Overlooked risks and opportunities for global protected areas revealed by mapping groundwatersheds

David Serrano¹[†], Xander Huggins^{1,2}[†]^{*}, Tom Gleeson^{1,3}, Sam Zipper⁴, Florian Jehn⁵, Melissa M. Rohde⁶, Robin Abell⁷, Kari Vigerstol⁶, Andreas Hartmann⁸

¹ Department of Civil Engineering, University of Victoria, Victoria, Canada

- ² Global Institute for Water Security, University of Saskatchewan, Saskatoon, Canada
- ³ School of Earth and Ocean Sciences, University of Victoria, Victoria, Canada
- ⁴ Kansas Geological Survey, University of Kansas, Lawrence (KS), USA
- ⁵ University of Freiburg, Freiburg, Germany
- ⁶ The Nature Conservancy
- ⁷ Conservation International
- ⁸ Institute of Groundwater Management, TU Dresden, Dresden, Germany
- † These authors contributed equally to this work.
- * Corresponding author: xanderhuggins@uvic.ca

ORCIDs:

| David Serrano: | 0000-0002-8293-7280 |
|-------------------|---------------------|
| Xander Huggins: | 0000-0002-6313-8299 |
| Tom Gleeson: | 0000-0001-9493-7707 |
| Sam Zipper: | 0000-0002-8735-5757 |
| Melissa M. Rohde: | 0000-0002-1252-0711 |
| Robin Abell: | 0000-0001-9407-7807 |
| Kari Vigerstol: | 0000-0003-1877-6133 |
| Andreas Hartmann: | 0000-0003-0407-742X |

Abstract

- Protected areas are a key tool for conserving biodiversity, sustaining ecosystem services and
- 2 improving human well-being. Global initiatives that aim to expand and connect protected areas
- 3 generally focus on controlling 'above ground' impacts such as land use, overlooking the
- 4 potential for human actions in adjacent areas to affect protected areas through groundwater
- 5 flow. Here, we assess the potential footprint of these impacts by mapping groundwatersheds, a
- 6 groundwater-modified watershed delineation. We find that most groundwatersheds (83%) of the
- 7 world's protected areas are partially unprotected and are overall only 52% protected by surface
- 8 area. These findings highlight a widespread potential risk to protected areas if activities affecting
- 9 groundwater are uncontrolled within their groundwatersheds, underscoring the need for
- 10 groundwatershed-focused protection measures. Delineating groundwatersheds can catalyze

needed discussions about protected area connectivity and effectiveness, and investments in
 groundwatershed conservation and management that can help ensure groundwater-dependent
 ecosystems are uncompromised by avoidable external underground threats.

14 Main Text

Protected areas are fundamental tools for safeguarding biodiversity and play an 15 important role in improving human well-being and sustaining ecosystem services¹⁻⁵. Yet, current 16 land protections have had clear limitations in regard to conserving freshwater ecosystems and 17 species, which have shown staggering declines^{6,7}. One often-cited reason for this inefficacy is 18 the lack of protection for hydrologically connected freshwater systems outside (i.e., upstream 19 and downstream) of protected areas^{8,9}. With the development of the Convention on Biological 20 Diversity's Post-2020 Global Biodiversity Framework¹⁰, members of the conservation community 21 have advocated for expansion of the network of protected areas to cover 30% of terrestrial, 22 inland water, and sea areas by 2030¹¹. The draft '30x30' target goes beyond coverage to also 23 include management effectiveness, yet the need to manage human activities in connected lands 24 and waters outside protected areas is absent from effectiveness discussions and indicators¹². 25 Examples of iconic protected areas like Doñana National Park¹³ and Grand Canyon National 26 Park¹⁴ illustrate how impacts from activities such as agricultural drainage, mining, and 27 28 groundwater pumping can affect internal protected area processes and compromise protection effectiveness. 29

As human land and water use intensifies around many protected areas^{2,15}, the management of surrounding groundwater becomes increasingly important. No systematic study has investigated the potential for human activities outside of protected areas to have impacts on protected areas through groundwater flow (Figure 1). Lateral groundwater flow supplies a significant proportion of water used by vegetation¹⁶, and changes in land use or land cover can impact downgradient terrestrial ecosystems by changing the quantity and distribution of

groundwater^{17,18}. Aquatic ecosystems can also be threatened by human activities transmitted
 through groundwater flow. Groundwater pumping, for instance, can reduce streamflow and drive
 streams from perennial to intermittent, ephemeral, or even disconnected¹⁹⁻²³. In addition, since
 groundwater provides distinct chemical and temperature attributes and can transmit
 contaminants such as nutrients²⁴, changes in groundwater levels and flow can introduce
 pollutants or otherwise alter water quality in protected areas²⁵.

42 In this study, we estimate the area from which human impacts may propagate via groundwater flow to protected areas. We employ a generic, reproducible workflow to derive 43 groundwatersheds (Box 1 and Supplementary Information) and apply this methodology to (i) 44 map and identify the groundwatersheds of the world's protected areas; (ii) assess physical 45 controls on the size of groundwatersheds; and (iii) identify risks to existing protected areas and 46 47 opportunities for improved conservation outcomes. By developing and applying the groundwatershed concept, we reveal areas contributing localized groundwater flow to the 48 world's protected areas. 49

Box 1: What are groundwatersheds?

Groundwatersheds are the area from which localized groundwater systems flow to a feature (Figure 1). Groundwatersheds are similar to surface watersheds, which are derived based on the topography of the land surface. Instead, groundwatersheds are derived from the topography of the water table. While the water table is generally understood as a subdued replica of the land surface topography, this assumption is not uniformly valid²⁶. Thus, the contributing groundwatershed and surface watershed can be spatially misaligned for the same draining feature²⁷. Groundwatersheds, like surface watersheds, can be identified for any feature (e.g., protected area, city, individual well, etc.) but unlike watersheds defined by static topography, groundwatersheds are dynamic in that their size and shape can change with the water table due to pumping, climate change, land use change, or seasonality. Therefore, groundwatersheds can be affected by a multitude of natural and human factors including aridity, infiltration capacity, recharge, evaporation rates, and land use. However, we expect the majority of each mapped groundwatershed to be static because fluctuations in the water

table will only correspond to changes in the groundwatershed extent if the location of divergent water table slopes are altered. We believe the groundwatershed concept was first introduced by Haitjema²⁸ to evaluate groundwater residence times, and similar concepts have been called *groundwater catchments*²⁹, *groundwater basins*³⁰, and mapping of *groundwater divides*³¹. However, the concept has seen limited uptake in water science and management likely because groundwater is often an overlooked resource. Mapping the groundwatersheds of protected areas is only one of many possible applications and therefore this work can serve as a proof-of-concept for wider application of groundwatersheds to inform a range of decisions, such as protecting drinking water sources.

In our parsimonious approach to derive groundwatersheds, it is only necessary to have a spatially distributed representation of the water table and the spatial location or extent of the feature(s) whose groundwatershed is to be determined. For this study, we rely on seven core global data sources to map groundwatersheds: a global database of protected areas³², a depth to water table map³³, a maximum rooting depth map³⁴, the water table and rooting depth studies' associated land surface digital elevation model, a map of groundwater-driven wetlands³⁵, a map of surface water bodies³⁶, and a line network of perennial rivers³⁷. We identify locations where groundwater is likely connected to terrestrial or aquatic ecosystems (herein called 'ecologically connected areas') if an area satisfies one of four possible criteria: if the root zone intersects the water table for at least one month per year, or if there exists a groundwater-driven wetland, perennial stream, or surface water body. This approach can be considered a globally consistent but rudimentary mapping of groundwater-dependent terrestrial and aquatic ecosystems, although we do not include subsurface ecosystems explicitly³⁸. We then use these identified locations within protected areas as 'outlets' for a watershed delineation algorithm using the water table surface in replacement of the land surface. Finally, we identify groundwatersheds for each protected area by spatially joining groundwatersheds for all ecologically connected areas within each protected area (see Methods).



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Here, we derive groundwatersheds for ecologically connected areas of the world's protected areas. We consider areas to be ecologically connected if roots reach the water table or if other features such as wetlands, lakes, or perennial rivers exist.



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And we use these metrics to report how the groundwatersheds of the world's protected areas vary around the world:



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52 Figure 1. Overview of the groundwatersheds concept, and our application of the concept

in this study. (a) Conceptual model of groundwatersheds for features of interest across a
 landscape. (b) Mapping groundwatersheds of ecologically connected features within a protected
 area. (c) Metrics to study controls and potential impacts for groundwatersheds.

56 Results

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Groundwatersheds of the world's protected areas

Groundwatersheds for protected areas are 83% larger (23.1 million km²) than the 58 combined size of the protected areas around the world that we considered (12.6 million km²: 59 Supplementary Figure 3). Almost all groundwatersheds extend beyond protected area 60 boundaries. Specifically, across all protected areas with an associated groundwatershed. 83% 61 (~31,200 of ~37,400 spatially contiguous sets of protected areas) have some proportion of their 62 groundwatershed unprotected. This corresponds to 71% of all protected areas globally, as 14% 63 of protected areas did not have an associated groundwatershed. A protected area has no 64 65 associated groundwatershed when no 'ecologically connected areas' are identified within the protected area (see Box 1). Potential cross-boundary impacts of protected areas are large as 66 overall protected areas only encompass 52% of their own groundwatersheds by area. 67 Groundwatersheds also span international boundaries and raise transboundary management 68 concerns: 494 groundwatersheds cross international borders despite their associated protected 69 area existing entirely within a single country. 70

To evaluate the potential importance of groundwatersheds and analyze their relationship 71 with protected areas globally, we defined two metrics (Figure 1c): relative groundwatershed size 72 73 (RGS) and the unprotected groundwatershed ratio (UPR). RGS is an ecohydrological index representing size of the groundwatershed relative to the ecologically connected area within the 74 groundwatershed (Figure 2a). UPR is a socio-hydrological conservation index that represents 75 the unprotected proportion of each groundwatershed (Figure 2f). Overall, groundwatersheds 76 77 tend to be larger in arid regions (Fig 2b) which is consistent with previous modeling of the impact of aridity on regional groundwater flow^{39,40}. Lower RGS values (e.g., as found in the 78 boreal forest of central North America) correspond to groundwatersheds where vegetation is 79 highly connected to the water table. In these humid (low aridity) regions, shallow water tables 80 constrain groundwatershed size (Figure 2b). Conversely, groundwatersheds with high RGS 81

values (e.g., central Sahel and western African, and the Iberian Peninsula) tend to be located in
 more arid regions. Larger groundwatersheds in arid regions suggest groundwater flow is of
 heightened importance for conservation initiatives in these regions.

85 The relationship between RGS and UPR implies that increasing relative groundwatershed size is related to a decreasing degree of protection (Figure 2g). UPR does not 86 significantly vary with the percentage of national land area protected (Supplementary Figure 87 88 4a), implying that even in countries where conservation targets have been met or where there is legislation directed at groundwater protection (such as Figure 2) with the EU Water Framework 89 Directive), groundwatersheds often remain unprotected through conventional protected areas. 90 Further, we find no relationship between UPR and subnational GDP per capita (Supplementary 91 Figure 4b), implying that increasing national wealth does not lead to increased groundwatershed 92 93 protection through formally designated areas. This partially echoes findings that greater increases in effective conservation extents are needed in developed economies than in 94 developing economies to safeguard biodiversity⁴¹. These possibly counterintuitive findings that 95 groundwatersheds may not be better protected in wealthier countries or in countries with greater 96 97 protected area coverage suggests a global misalignment between protected areas and their connected groundwater flow systems and underscores the challenge of conserving protected 98 area ecosystems above and below ground without consideration of groundwater flow. 99

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Figure 2. Mapping the groundwatersheds of the world's protected areas. (a-e) Relative groundwatershed size (RGS). (a) RGS of protected areas, plotted as a point at the centroid of each protected area. (b) Distribution of RGS across aridity classes. (c-e) Extent of groundwatersheds and ecologically connected areas, which are the two inputs used to calculate RGS, shown for (c) central North America, (d) central West Africa, and (e) the Iberian Peninsula. (f-j) Unprotected area. (g) Relationship between RGS and UPR for all protected areas. (h-j) Extent of unprotected groundwatershed area and protected groundwatershed area, which

are the inputs used to calculate UPR, shown for (h) central North America, (i) central West
 Africa, and (j) the Iberian Peninsula.

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Degree of human activity within groundwatersheds

The concept and application of groundwatersheds reveals potential long-range and long-113 term subsurface impacts on features of interest. Activities such as mining, agriculture, and 114 urban expansion, captured in the human modification gradient⁴² (Figure 3a), play a role in 115 determining the potential risk to the quality and quantity of groundwater flow to protected areas. 116 Conceptually, the potential vulnerability of protected areas can be represented by the human 117 modification gradient within unprotection portions of their groundwatersheds (Figure 3b). 118 Specifically, ecologically connected areas within protected areas could be affected most directly 119 by groundwater pumping and contamination, and indirectly via land use or climate change 120 through, for instance, changes to groundwater recharge. The timing and severity of these 121 cumulative impacts would be a function of the type, location and magnitude of the specific 122 stressor, which is beyond this study's scope, but could enable improved management as we 123 describe below. 124

Overall, we see considerable variability in both UPR and the modification gradient for both individual protected areas and when summarized to terrestrial ecoregions of the world (Figure 3b). Regions of greatest concern, where we find high human modification gradients within predominantly unprotected groundwatersheds (i.e., protected areas with high UPR values), include the Midwest to east coast of the USA, across the British Isles and Europe, Western Africa, Northern India, Pakistan, and the east coast of Brazil (Figure 3c).

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Groundwatershed coverage by lower levels of protection

Herein, we have focused on higher levels of protection (IUCN protected area
 management categories I-III). However, expanding our analysis to include lower levels of
 protection (categories IV-VI) reveals that while most groundwatersheds remain unprotected
 when considering lower levels of protection, there are a small set of nations whose lower levels

of protected areas encompass significant proportions of the groundwatershed we have mapped. 136 137 The median national percentage of unprotected groundwatershed surface area (by high levels of protection) that is already protected by lower levels of protection is only 4%. However, 138 Germany, Uruguay, Central African Republic, Myanmar, and South Korea are among a few 139 nations whose lower levels of protected areas cover over 30% of the groundwatersheds that lie 140 outside of their IUCN category I-III protected area (Supplementary Figure 5). While expanding 141 formal area-based protection of groundwatersheds is one approach for mitigating groundwater 142 threats to a protected area that could contribute to the post-2020 Global Biodiversity Framework 143 (Supplementary Figure 6), that approach could be feasible or inappropriate in many contexts 144 and may in fact be unnecessary if activities can be regulated through other means. Prioritizing 145 groundwatersheds for protection would require additional information about timescales and 146 magnitudes of impacts on the protected area. 147



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Figure 3. Implications of groundwatersheds on conservation initiatives. (a) The human modification gradient within the unprotected portion of groundwatersheds for global protected areas. Protected areas with no unprotected groundwatershed area are not shown. (b, c) The

relationship between UPR and the human modification gradient within unprotected portions of
 groundwatersheds, summarized across the terrestrial ecoregions of the world⁴³. (b) A
 scatterplot of UPR against modification gradient split into quadrants based on median ecoregion
 values of each axis dimension, which corresponds to the color scheme of the mapped
 ecoregions in (c).

157 **Discussion**

The variability of potential human impacts and the social, economic and political 158 differences across regions implies a portfolio of approaches are available for protecting 159 groundwatershed water quality and quantity, in addition to formal protected areas. Enhanced 160 161 protection of groundwatersheds could be achieved through strategies such as groundwater regulation (e.g., well permitting), sustainable water policies (e.g., Sustainable Groundwater 162 Management Act in California, USA), source water protection (e.g., Edwards aquifer protection, 163 in Texas, USA), Indigenous-led land and water management and monitoring (e.g., Guardian 164 programs such as northwestern Australia), conservation or regenerative agriculture (e.g., 165 practices that reduce groundwater pumping), and nature-based solutions (e.g., invasive species 166 removal for the Greater Cape Town water fund in South Africa). Management strategies could 167 be borrowed or adapted from these and other conservation and source water protection 168 approaches, rather than developing entirely new policy or management approaches. Selecting 169 an appropriate strategy depends on the social, economic and political context as well as the 170 degree of possible impacts, from severe (nearby, large magnitude pumping or contamination) to 171 less impactful (distant or minor land use change). 172

Our results importantly 'daylight' the connection between groundwater and protected areas and highlight the vulnerability of protected areas to potential groundwater impacts. However, our approach has limitations (see Supplementary Information). For instance, we used a simplified approach to identify potential groundwater-dependent ecosystems, focused on higher levels of protection (IUCN protected area categories I-III), and mapped only the possible spatial extent but not the timing of groundwatershed-protected area connections. Thus, this first-

| 179 | order global analysis is not intended to lead to recommendations for specific protected areas but |
|-----|---|
| 180 | rather explores global trends in these relationships and possible strategies. As governments |
| 181 | around the world commit to new protected area targets, and other actors like companies make |
| 182 | their own conservation commitments, our analysis can serve as a reminder that protection stops |
| 183 | neither at protected area borders nor at the ground surface. The concept of groundwatersheds, |
| 184 | equally applicable to any groundwater-connected feature, has strong potential with further |
| 185 | refinement to inform sustainability planning and resilience-building around the world. |

186 **Methods**

We sought to implement a simple geospatial methodology using best-available, openly
accessible global data to map the groundwatersheds of the world's protected areas. The study
approach is described in detail in Supplementary Section 1. All data used in this study were
obtained from published, open-access data sets and are described in Supplementary Table 1. A
flow chart of this study's methodology is shown in Supplementary Figure 1. All analyses in this
study were performed at 30 arc-second resolution (~1 km at the equator).

193 <u>A computationally simple approach to groundwatershed mapping</u>

Groundwatersheds were derived by making minor modifications to a conventional 194 surface watershed delineation method. Whereas surface watersheds are derived using an outlet 195 location (or 'pour point') and a digital elevation model of the land surface, groundwatersheds are 196 derived using an outlet location and the water table surface. Whereas a surface watershed 197 identifies the contributing area of overland flow to a point of interest, a groundwatershed 198 identifies the contributing area of local groundwater flow to a feature of interest. Our 199 methodology does not identify contributing areas of subregional and regional groundwater flow, 200 as discussed in study limitations (see Supplementary Information) and as shown in 201 Supplementary Figure 2. In the following sections, we summarize our methods to identify 202 203 groundwatershed outlet locations and to derive groundwatersheds.

204 Groundwatershed outlet preparation

Water table: The water table depth data contains two data sets: mean monthly water table depths and mean annual water table depth, both averaged over a 10-year model run. As required for groundwatershed delineation, we converted water table depth to water table elevation by subtracting water table depth from the land surface elevation. We used the mean monthly water table elevation data in our derivation of ecologically connected areas and in our groundwatershed uncertainty analysis and the overall mean water table elevation data in our core groundwatershed delineation.

Root zone: Similar to water table depth, we converted rooting depth to rooting elevation by
 subtracting rooting depth from the land surface elevation. This elevation represents the
 elevation of the bottom of the root zone. This rooting zone elevation is used in the derivation of
 ecologically connected areas.

Protected areas: From the World Database on Protected Areas (see Supplementary Table 1), 216 we subset two groups of protected area categories: those with relatively high degrees of 217 protection and those with lower degrees of protection. We considered IUCN terrestrial protected 218 area categories: la (Strict Nature Reserve), lb (Wilderness Area), ll (National Park), ll (National 219 Monument or Feature), as well as protected areas with "Not Reported" or "Not Assigned" 220 categories as areas with high degrees of protection. We included "Not Reported" and "Not 221 Assigned" protected areas in this high protection class following a UNEP recommendation and 222 as we found these categories to be more prevalent in the Global South where reporting of 223 protected areas may be less comprehensive. By including these categories, we retained a 224 225 greater global coverage within the protected areas data set. The remaining protected area categories: IV (Habitat/Species Management Area), V (Protected Landscape/Seascape), VI 226 (Protected area with sustainable use of natural resources), and "Not Applicable", are grouped 227 into a class representing lower levels of protection. 228

With these two simplified protected area classes, we rasterized both sets to our 229 operating resolution, including all grid cells touched by a protected area. As the grain of our 230 analysis is 30 arc-seconds (~1 km), we additionally filtered out any protected areas with a 231 reported surface area <1 km² before rasterization. Lastly, we identified all spatially contiguous 232 protected areas, which we used as the protected area layer to calculate our derived metrics 233 (see Box 1) and report summary statistics. We opted to identify contiguous protected areas 234 rather than use the unique identities of individual protected areas as some protected areas 235 overlap or abut one another. Using this spatially contiguous but flattened representation of 236 protected areas provided a more streamlined approach to handle and report global protected 237

area results. However, these contiguous protected areas differ in total count from the original 238 239 protected area dataset. We primarily used the "high level of protection" class of protected areas in our analysis. The "low level of protection" class was used in our post-hoc analysis. 240 Ecologically connected areas: Though we sought to identify the groundwatersheds of the 241 world's protected areas, we opted not to delineate groundwatersheds using the entire extent of 242 protected areas as outlet features. Rather, we identified and used areas within the protected 243 areas where it is reasonable to assume there are interactions with groundwater. To identify such 244 areas, which we refer to as "ecologically connected areas", we considered: (i) the interaction 245 between rooting depths and the water table, (ii) the intermittency of rivers, (iii) the presence of 246 groundwater-related wetlands, and (iv) other surface water bodies. These considerations, 247 together, represent various mechanisms that link groundwater to surface processes, including 248 root water uptake and groundwater-surface water interactions. 249

We identified areas where root systems are likely sourcing groundwater by comparing 250 mean monthly water table elevations with the elevation of the bottom of the root zone. We 251 considered any grid cell in which the root zone intersects the water table for at least one month 252 per year as an ecological connection. We then identified areas where groundwater-surface 253 water interactions are likely to occur. We did so by considering the location of perennial rivers, 254 groundwater-related wetlands, and lake extents. The combination of these locations: where root 255 zones intersect the water table, where groundwater-related wetlands exist, and where 256 groundwater-surface water interactions are likely to occur represent the 'ecologically connected 257 areas' we used as outlets in our groundwatershed delineation. Though not all rivers and surface 258 water bodies depend on groundwater discharge (e.g., losing river reaches), these are reflected 259 by lower surrounding water table levels and thus will not receive an associated contributing 260 groundwatershed beyond the ecologically connected cell(s). As we are only concerned with 261 identifying the groundwatersheds of protected areas, our final preparation step was to mask all 262

ecologically connected cells to the extent of protected areas before use in the groundwaterdelineation process.

265 Groundwatershed delineation

266 Our groundwatershed delineation process followed conventional watershed delineation approaches that generate a flow direction raster which is used to derive watersheds for 267 specified features. However, and as aforementioned, we substituted the derived water table 268 surface for the land surface elevation when deriving the flow direction raster. We did not apply 269 additional hydrological preconditioning steps to the water table surface, such as the removal of 270 depressions, as depressions in the water table represent local water table gradients which we 271 sought to represent in our study. The flow direction raster was generated using the D8 flow 272 direction method which can represent 8 possible flow directions to adjacent cells according to 273 274 the direction of the steepest water table gradient. Though the D8 algorithm has known limitations, such as generating parallel flow paths and poorly depicting watersheds in coastal 275 and endorheic basins, it remains a common, simple, and widely used approach to derive flow 276 direction. Secondly, improving the sophistication of our flow direction derivation may not be 277 278 warranted as our analysis was performed at a coarse spatial resolution (30 arc-second), which is much coarser than watershed-specific delineation studies that are often conducted at <100 m 279 resolution. 280

The groundwater flow direction raster was used to derive groundwatersheds in 281 combination with the derived ecologically connected cells. Each ecologically connected cell was 282 converted to a spatial point file at the centroid of the grid cell. Each point was used as a 'pour 283 point' in the watershed delineation algorithm. Once groundwatersheds were derived for 284 individual pour points, they were merged based on their associated contiguous protected area. 285 286 For flow direction raster and groundwatershed delineation steps, we used the 'D8Pointer' and 'Watershed' tools in the Hydrological Analysis toolbox of the open source geospatial platform 287 Whitebox Geospatial⁴⁴. 288

289

Uncertainty analysis

290 As groundwatersheds are dynamic (i.e., can fluctuate with the water table) we performed an uncertainty analysis to quantify the degree to which the extents of groundwatersheds change 291 throughout a typical year. For this, we used mean monthly water table depths rather than the 292 mean annual water table depth and repeated our groundwatershed delineation process for all 293 months. While we observed month-to-month variation in groundwatershed extent across most 294 groundwatersheds, we found that the total area of groundwatersheds for the world's protected 295 areas fluctuates little throughout the year (Supplementary Figures 7, 8). These small 296 fluctuations in total groundwatershed size indicate the robustness of our first-order analysis of 297 global groundwatershed mapping. However, these uncertainty results simultaneously 298 underscore the need for methodological advances to map groundwatersheds using improved 299 process representation in future studies to refine these estimates and allow for consideration of 300 regional and complex groundwater flow systems. 301

302 Data availability

Source data are documented in Supplementary Table 1 and can be downloaded from the
 persistent web-links provided. Groundwatershed data produced in this study will be uploaded to
 an open-access repository upon manuscript acceptance.

306 **Code availability**

307 Code used to produce all results in this study is available at

308 <u>https://github.com/XanderHuggins/groundwatersheds-for-PAs</u>. This repository will be archived

- 309 on a dedicated archiving service (such as Zenodo) upon manuscript acceptance. All analyses
- ³¹⁰ were conducted using the R project for statistical computing⁴⁵. R packages necessary for
- analysis and visualization include: terra⁴⁶, gdalUtilities⁴⁷, rasterDT⁴⁸, whitebox^{44,49}, ggplot2⁵⁰,
- ³¹² tmap⁵¹, scico^{52,53}, and MetBrewer⁵⁴. Composite figures were assembled in Affinity Designer
- 313 (<u>https://affinity.serif.com/en-us/designer/</u>).

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- The study was conceived by T.G. A.H., S.Z., and F.J. The methods were developed by T.G.,
- 447 X.H., S.Z., A.H., F.J., and D.S. Analysis was performed by X.H., D.S., and F.J. Figures were
- developed by X.H., T.G., and D.S. All authors, D.S., X.H., T.G., S.Z., M.M.R., K.V., R.A., A.H.,
- and F.J., discussed results and edited the manuscript at multiple stages.

450 Competing Interests Statement

451 The authors declare that they have no competing interests.