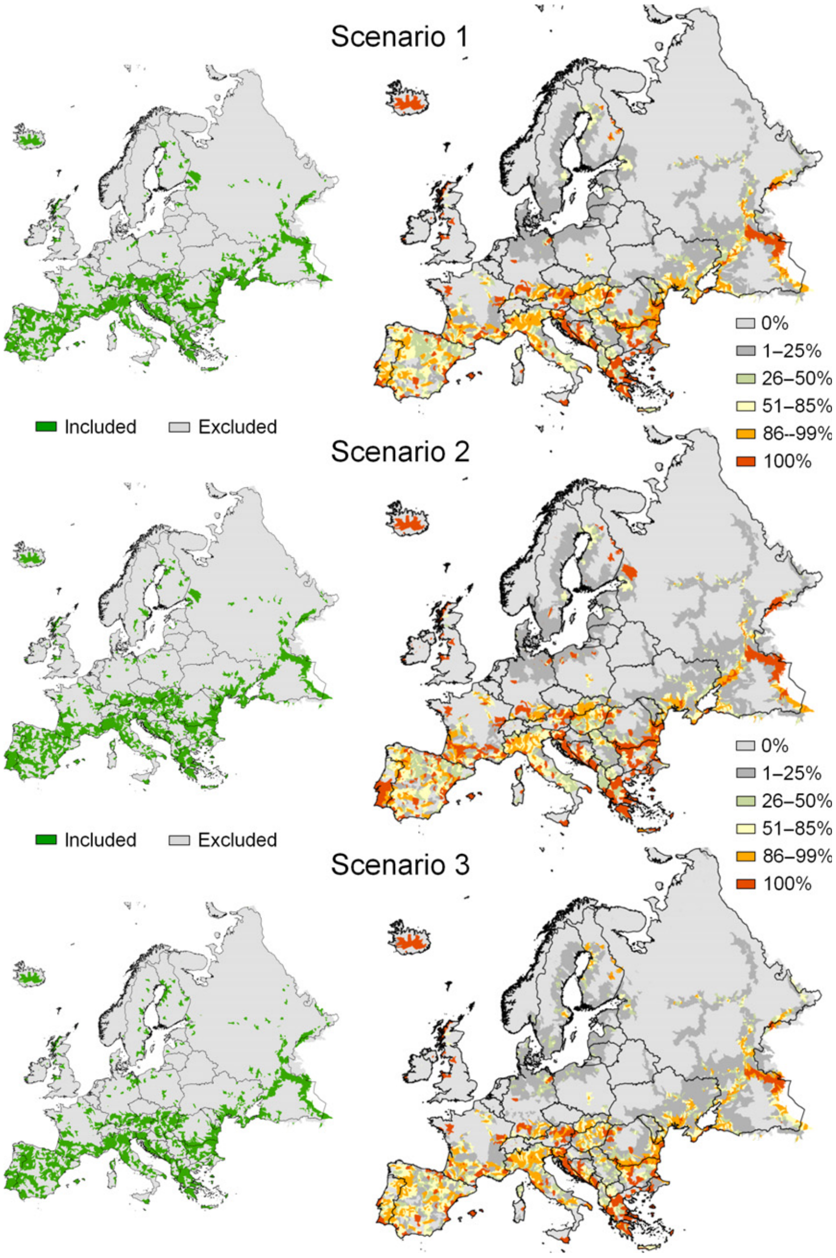

Fig. 2. Catchments included in the best solution of 1000 Marxan prioritisations (left column) and catchment irreplaceability as estimated by selection frequency (%) in 1000 runs of Marxan (right column) in the three scenarios. [Colour figure can be viewed at wileyonlinelibrary.com]

the Critical Catchments were unique to Scenario 1 and 773 were unique to Scenario 2 (see Fig. S3), and 718 Critical Catchments were shared by all three Scenarios.

A visual examination revealed little difference among the three scenarios (Fig. 2). The proportion of Critical Catchments returned as Irreplaceable was highest in Scenario 2 (1408 catchments or 40% of 3401 catchments), lower in Scenario 1 (902 or 27% of 3492) and lowest in Scenario 3 (741 or 20% of 3776). There was a slightly higher emphasis on northern catchments (e.g. Finland, northern Russia, Sweden), south-western catchments (southern Portugal, southern France) and south-eastern catchments (lower Danube) in Scenario 2 compared to Scenario 1. This was not surprising because in Scenario 2, the prioritisation was started with the best protected 5% of Critical Catchments (n = 435) locked in and Marxan tends to select areas neighbouring locked-in catchments as it aims to minimise boundary costs.

The proportion of threatened (CR, EN, VU) species for which targets were met was 97·1% in Scenario 1, 98·2% in Scenario 2 and 96·8% in Scenario 3 (total $n = 556$ threatened species). The number of threatened species for which targets were not met was 16 in Scenario 1, 10 in Scenario 2 and 18 in Scenario 3 (Table 2). However, for almost all of these species, many of which were charismatic, locally rare fish with large distribution ranges (e.g. sturgeons *Acipenser* spp.), at least 100 000 km^2 of the native range and/or at least 60% of the native range was covered by the best network (Table 3). We thus concluded that the optimal network identified by Marxan adequately covered the ranges of the large majority of threatened species in each scenario.

Table 2. Number of species for which targets were met or not in the three scenarios

Red List status	Scenario 1 Met	Scenario 1 Not met	Scenario 2 Met	Scenario 2 Not met	Scenario 3 Met	Scenario 3 Not met
CR	144	8	147	5	142	10
EN	141	5	144	2	142	4
VU	255	3	255	3	254	4
NT	96	11	96	11	97	10
LC	521	33	521	33	535	19
DD	60	19	60	19	62	17
Total	1217	79	1223	73	1232	64

GAP ANALYSES

In our first gap analysis, we found that 23% of Critical Catchments (n = 8423) were not spatially covered by protected areas, and 73% had less than 20% overlap with protected areas. Only about 6% of Critical Catchments, including 11 AZE catchments, had more than 70% coverage by protected areas. Critical Catchments representing gaps in protected area coverage are mostly located in the Balkans and eastern Europe (Fig. 3). The Drin AZE catchment in Montenegro, home to the last population of the mollusc *Saxurinator orthodoxus*, has no protected area coverage. In contrast, Lake Vistonis AZE and Lake Ioannina AZE in Greece, home to the only populations of fish species *Alosa vistonica* and *Pelasgus epiroticus* respectively, are 100% covered by protected areas. A total area of 15 916 km^2 of Critical Catchments is overlapped by Ramsar sites. The area of Critical Catchments covered by Ramsar sites but not covered by Natura 2000 is 3941 km^2. These are mainly located in the Balkans, Switzerland and small areas of Portugal, Norway and Monaco.

In our second gap analysis, we found that 44% of the full set of Critical Catchments we identified (n = 8423) had no spatial overlap with any protected area. In Scenario 1, where the best Critical Catchments were chosen, 42% were not covered by any protected area. In Scenario 2, where Critical Catchments with at least 70% spatial overlap with protected areas were locked in, the percentage of gaps dropped slightly to 38%. In Scenario 2, over half (58%) of the Critical Catchments had less than 10% spatial overlap with Natura 2000 areas (see Table S2 for country results). There were 87 CR (n = 42) or EN

Table 3. Number of occurrences ('No. occ.'), area and per cent of range covered by the best Marxan solution for threatened species (CR, EN, VU) for which targets were not met

Species name	Red list status	Native range		Scenario 1			Scenario 2			Scenario 3		
		No. occ.	km^2	No. occ. Covered	Range covered km^2	Range covered %	No. occ. Covered	Range covered km^2	Range covered %	No. occ. Covered	Range covered km^2	Range covered %
Acipenser gueldenstaedtii	CR	675	376 908	648	339 747	90·1	629	327 476	86·9	616	291 577	77·4
Acipenser nudiventris	CR	126	91 634	123	87 358	95·3	124	89 449	97·6	120	81 001	88·4
Acipenser persicus	CR	213	162 252	189	129 834	80·0	187	124 698	76·9	183	114 496	70·6
Acipenser stellatus	CR	767	431 860	681	351 503	81·4	662	340 118	78·8	674	309 485	71·7
Acipenser sturio	CR	50	34 681	48	31 113	89·7				43	22 782	65·7
Coregonus trybomi	CR	30	11 192							28	9 198	82·2
Huso huso	CR	334	201 237	327	191 981	95·4				324	178 989	88·9
Iberochondrostoma lusitanicus	CR	45	29 024	40	22 692	78·2				40	22 937	79·0
Margaritifera auricularia	CR	153	64 066	128	48 298	75·4	145	58 467	91·3	131	48 560	75·8
Pyrrhosoma elisabethae	CR	25	18 959							24	17 482	92·2
Boyeria cretensis	EN	9	8657	8	5394	62·3						
Bythinella viridis	EN	6	5450	5	3967	72·8						
Cobitis calderoni	EN	386	203 908	282	119 515	58·6	289	131 018	64·3	311	126 993	62·3
Hucho hucho	EN	222	143 913	171	100 866	70·1				155	88 062	61·2
Squalius lucumonis	EN	55	41 042							45	28 513	69·5
Theodoxus transversalis	EN	703	387 681	497	241 054	62·2	496	240 831	62·1	533	234 013	60·4
Acipenser ruthenus	VU	1659	842 414	839	371 937	44·2	752	335 353	39·8	885	353 955	42·0
Alisma wahlenbergii	VU	111	58 433							80	27 573	47·2
Coregonus maraena	VU	1868	864 090	166	61 885	7·2	260	84 543	9·8	285	77 395	9·0
Cyprinus carpio	VU	2201	1 305 623	1189	537 980	41·2	1054	480 012	36·8	1206	491 621	37·7

Empty cells indicate that targets were met.

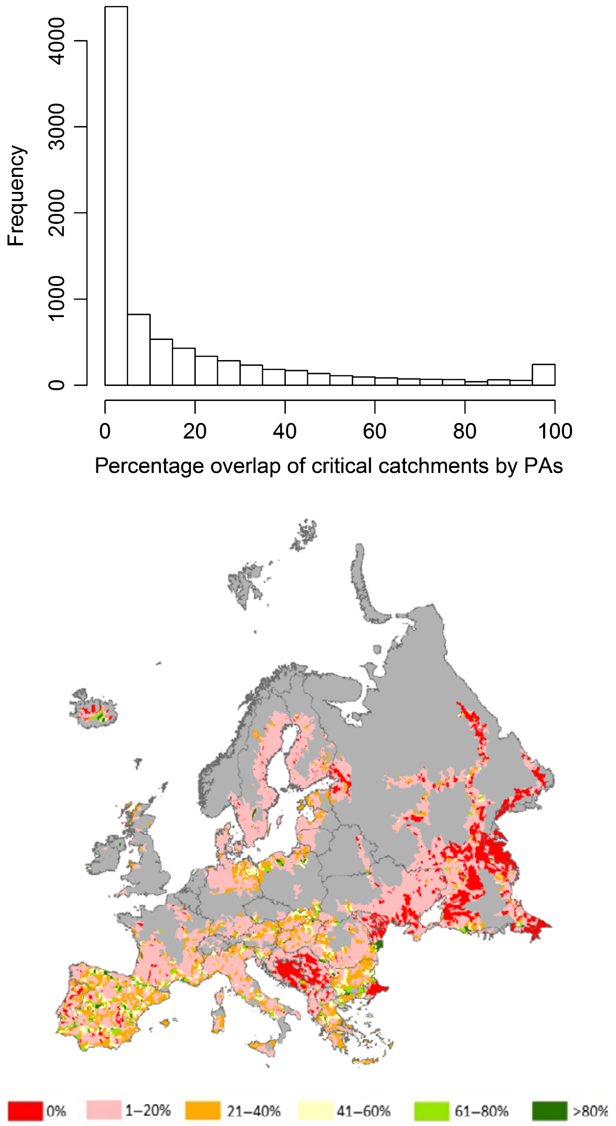

Fig. 3. Frequency distribution and spatial patterns in the percentage of overlap of Critical Catchments by protected areas (PAs). [Colour figure can be viewed at wileyonlinelibrary.com]

(n = 45) species that had no coverage by Natura 2000 areas, comprising 28 fishes, 58 molluscs and 1 plant species (see Table S3). Similarly, 20% of the 65 AZE catchments and 31% or 435 of the irreplaceable catchments did not overlap with Natura 2000 areas. Seventy-one per cent (n = 2486) of the Critical Catchments selected in Scenario 2 contained fewer than five trigger species. Of those with more than five trigger species, 37% had no spatial coverage by Natura 2000 areas, including all but one of the 17 Critical Catchments with the most trigger species.

Discussion

Our study highlights the spatial mismatch between freshwater biodiversity and the protected areas of Europe. Our findings suggest that protected areas do not currently provide sufficient coverage to the most important Critical Catchments. With no improvements to the current configuration and perhaps management, European countries are unlikely to meet international obligations to reverse the loss of biodiversity.

We suggest several ways in which our results can be utilised to identify threats to freshwater biodiversity and shortfalls in conservation and management. First, the trigger species we identified (i.e. threatened, restricted range and ecoregion-restricted species) should become the focus of/require conservation and/or management. With minimum estimates of 44% of freshwater mollusc species, 37% of freshwater fish species, 15% of dragonflies and 7% of aquatic plants threatened in Europe (Cuttelod, Seddon & Neubert 2011), it is crucial that the freshwater species we identified are targets for conservation (see ‘Data accessibility’ for trigger species lists).

Second, at the time of writing, 23 member states are yet to complete the EC requirement for identifying and designating new Natura 2000 areas (Crofts 2014). We suggest there is now an opportunity for member states and the European Environment Agency to utilise our results to guide the strategic expansion of Natura 2000 areas. As well as designating new sites, gaps may be addressed by expanding existing sites to include nearby freshwater features (Juffe-Bignoli *et al.* 2016). Ideally, a conceptual shift away from the terrestrial focus is necessary when managing freshwater ecosystems (Abell, Allan & Lehner 2007). Catchment-scale management of both biodiversity and human activities is required (Moss 1999; Nel *et al.* 2009). This concept directly aligns with the principles of ‘wider countryside measures’ of the EU Habitats Directive and the provisions for whole catchment management in the EU Water Framework Directive (WFD) (Crofts 2014). Our prioritisation and gap analysis can contribute to improvements in coverage.

Third, once delineated within Critical Catchments, the recognition of freshwater KBAs (for instance on https://www.ibatforbusiness.org/), especially those that are not covered by protected areas, may facilitate environmental safeguards to be met by the private and public sectors. Raising the awareness of stakeholders that affect the water quality and flow regime of the Critical Catchments will be as key to protecting freshwater biodiversity as the integrity of a protected area network.

Fourth, we found that about 94% of Critical Catchments have less than 30% spatial overlap with protected areas. We thus propose that a good starting point for identifying potential restoration targets could be those Critical Catchments that are irreplaceable and have limited spatial overlap with protected areas. Critical Catchments can thus help to address the Aichi Biodiversity Target 15 and Target 2 of the EU Biodiversity Strategy to 2020 which aim to restore ‘at least 15% of degraded ecosystems’. This also aligns with the objective of the WFD to achieve ‘good ecological status’ for all surface waters by 2015, although questionable implementation of the WFD habitat monitoring requirements is hampering the achievement of this goal (Moss 2008; EC, 2012). Highlighting Critical Catchments for potential restoration may help to focus the WFD's habitat monitoring and to guide restoration efforts to those catchments where favourable outcomes could be greatest while also contributing to the implementation of the EU Blueprint to Safeguard Europe's Water Resources. This is especially important for improving habitat quality and connectivity for catchments outside the Natura 2000 network. Future studies could integrate restoration into prioritisation. For example, Linke *et al.* (2012) focused on conservation targets in the catchments in the best condition by integrating area scaled by threat into a cost metric such that area was discounted if the threat level was low.

Our framework for the conservation of European freshwater biodiversity can be developed further in several ways. The Critical Catchments we identified represent the management zones for future freshwater KBAs that are of importance for the global persistence of freshwater biodiversity. However, some Critical Catchments may be sub-optimal for protection due to intensive land use, urbanisation or altered hydromorphology (e.g. dams) within catchments. Thus, prioritisation trading off catchments based on conservation feasibility, catchment vulnerability and opportunity costs would help to further refine 'conservation' priorities. In addition, an approach that includes common species that may be threatened in the future, environmental gradients acting as coarse filters to capture poorly sampled species and habitats or ecosystems necessary to maintain threatened species would also be desirable (Khoury, Higgins & Weitzell 2010). We therefore recommend that future studies apply systematic conservation planning (SCP) to build on this study. It is important to note that spatial prioritisation provides only possible outcomes of scenarios and not the final answer to a conservation planning problem. Prioritisation is usually a place to start SCP, and needs to be iterated as better knowledge on model parameters and stakeholder input becomes available during the process (Margules & Pressey 2000). For example, future studies could incorporate socioeconomic data to achieve the same biodiversity targets while minimising conflict or opportunity costs with human activities such as mining, forestry and agriculture (Carwardine *et al.* 2008a). Furthermore, ecosystem service targets and their overlap with biodiversity targets can be used to build a stronger economic case for catchment protection. Moreover, incorporating species distribution shifts expected under different climate scenarios into the prioritisation would allow detecting catchments that are suitable for climate change adaptation (Groves *et al.* 2012; Markovic *et al.* 2014). Finally, species-based approaches may have limitations, for example, by focusing on threatened species only. More proactive approaches that use alternative methods could focus on ecosystem status or condition or on species assemblages representative of different regions before they become threatened (e.g. Khoury, Higgins & Weitzell 2010). For example, hierarchical methods can represent species and ecosystems across both regional environmental gradients and species assemblages by the stratification of species occurrences across gradients (Higgins *et al.* 2005). However, the inclusion of information on ecosystem status or condition may identify an alternative set of catchments which may lead to results that are more realistic for conservation actions but are poorer for species representation (Heiner *et al.* 2011).

We acknowledge that gap analysis based on protected area coverage alone does not necessarily reflect efficacy. For instance, Geiger *et al.* (2014) suggest that fish species *A. vistonica* and *P. epiroticus* may have recently gone extinct, despite 100% of their lake habitats being protected in Greece. This demonstrates that site protection alone is insufficient to safeguard freshwater biodiversity. Furthermore, many Natura 2000 sites in freshwater ecosystems are in 'bad' condition (Eionet, 2009) suggesting a poor outlook for freshwater biodiversity despite the overlap with protected areas. We further caution that our estimates of gaps were likely underestimated, as overlap of part of a Critical Catchment does not necessarily mean overlap of the freshwater features of interest. We suggest review of management plans in addition to coverage to obtain a more in-depth evaluation of the benefits provided by each protected area (Thieme *et al.* 2016). Finally, the gap thresholds can also be tailored to the specific requirements of different species (see Rodrigues *et al.* 2004 for examples of species specific considerations of thresholds for gap species). Our approach is justifiably conservative – the level of effective protection for freshwater biodiversity is likely to be far less than assumed here. Nevertheless, we use this study to indicate a theoretical best case scenario since any arbitrary threshold of coverage is not necessarily an accurate representation of protection, if any. For instance, many protected areas could be 'paper parks' or they could have management plans with little, if any, focus on freshwater biodiversity. Generally, it is increasingly acknowledged that enlarging protected areas may not be sufficient to protect freshwater biodiversity and to meet the ambitious goals of international policies (Thieme *et al.* 2016). Often there is a need for additional conservation actions.

Hydrological connectivity among catchments is an important issue for freshwater ecosystems, both across and within country borders (Hermoso *et al.* 2011). Incorporating connectivity would allow for spatial clumping along connected river networks scaled by distance to the selected catchment with closer catchments having a higher penalty factor. Incorporating connectivity would likely change our results by increasing the irreplaceability of a larger number of suitable catchments within only a few river systems, resulting in a spatially more compact solution (Hermoso *et al.* 2011). Connectivity based on upstream, downstream or bi-directional connectivity is possible to specify in Marxan (Beger *et al.* 2010) and Zonation (Moilanen, Wilson & Possingham 2008) if a fully resolved topology of the river network is available. For simplicity, Linke *et al.* (2012) applied upstream connectivity only, while a heuristic whole catchment approach was taken in Linke *et al.* (2007). Although the BLM used in our prioritisations provides an approximation to connectivity, it does not consider the river network, and clumping may take place across unconnected catchment boundaries. For these reasons, we recommend inclusion of connectivity in future studies to ensure adequate upstream protection of Critical Catchments.

The identification of Critical Catchments, and their component KBAs, provides a powerful new tool for focusing greater investment on the conservation of freshwater species and their habitats and for meeting international conservation targets such as in the CBD and the EU Biodiversity Strategy (EC, 2011). We show how Critical Catchments for freshwater biodiversity are distributed across Europe and that there are opportunities to strengthen protection at these sites. We proposed an initial step in how Europe could prioritise globally important Critical Catchments to meet the Aichi 17% protection target while making best use of existing protected areas, and identified where such catchments might alternatively provide a focus for habitat restoration targets. Our study highlights the potential areas where this approach could work effectively in developing solutions through the science-policy-interface and we hope it will serve as a model for others to follow. Efforts are now needed to engage EU stakeholders in fine-tuning and ultimately implementing a strategy that addresses the ongoing loss of freshwater biodiversity in Europe. This study represents an important first step in this direction.

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Data accessibility

Critical Catchment factsheets including trigger species lists: http://www.birdlife.org/datazone/freshwater

HydroBASINS layer ('Format 2'): http://hydrosheds.org/page/hydrobasins

The species distribution data are available from: https://www.iucn.org/theme/species/our-work/freshwater-biodiversity/what-we-do/biofresh-0

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Supporting Information

Details of electronic Supporting Information are provided below.

Data S1. Methods.

Table S1. AZE catchments and species in Europe.

Table S2. Critical Catchments area and proportion of coverage by Natura 2000 areas in EU member states.

Table S3. List of CR and EN species not covered by Natura 2000 areas.

Fig. S1. Critical Catchments for fishes, molluscs, aquatic plants and odonates.

Fig. S2. Location of AZE catchments.

Fig. S3. Critical Catchments common in Scenarios 1 and 2 and specific to Scenario 1 or 2.