

1 **Title Page**

2  
3 **Title:** An environmental resistance model to inform the biogeography of aquatic invasions in  
4 complex stream networks

5  
6 **Running title:** Environmental resistance to invasions

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17  
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27  
28 **Abstract**

29 **Aim** Freshwater invasions are a global conservation issue. Emerging tools for biogeographic  
30 analyses can provide critical information for their effective management and monitoring. Here,  
31 we propose a method to assess the distribution of environmental resistance of stream ecosystems  
32 to biological invasions by coupling multi-stage habitat potential models for non-native species.

33 **Location** Andean Patagonia (Chile and Argentina).

34 **Taxa** North American beaver (*Castor canadensis*), Chinook salmon (*Oncorhynchus*  
35 *tshawytscha*), and coho salmon (*O. kisutch*).

36 **Methods** Environmental resistance to invasive species was mapped throughout a large region of  
37 Patagonia by stacking multi-stage habitat relationships for each target species and assessing the  
38 complementation between critical habitats at multiple scales. We generated an environmental  
39 model of stream networks derived from high-resolution topographic and climatic data  
40 representing 15,406 drainage basins (> 1 km<sup>2</sup>) covering an area of 369,791 km<sup>2</sup>. We quantified  
41 the intrinsic potential of stream reaches (100 m and 1,000 m) to sustain high-quality habitats and  
42 assessed habitat complementation (i.e., abundance and proximity) at the sub-basin scale as a  
43 proxy for environmental resistance.

44 **Results** Our model revealed high heterogeneity in the distribution of environmental resistance to  
45 invasions throughout the study region, providing case-specific insights for the research and  
46 management of invaders.

47 **Main conclusions** Environmental resistance modelling is a novel method to study the  
48 biogeography of riverine invasions. Our approach is compatible with additional sources of  
49 information about species and the environment, and shows versatility to diverse invasion  
50 scenarios and data sources. This method can be useful in prioritising research and management  
51 of incipient and spreading invasions, especially for large and data-poor regions.

52 **Keywords:** aquatic, complementarity, hydrogeomorphology, invasibility, lotic, non-native, risk,  
53 resistance, riverscapes, suitability

54

## 55 **1. Introduction**

56 Biological invasions are a primary driver of global ecological change (Lockwood et al., 2013)  
57 and a source of increasing attention in biogeographic studies (Hastings et al., 2005; Acevedo et  
58 al., 2016). Spatially explicit habitat modelling can provide valuable information for risk  
59 assessment and spatial prioritisation of monitoring and management of invasions (Jeschke &  
60 Strayer, 2008; Jiménez-Valverde et al., 2011). However, the apparent idiosyncrasies and lack of  
61 predictability of invasions in freshwater ecosystems (Moyle & Light, 1996; García-Berthou,  
62 2007) and the high structural complexity of stream networks (Fausch et al., 2002; Wiens, 2002)  
63 present additional challenges to modelling the spatial distribution of aquatic invaders. The  
64 management and control of introduced species depend on introduction intensity (propagule  
65 pressure), the invasive traits of introduced species (e.g., vagility, fertility, phenotypic plasticity;  
66 Kolar & Lodge, 2001), and the compatibility of their life-history requirements with critical  
67 attributes of the receiving ecosystem (e.g., suitability, connectivity). Therefore, habitat modelling  
68 applied to freshwater invasions warrants the consideration of unique ecological relationships  
69 between introduced species and the spatial structure of freshwater ecosystems.

70 In the absence of empirical information about presence/absence, mapping the habitat  
71 suitability for invaders in stream networks can be approached using mechanistic knowledge of  
72 the interplay between landscapes, populations, and behaviour as seen in native ranges (Poff,  
73 1997; White et al., 2014). Conceptually, riverscapes represent freshwaters running through  
74 landscapes (Ward, 1998; Fausch et al., 2002; Wiens, 2002) as highly confined, linear, and  
75 hierarchical stream networks (Ward, 1998; Montgomery, 1999; Fausch et al., 2002; Benda et al.,  
76 2004; Humphries et al., 2014). The biophysical heterogeneity (Ward, 1989) of riverscapes is  
77 shaped by multiple longitudinal (i.e., upstream-downstream), lateral (i.e., channel-floodplain),  
78 vertical (i.e., surface-hyporheic), and temporal dimensions. Yet, the distribution and dispersal of  
79 freshwater species are generally shaped by the longitudinal dimension of riverscapes (Huet,  
80 1959; Vannote et al., 1980; Penaluna et al., 2021). Predictive models able to assess these critical  
81 components of the longitudinal distribution of stream habitats can be used to evaluate the  
82 propensity of receiving riverscapes to support novel species.

83 The habitat intrinsic potential model is a mechanistic approach to characterise the  
84 structural capacity of individual stream sections to provide high-quality habitats for a target  
85 species (Burnett et al., 2007). In native ranges, this approach has been used to identify historical  
86 (Agrawal et al., 2005) and degraded (Burnett et al., 2007) habitats and to monitor habitats for  
87 juvenile animals (Matter et al., 2018), species relocations (Dittbrenner et al., 2018), and  
88 population abundances (Flitcroft et al., 2012; Petro et al., 2018; Romey, 2018). In addition, this

89 approach has been expanded to represent both multiple spatial scales (Firman et al., 2011) and  
90 species' life stages (Flitcroft et al., 2012). The use of the intrinsic potential approach in invasion  
91 biology is promising, for example, in predicting possible interactions between native and  
92 introduced species (Jalbert et al., 2021; Manning et al., 2022). Yet, the lack of standard protocols  
93 to assess the spatial distribution of ecologically-relevant hydrogeomorphic processes, as well as  
94 the inclusion of multiple invaders' life stages, have hindered the use of intrinsic potential models  
95 to answer questions about the biogeography of aquatic invaders.

96 Species relate to their ecosystems at multiple spatial-temporal scales, and species-specific  
97 relationships between invaders and their landscapes are essential to develop meaningful invader-  
98 habitat models (Brown et al., 2008; Vicente et al., 2019). Every species requires specific  
99 environmental conditions and resources, and those requirements can present predictable  
100 ontogenic changes. For instance, species often require multiple habitat types for the completion  
101 of their life cycles in stream networks (e.g., Schlosser, 1995a), a process known as "habitat  
102 complementation" (Dunning et al., 1992). The availability of complementary habitats can be  
103 viewed as an environmental filter to invasions (Moyle & Light, 1996). Therefore, a  
104 comprehensive understanding of the relationships between species life-histories and relevant  
105 landscape attributes is critical for assessing a region's vulnerability to the colonisation and  
106 expansion of introduced species. Under this paradigm, the traditional intrinsic potential approach  
107 using single life-stage characterisations of habitat suitability provides an incomplete  
108 representation for species with complex life histories. Thus, habitat models incorporating habitat  
109 complementation requirements can enhance intrinsic potential models to map and quantify  
110 environmental resistance to invasions of species with complex life histories.

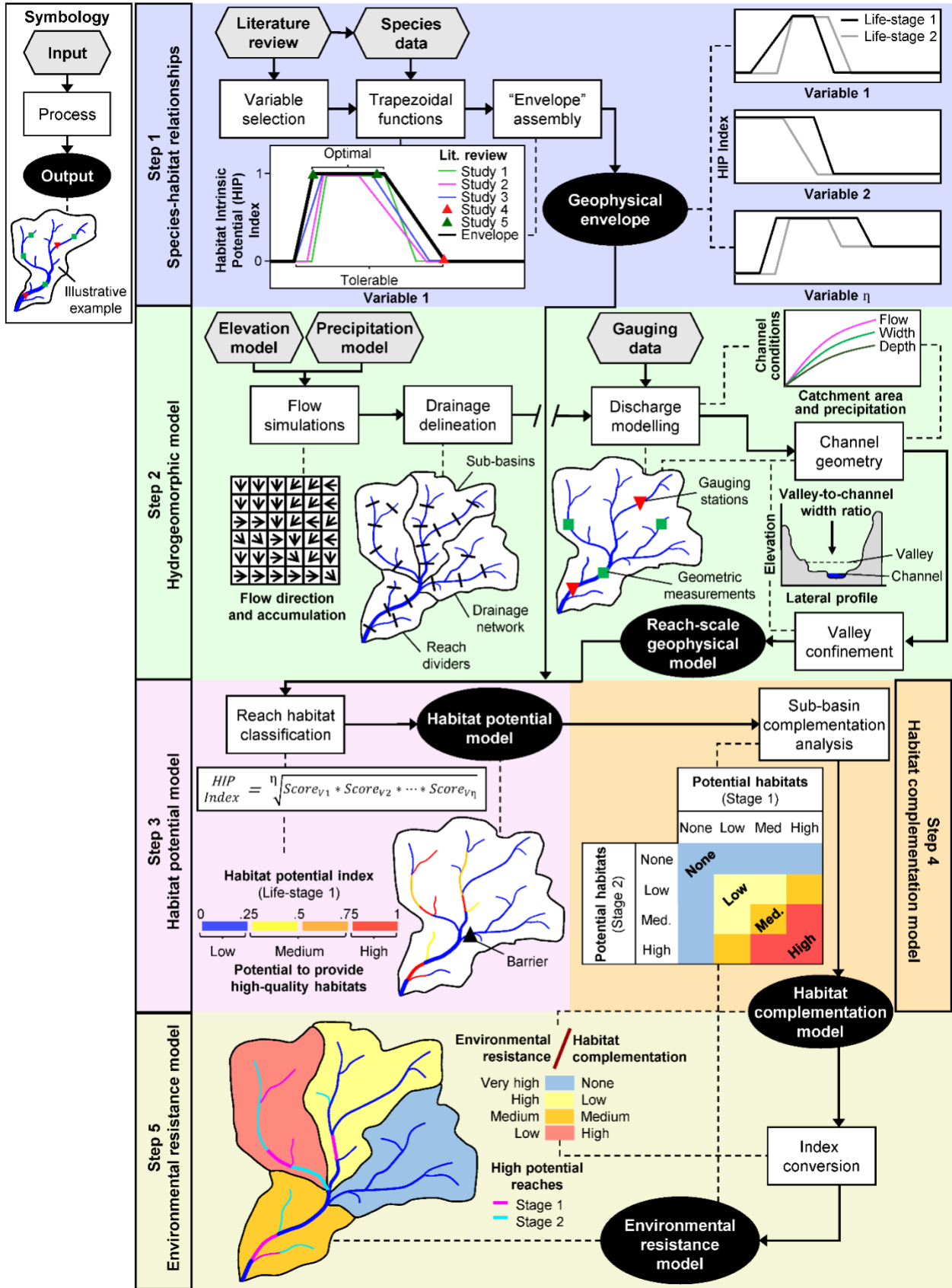
111 Here, we develop and implement a method for mapping environmental resistance to  
112 invasions based on habitat intrinsic potential and habitat complementation models at different  
113 spatial scales. Our models include a clear description of standard steps and procedures that will  
114 ensure reproducibility. We provide a proof-of-concept and partially validate our model using  
115 three species introduced in freshwater environments of southern South America, including the  
116 North American beaver (*Castor canadensis* Kuhl, 1820), Chinook salmon (*Oncorhynchus*  
117 *tshawytscha* Walbaum, 1792), and coho salmon (*O. kisutch* Walbaum, 1792). Our approach is  
118 transferable across species and ecosystems and aims to advance the understanding of spatial  
119 patterns of these and other aquatic invasions by prioritising surveillance efforts for regions at  
120 high risk, but too large to be sampled comprehensively.

121

## 122 **2. Materials and Methods**

123 We mapped the distribution of environmental resistance to the invasion of non-native species  
124 following five sequential steps (**Fig. 1**). In Step 1, we assembled multi-stage models of species-  
125 habitat relationships. In Step 2, we characterised habitats at stream reach and basin scales using a  
126 hydro-geomorphic model. In Step 3, we classified the intrinsic potential for each life stage for  
127 each reach. In Step 4, we assessed habitat complementation at the sub-basin scale. In Step 5, we  
128 mapped the distribution of environmental resistance to species invasion.

129



131 **Figure 1.** Workflow diagram of our spatially-explicit modelling framework to map the  
132 distribution of environmental resistance to the invasion of non-native species in stream networks  
133 showing 5 key steps.

134

## 135 **2.1 Study area**

136 Our study area encompassed the Andean Patagonian region, including all Pacific basins and the  
137 archipelago of Tierra del Fuego (**Fig. 2**). This region is characterised by complex mountainous  
138 terrain and high heterogeneity in geophysical and bioclimatic conditions (Amigo & Ramírez,  
139 1998; Olson et al., 2001). The region's physiography has been shaped by the Andes Mountains,  
140 featuring active volcanos, fjords, glacial fields, islands (>40,000), and diverse valley types  
141 (Börgel, 1965). The extensive latitudinal range of our study region (36-55 °S) includes multiple  
142 climates and hydrological conditions (Abell, 2002). Most human-related influences are  
143 concentrated in the north (38-41°S), whereas pristine protected areas predominate throughout the  
144 south (41-55°S).

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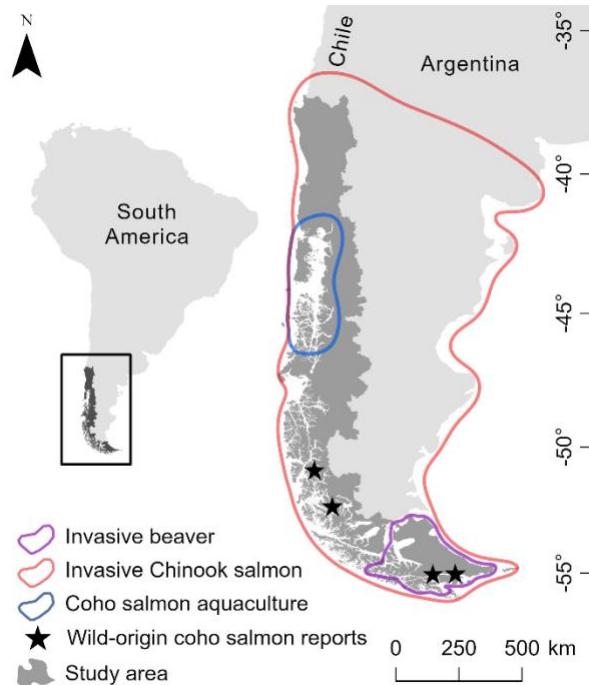
## 146 **2.2 Target species used to illustrate our modelling procedure**

147 North American beaver and Pacific salmon (Chinook and coho salmon in this study) are  
148 ecological engineers and keystone species in their native ranges. Thus, the potential  
149 consequences of their introductions in novel environments will likely result in far-reaching  
150 impacts on receiving systems. For instance, beavers can alter ecosystems across multiple  
151 organisation levels, from the geomorphology of channels to water chemistry to the entire  
152 composition of aquatic and terrestrial fauna (Naiman et al., 1988; Anderson et al., 2020; Brazier  
153 et al., 2021). Similarly, Pacific salmon contribute marine-derived nutrients to terrestrial and  
154 freshwater ecosystems sustaining many species and communities (Naiman et al., 2002). In  
155 addition, these focal species could interact symbiotically in invaded regions. Beaver ponds can  
156 improve local habitat conditions (Alexander, 1998), growth (Arismendi et al., 2020), abundance  
157 (Virbickas et al., 2015), spatial distribution (Leidholt-Bruner et al., 1992; Mitchell & Cunjak,  
158 2007), and overall population productivity of salmonids (Pollock et al., 2004). In contrast, beaver  
159 dams can also influence connectivity for dispersal and spawning migrations (Lokteff et al.,  
160 2013). Therefore, environmental models generated jointly for these invasive species could have  
161 synergistic advantages for studying their biogeography.

162 Pacific salmon (Basulto, 2003) and the North American beaver (Skewes et al., 2006)  
163 have been introduced in South America (Chile and Argentina) during the last century. They have  
164 had different levels of invasion success, ecological impacts, and societal values. See **Appendix**  
165 **S1 in Supporting Information** for a summary of the history of introduction, invasion success,  
166 and effects of these species in the study region.

167

168



169  
 170 **Figure 2.** Map of the study area in Andean Patagonia (Chile and Argentina, 36.8 – 55.7 °S)  
 171 encompassing a total area of 369,791 km<sup>2</sup>, and the generalised geographic ranges of our three  
 172 non-native target species. For North American beaver and Chinook salmon, coloured lines  
 173 represent reportedly invaded ranges, and for non-native coho salmon, coloured areas represent  
 174 the distribution of potential propagule sources from aquaculture production during the last ten  
 175 years (2010-2019). Black stars indicate the locations of potentially naturalised coho salmon  
 176 detections (Górski et al., 2017; Chalde et al., 2019). Map projection: South America Albers  
 177 Equal-Area Conic.

178  
 179 **2.3 Step 1: species-habitat relationships**

180 The development of mechanistic species-habitat relationships requires the identification of  
 181 variables determining the quality of physical habitats using remote sensing data and Geographic  
 182 Information Systems (GIS; Lunetta et al., 1997). The habitat intrinsic potential model requires  
 183 the delineation and characterisation of stream networks based on high-resolution elevation data  
 184 (< 30-m, **Fig. 1**) and uses simple geohydrological variables (e.g., discharge, gradient, valley  
 185 confinement) that can predict suitable environments (e.g., flow velocity, substrate size, hyporheic  
 186 exchange, pool-riffle ratio). This procedure allows for the customisation of species-habitat  
 187 relationships for different life stages that can be transferred to any region of interest.

188 We revised all intrinsic potential models published for our three target species to develop  
 189 transferable species-habitat relationships for applications related to introductions to novel regions  
 190 outside their native ranges. For the North American beaver, these models have been successfully  
 191 implemented to map the potential of streams to support dam-building habitats in Oregon and  
 192 Washington, USA (Suzuki & McComb, 1998; Dittbrenner et al., 2018; Petro et al., 2018). For  
 193 Chinook (Agrawal et al., 2005; Busch et al., 2013; Bidlack et al., 2014; Matter et al., 2018) and  
 194 coho salmon (Burnett et al., 2007; Romey, 2018), intrinsic potential models have been described  
 195 for different populations, phenotypes, and life stages. The differences in species-habitat  
 196 relationships among these studies make it difficult to choose a single species-habitat model for

197 applications outside their native ranges, especially considering the mixed genetics of Pacific  
198 salmon introductions in Patagonia (Neira et al., 2014; Correa & Moran, 2017; Gomez-Uchida,  
199 Cañas-Rojas, et al., 2018). Instead, we combined species-habitat relationships from native ranges  
200 to incorporate the variability of tolerable and optimal conditions described for different  
201 phenotypes of the same target species. Using this approach, we combined trapezoid-shaped  
202 piece-wise linear functions (i.e., trapezoidal functions) by enveloping the whole area under the  
203 curve described for the relationship between each species and environmental variable (i.e.,  
204 envelope assembly; **Fig. 1, Step 1**). This simple aggregation technique acknowledges the high  
205 degree of uncertainty in predicting patterns that might occur in the receiving ecosystems. In  
206 addition, it gives value to species plasticity traits (i.e., related to environmental requirements),  
207 which have been highly associated with invasion success (Alcaraz et al., 2005; Olden et al.,  
208 2006; Strayer, 2010; Arismendi et al., 2014). The resulting species-habitat functions were  
209 interpreted as representations of all known tolerable (trapezoid's feet) and optimal (trapezoid's  
210 shoulders) environmental ranges described for each species and life stage. More details of this  
211 procedure are provided in **Appendix S2**.

212

#### 213 **2.4 Step 2: hydrogeomorphic model**

214 There are no publicly available datasets of stream networks in South America to support the  
215 creation of habitat intrinsic potential models. Thus, we used publicly available topographic and  
216 climatic datasets to delineate and characterise the stream networks of our study region (**Fig. 1,**  
217 **Step 2**). For this purpose, we developed a customised processing toolbox in ArcGIS Pro 2.8  
218 (Esri, 2022) through 'arcpy' (code available at <https://doi.org/10.5061/dryad.3tx95x6jf>). We  
219 followed similar procedures described by Miller (2003) for hydrogeomorphic watershed analysis  
220 based on Digital Elevation (DEM) and precipitation models (*sensu* Benda et al., 2007; Clarke et  
221 al., 2008).

222 Based on a DEM of 12.5-meter resolution (downscaled from 30-m SRTM DEM by the  
223 Alaska Satellite Facility; <https://asf.alaska.edu>) and a mean annual precipitation model (30 arc-  
224 seconds; Fick & Hijmans, 2017), we generated a spatially explicit model of the stream networks  
225 of Andean Patagonia (36.8 – 55.7 °S). This environmental model covered an area of 369,791  
226 km<sup>2</sup> comprised of 15,406 river basins (> 1 km<sup>2</sup>). The digital drainage network represented  
227 671,971 linear km of streams > 0.01 m<sup>3</sup>s<sup>-1</sup>. Stream reaches were characterised at two spatial  
228 resolutions (i.e., 100 m and 1,000 m line sections) based on the most frequently applied variables  
229 for our target species in the scientific literature (see **Appendix S2**), including 1) *mean annual*  
230 *discharge*, 2) *channel gradient*, 3) *channel width*, 4) *valley width*, 5) *valley confinement*, and 6)  
231 *anadromous connectivity*. For an expanded description of environmental modelling steps, see  
232 **Appendix S3**.

233

#### 234 **2.5. Step 3: habitat potential model**

235 Using the species-habitat relationships for each of our three target species (**Fig. 3**), we scored  
236 reach-scale geophysical attributes ranging from 0 (low) to 1 (high) based on their potential to  
237 sustain habitats at any given time. Scores were combined using geometric means to calculate a  
238 stream reach intrinsic potential index (**Fig. 1, Step 3**). This averaging method enabled the  
239 combination of partially compensatory environmental variables in determining the presence of  
240 suitable habitats. For instance, optimal discharge and valley conditions can compensate for sub-  
241 optimal channel gradients. However, if another variable's score approximates zero (i.e., limiting

242 factor), its weight is higher in the final intrinsic potential index (more details in **Appendix S3,**  
243 **section 2.5**).

244

#### 245 **2.6. Step 4: habitat complementation model**

246 Pacific salmon require different lotic habitats to complete life cycles (Flitcroft et al., 2019). Thus,  
247 an approach that includes habitat complementation (Schlosser, 1995b) is warranted to better  
248 address ecological questions in riverscapes (Fausch et al., 2002). Here, we evaluated the  
249 complementation of freshwater habitats for Pacific salmon by estimating the intra-basin  
250 abundance and proximity of potential spawning and rearing habitats. For North American  
251 beaver, given habitat intrinsic potential models were only available for a single life stage (i.e.,  
252 dam building), we assessed habitat complementation between high-potential aquatic and  
253 terrestrial environments (i.e., forest cover) as shown in high-resolution land cover data (10-  
254 meter, Karra et al., 2021). The spatial density of high-potential habitats (linear km/sub-basin area  
255 for beavers, linear km/accessible linear km for salmon) for different life stages were  
256 compounded in a Habitat Complementation Index (HCI). The HCI consisted of four discrete  
257 classes (**Fig. 1, Step 4**), namely no habitat complementation (HCI = 1; missing potential habitats  
258 for one or both stages), low habitat complementation (HCI = 2; potential habitats are available,  
259 but in low densities, overall), medium habitat complementation (HCI = 3; potential habitats are  
260 available in moderate densities, overall), and high habitat complementation (HCI = 4; high  
261 density of potential habitats, overall). More details about the calculation of HCI for each species  
262 are provided in **Appendix S3, section 2.6**.

263

#### 264 **2.7 Step 5: Environmental resistance model**

265 We adapted this habitat complementation model to map the distribution of environmental  
266 resistance to species naturalisation and invasion (**Fig 1, Step 5**). We estimated environmental  
267 resistance as the inverse of the HCI, resulting in an Environmental Resistance Index (ERI) with  
268 four discrete classes. Areas providing high habitat complementation were classified as having  
269 low environmental resistance to invasion (ERI = 1). In contrast, areas with no habitat  
270 complementation were classified as having very high resistance to invasion (ERI = 4).

271

### 272 **2.8 Model applications**

#### 273 *2.8.3 North American beaver*

274 We mapped the distribution of environmental resistance to the invasion of beavers in the Tierra  
275 del Fuego archipelago (**Fig. 4c**) and compared it with current beaver distribution data (**Fig. 4a;**  
276 Huertas Herrera et al., 2020) and priority management zones (**Fig. 4b;** Parkes et al., 2008).  
277 Priority areas for the management of invasive beavers were designed by the Chilean Agriculture  
278 and Cattle Service (Servicio Agrícola y Ganadero, SAG) to prevent the expansion of the species  
279 to the mainland (Parkes et al., 2008). We identified high priority areas that were still uninvaded  
280 by beavers but presenting low resistance to beaver invasion. This application provides explicit  
281 information for the spatial narrowing of surveillance and prevention efforts of beaver  
282 colonization.

283 We also tested the predictive potential of environmental resistance modelling using an  
284 invasive beaver dam occurrence dataset for Tierra del Fuego (Huertas Herrera et al., 2020). This  
285 dataset consisted of 206,203 locations of active and abandoned beaver dams digitised from high-  
286 resolution satellite imagery. We fitted logistic linear regressions to test the sensitivity and  
287 specificity of our beaver habitat model to predict the presence-absence of beaver dams at sub-



288 basin and stream reach (1 km scales, using HCI indexes and available linear km of potential  
289 habitats as explanatory variables. Additionally, we assessed the performance of our  
290 environmental resistance model for identifying degrees of invasion (based on sub-basin dam  
291 densities) using Mann-Whitney U tests for contiguous classes (**Fig. 4c**).

292  
293

#### 294 *2.8.1 Chinook salmon*

295 We mapped and quantified the abundance and proximity of potential habitats for the rearing and  
296 spawning life stages of Chinook salmon. We identified areas with the lowest environmental  
297 resistance to a continued invasion of Chinook salmon, and areas with decreased habitat potential  
298 and connectivity, i.e. high resistance. In addition, we illustrated our approach to answering  
299 management questions at smaller spatial extents (i.e., basin level). Using the case of the Toltén  
300 River basin, we mapped the distribution of environmental resistance in a system that supports a  
301 self-sustaining, naturalised Chinook salmon population. The Toltén River basin supports  
302 emergent recreational and artisanal fisheries of growing interest for public agencies and scientists  
303 (Cid-Aguayo et al., 2021). We combined our environmental resistance assessment with current  
304 land and water uses to illustrate model applications for different management scenarios affecting  
305 the biogeography of this salmon fishery.

306  
307

#### 307 *2.8.2 Coho salmon*

308 We combined our environmental resistance assessment with current information about coho  
309 salmon propagule pressure represented by salmon farming production in marine net-pens  
310 between 2010 and 2019. We summarised historical data of massive salmon escapes and total  
311 aquaculture production (a surrogate for leakage escapes) at aquaculture management zones from  
312 Los Lagos and Aysén districts (41-47°S), where most coho salmon aquaculture exists (Soto et  
313 al., 2022). The overlap between areas with low environmental resistance and high propagule  
314 pressure can be interpreted as areas at risk of non-native coho salmon naturalisation. In addition,  
315 we overlapped our environmental resistance assessment with the most recent reports of likely  
316 naturalised salmon (Górski et al., 2017; Chalde et al., 2019) to illustrate the proximity of  
317 freshwater habitats that could support these self-sustaining populations. These maps can assist  
318 decision-makers in the spatial allocation of surveillance and pre-emptive management efforts.

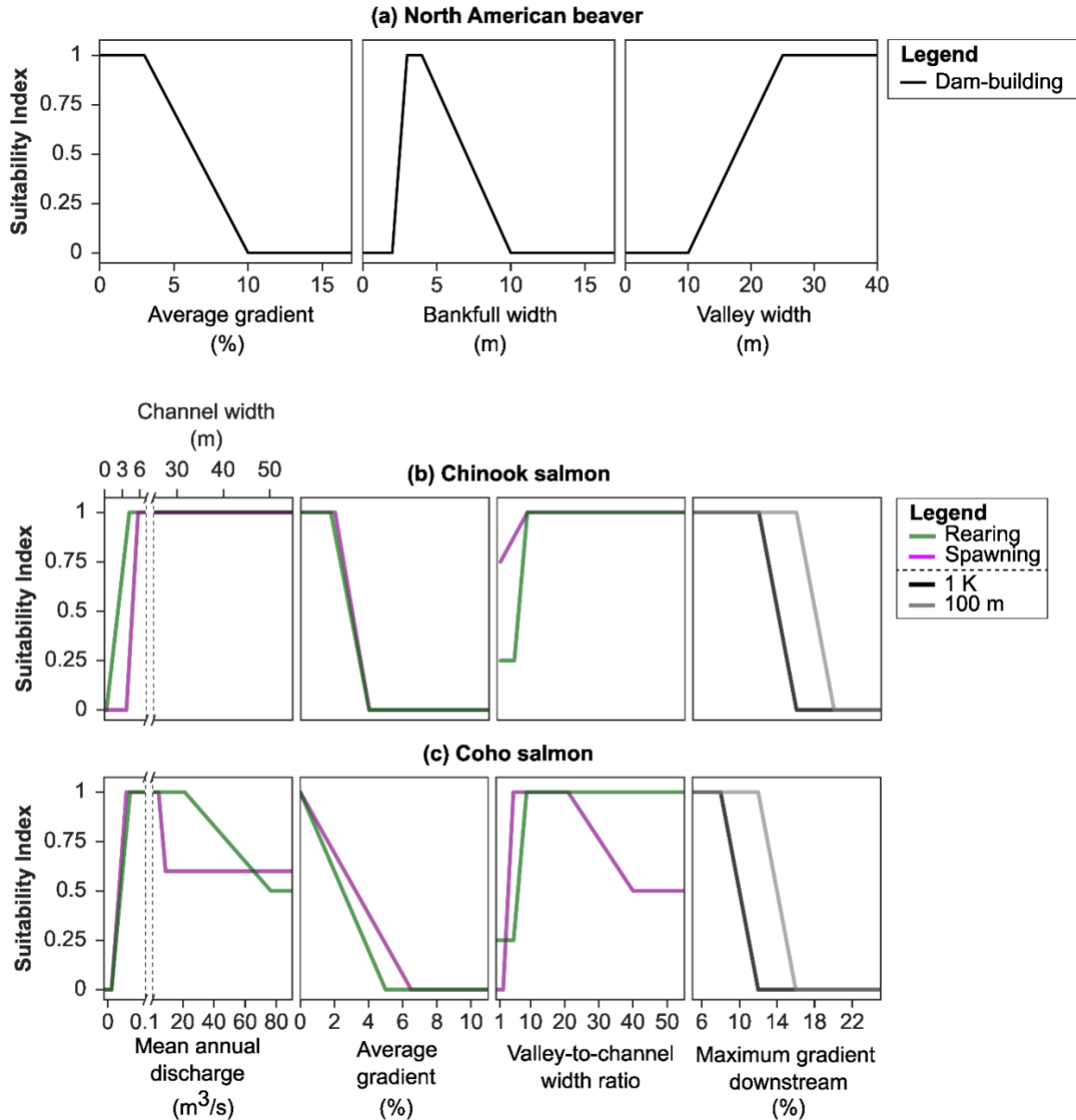
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### 320 **3. Results**

#### 321 **3.1 Species-habitat relationships for our three target species**

322 In our review of the intrinsic potential modelling literature, we identified 17 original studies  
323 modelling the relationships between reach-scale geomorphic variables and the habitats of our  
324 three target species (**Fig. 3**; Table S1). All available studies focused on native ranges. Studies  
325 showed differences among species, populations, and life stages, as well as in their selection of  
326 geophysical variables and the shape of habitat functions (more details in **Appendix S2**).

327



328  
 329 **Figure 3.** Species-habitat suitability relationships obtained from a literature review to classify  
 330 geophysical conditions based on their potential to provide habitats for our three target species.  
 331 The upper panel shows suitability curves for classifying dam-building habitats for North  
 332 American beaver (a). The lower panels show Chinook (b) and coho salmon (c) rearing (green  
 333 line) and spawning (purple line) suitability curves. Rearing suitability curves for both species  
 334 shared discharge, gradient, and valley constraint variables, while Chinook salmon spawning  
 335 models predominantly used channel width instead of discharge. Our habitat model included two  
 336 suitability curves for each salmon species representing the swimming capacity of adult migrants  
 337 through stream gradients at two different scales: 100-m (grey line) and 1,000-m stream reaches  
 338 (black line).

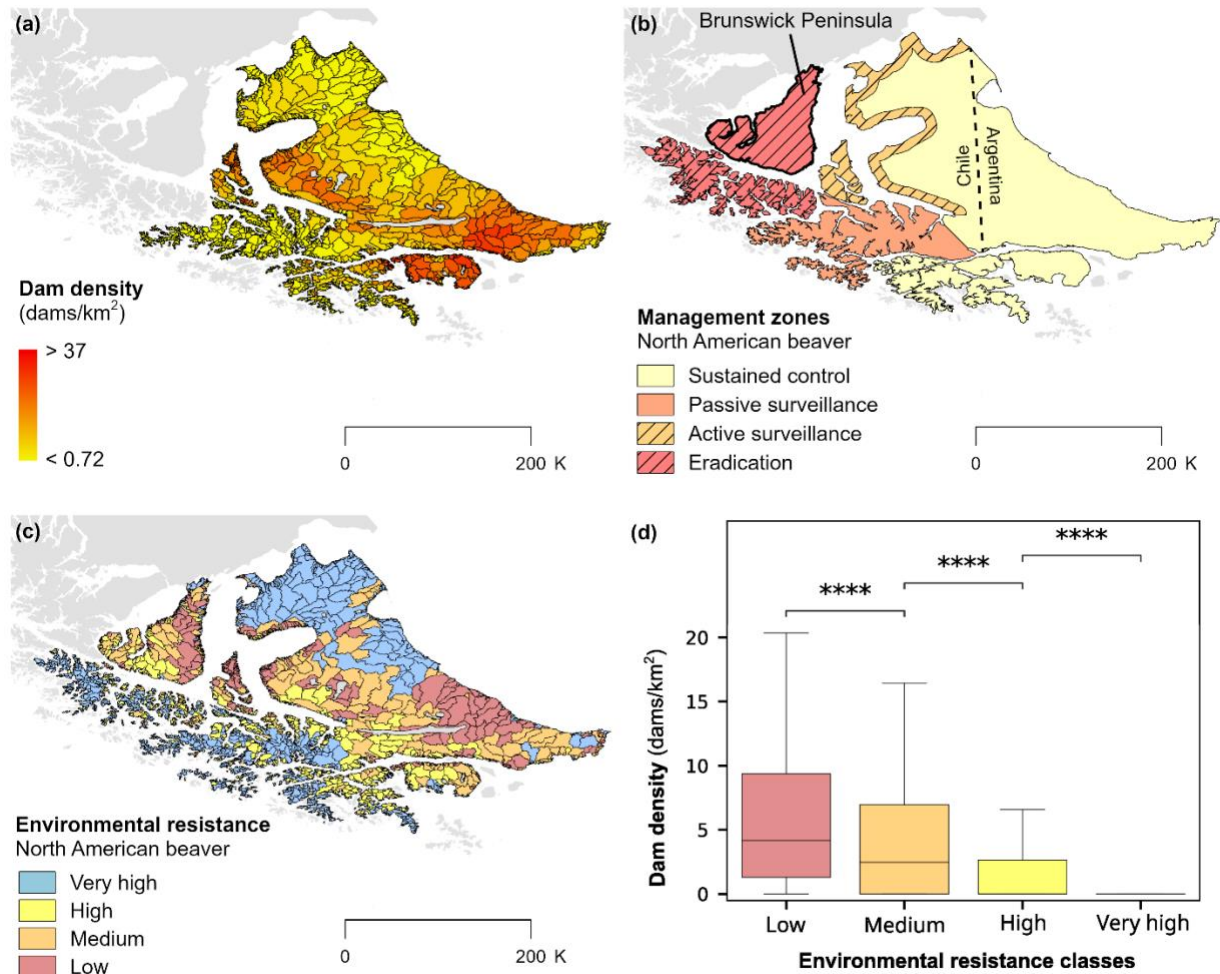
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340

341 **3.2 Distribution of environmental resistance for target species and illustrative applications**

342 *3.2.1 North American beaver*

343 We focused on the archipelago of Tierra del Fuego and adjacent areas where beavers have not  
344 yet colonised. In this region, we delineated 3,647 basins draining directly to the ocean and  
345 subdivided basins > 50 km<sup>2</sup> into units averaging 120 km<sup>2</sup>. Our model identified 32,163 stream  
346 km with high geophysical potential to sustain dam-building beaver habitats, representing 41.5%  
347 of the modelled stream network. At the sub-basin level (**Fig. 4c**), our model returned 18.9%  
348 (11,645 km<sup>2</sup>) of the area having low resistance (ERI = 1) to the invasion of beavers, 27.5%  
349 (16,966 km<sup>2</sup>) showed moderate resistance (ERI = 2), 16% (9,851 km<sup>2</sup>) showed high resistance  
350 (ERI = 3), and 37.6% (23,235 km<sup>2</sup>) showed a very high resistance (ERI = 4). Areas of low  
351 environmental resistance were concentrated in south-eastern and central-western parts of the  
352 main island and the Brunswick Peninsula. The comparison of environmental resistance with  
353 priority management zones (by SAG; **Fig. 4b**) showed high overlap of low environmental  
354 resistance with top priority areas for the containment of beaver invasion (i.e., removal zones),  
355 suggesting an increased risk of expansion into the continent. Further, logistic regressions showed  
356 satisfactory performance in identifying beaver occurrences at the sub-basin (Area Under the  
357 Curve of the Receiver Operating Characteristic, AUC = 0.82, 64% sensitivity, 82% specificity)  
358 and reach scales (AUC = 0.86, 83% sensitivity, 73% specificity). Lastly, Mann-Whitney U tests  
359 showed a high discrimination rate in the degree of invasion (**Fig. 4a**) among environmental  
360 resistance classes ( $p$ -values < 0.000001; **Fig. 4d**), proving helpful predicting the distribution of  
361 beaver invasions at the sub-basin scale.



362  
 363 **Figure 4.** Model results for North American beaver, showing (a) map of environmental  
 364 resistance at the sub-basin level. Plot (b) shows priority management zones for invasive beaver  
 365 by the Chilean Agriculture and Cattle Service (Servicio Agrícola y Ganadero, SAG), here  
 366 extending the “sustained control” zone into Argentina. (c) shows sub-basin beaver dam densities  
 367 based on the occurrence dataset by Huertas Herrera (2020). The boxplot in (d) compares dam  
 368 densities at each environmental resistance class (without outliers) using the same colours as in  
 369 (c), with red depicting low resistance, yellow medium resistance, and orange showing low  
 370 resistance sub-basins. \*\*\*\* denotes high significance levels ( $p$ -values < 0.0001) in class  
 371 discrimination obtained from Mann Whitney U tests. Map projection: South America Albers  
 372 Equal-Area Conic.

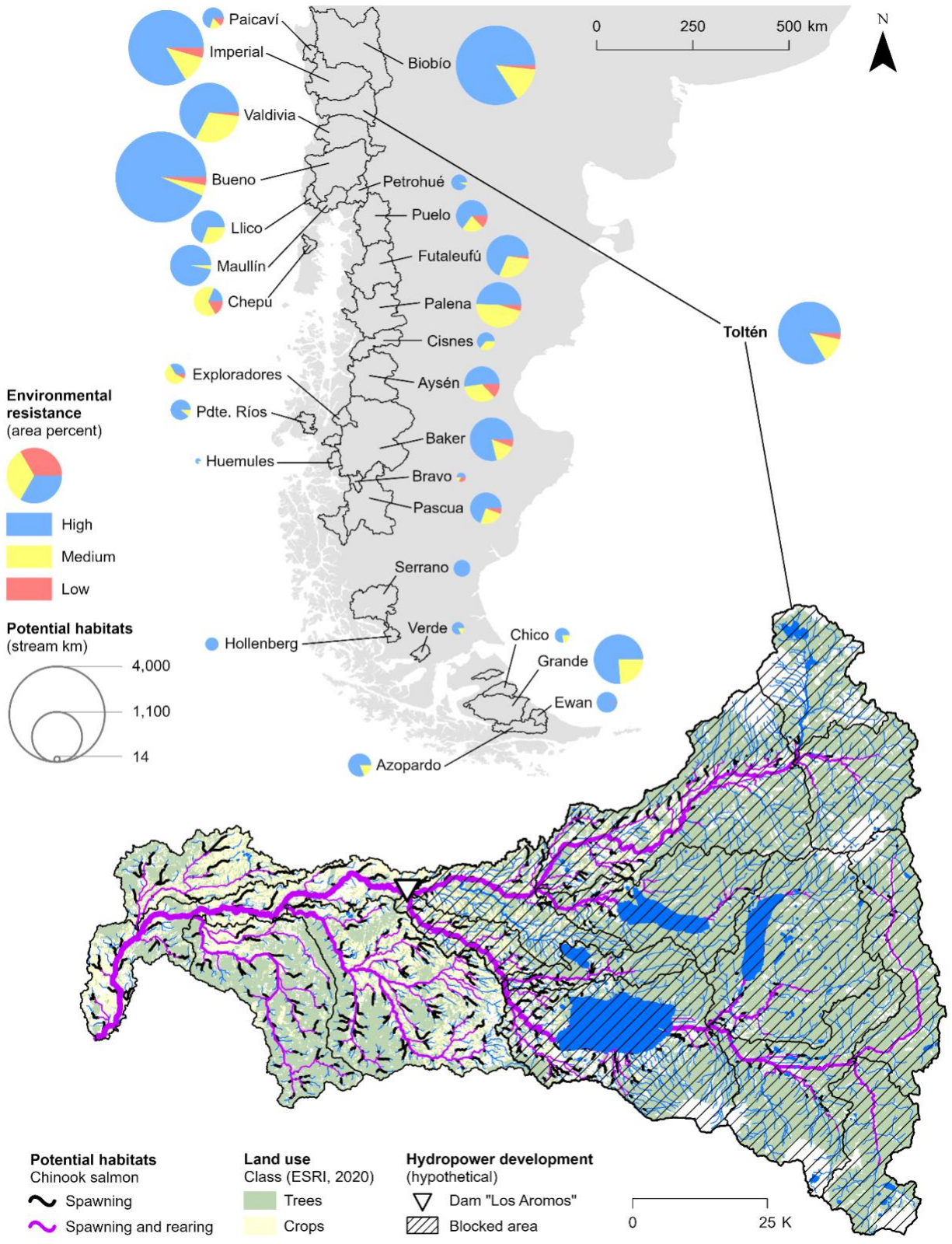
373  
 374 *3.2.2 Pacific salmon*

375 We mapped the distribution of environmental resistance to Pacific salmon (Chinook and coho  
 376 salmon) invasions for the entire study area (Web Map available at <https://arcegis.com/1WuqDH>). No  
 377 areas were excluded based on our air temperature exclusion criterion (see **Appendix S3, section**  
 378 **2.3**), whereas approximately 8.1% (54,437 stream km) were excluded due to exceedingly high  
 379 glacial influence.

380  
 381 *3.2.2.1 Chinook salmon*

382 The anadromous connectivity analysis for Chinook salmon in Andean Patagonia showed high  
383 access potential (reaches with anadromous connectivity scores  $> 0.75$ ) of 167,736 stream km.  
384 The intrinsic potential classification showed that 31,540 km had a high potential to sustain  
385 Chinook salmon rearing habitats, and 45,434 km had a high potential for spawning habitats.  
386 Most sub-basins (46.1%, 165,739 km<sup>2</sup>) had a very high resistance (ERI = 4) to Chinook salmon  
387 invasion (mostly systems that were not accessible to anadromous salmon). Sub-basins with high  
388 resistance to invasion (ERI = 3) covered 25.4% (91,317 km<sup>2</sup>) of the study area, while those with  
389 medium environmental resistance (ERI = 2) corresponded to 18.9% (67,942 km<sup>2</sup>), and those with  
390 low resistance (ERI = 1) comprised only 9.6% (34,684 km<sup>2</sup>). Results for large basins ( $>1,000$   
391 km<sup>2</sup>) are summarized in **Fig. 5a**.

392 We mapped the interaction of potential habitats for Chinook salmon with different land  
393 use (i.e., forest, agriculture) and a hypothetical scenario of hydropower development in the  
394 Toltén River Basin (**Fig. 5b**). There were 2,071 km of high potential habitat for Chinook salmon  
395 in this basin representing low resistance to its invasion, from which 15% overlapped with  
396 agricultural lands and 16.4% with forest cover. In the hypothetical scenario of hydropower  
397 development, our model showed access obstruction to almost half of potential spawning habitats  
398 (51.4%, 1,065 km) and 38.3% (794 km) of potential rearing habitats (**Fig. 5b**). This hydropower  
399 scenario would block Chinook salmon access to 38% (129 km) of high potential streams co-  
400 occurring with forest cover.



401  
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 404

**Figure 5.** Chinook salmon potential habitats and environmental resistance. Panel (a) shows the distribution of environmental resistance in large basins (> 1,000 km<sup>2</sup>) throughout the study area. Very high resistance class sub-basins are not displayed since most are not accessible to

405 anadromous salmon). This was the dominant class for most basins. Panel (b) zooms into the  
406 Toltén River basin (8,398 km<sup>2</sup>), displaying rivers coloured based on their potential for spawning  
407 and rearing. Terrestrial pixels represent optimal (trees, green) and suboptimal (crops, yellow)  
408 land covers for salmon. Blocked environments by the hypothetical hydropower development  
409 scenario appear as hatched areas. Map projection: South America Albers Equal-Area Conic.

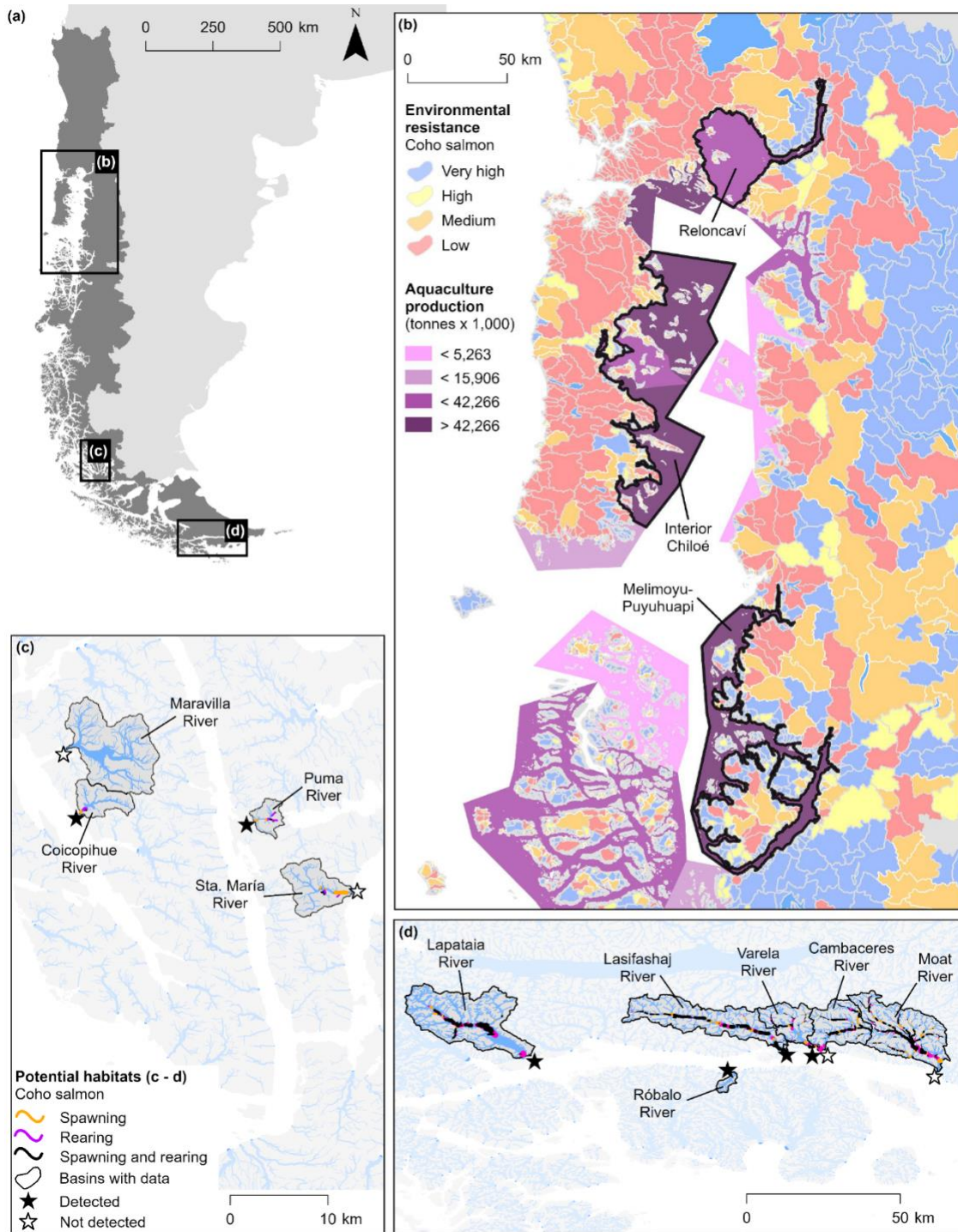
410

#### 411 3.2.2.2 *Coho salmon*

412 There were 153,222 stream km accessible to coho salmon in the study area (**Fig. 6a**). These  
413 environments included 58,414 stream km with a high potential to sustain coho salmon rearing  
414 and 62,356 km with a high potential for spawning. Sub-basins with very high resistance (ERI =  
415 4) to coho salmon invasion represented 43.5% (156,641 km<sup>2</sup>) of the study area, whereas high  
416 resistance sub-basins corresponded to 6.3% (22,506 km<sup>2</sup>). Medium resistance (ERI = 2) sub-  
417 basins covered 21.3% (76,610 km<sup>2</sup>), and low resistance sub-basins were 28.9% (103,925 km<sup>2</sup>) of  
418 the study area.

419 We mapped environmental resistance to the invasion of coho salmon in the Lakes district  
420 of southern Chile, a region with high historical aquaculture production (therefore, high levels of  
421 propagule pressure due to aquaculture escapes). We identified three areas presenting a high risk  
422 to the establishment of coho salmon populations, including the Reloncaví fjord and bay, the  
423 interior river basins of Chiloé, and the area of Melimoyu-Puyuhuapi (**Fig. 6b**). In these three  
424 areas, coho salmon aquaculture production has surpassed 40 million tonnes during the last three  
425 decades and is associated to persistent fish escapes from aquaculture facilities (Soto et al., 2001;  
426 Sepúlveda et al., 2013; Gomez-Uchida, Sepúlveda, et al., 2018). The proximity of salmon farms  
427 to low-resistance freshwater systems for coho salmon breeding and recruitment suggests a higher  
428 likelihood for their success in establishing naturalised populations.

429 We also mapped potential habitats for coho salmon in basins near reported naturalised  
430 salmon in northern Magallanes (Górski et al., 2017; **Fig. 6c**) and the Beagle Channel (Chalde et  
431 al., 2019; Maldonado-Márquez et al., 2020); **Fig. 6d**). From these reports, we evaluated  
432 environmental resistance for ten basins, including four basins where coho salmon were not  
433 detected (i.e., Maravilla River, Santa María River, Cambaceres River, Moat River). In basins  
434 with coho salmon detections, our model showed that 56% of the area consisted of sub-basins  
435 with low environmental resistance. In basins with no detections, only 35% of their area had low  
436 resistance. Basins with the highest percentage of low environmental resistance areas included the  
437 Coicopihue (100%), Puma (100%), Santa María (100%), and Varela (75%) river basins.



438  
 439 **Figure 6.** Coho salmon habitat and environmental resistance. Panel (a) shows the three areas  
 440 where we provide illustrative applications of our approach for coho salmon. Panel (b) shows the  
 441 distribution of environmental resistance relative to coho salmon aquaculture production between  
 442 the years 2010-2019 (Soto et al., 2022) and three labelled areas with the highest risk of invasion,  
 443 (c) the distribution of potential stream habitats for rearing and spawning near areas where  
 444 naturalised coho salmon have been captured (Górski et al., 2017), and (d) areas with detection of



445 coho salmon using environmental DNA (Chalde et al., 2019) and live captures (Maldonado-  
446 Márquez et al., 2020). Map projection: South America Albers Equal-Area Conic.

447

#### 448 **4. Discussion**

449 Region-wide surveillance and monitoring of invasive species are logistically unfeasible and cost-  
450 prohibitive, making spatial prioritisation tools extremely useful for increasing efficiency in the  
451 allocation of resources. We present a mechanistic habitat model to map environmental resistance  
452 to riverine invasions based on the availability and connectivity of potential habitats for multiple  
453 life stages of target species. We illustrate the benefits of this method with applications to three  
454 case studies of non-native species with varying environmental requirements, propagation history,  
455 invasion success, and perceived impacts on receiving ecosystems.

456 Our approach has advantages for invasion modelling due to its effective leveraging of  
457 publicly available, high-resolution satellite data, and the simplicity of its interpretation. By  
458 employing relatively static geomorphic predictors and long-term averaged climatic models, the  
459 habitat intrinsic potential approach quantifies the geophysical capacity of freshwater habitats to  
460 sustain certain biotic conditions at any given time or management scenario (Burnett et al., 2007).  
461 Invasion risk assessments based on this modelling approach require fewer updates over time  
462 while still allowing the integration of temporally dynamic data (e.g., propagule pressure, land  
463 cover, future climatic scenarios) as complementary determinants of the expression of that habitat  
464 potential for different target species.

465 The described “geophysical envelope” model assembly method can leverage disparate  
466 information sources to generate transferable species-habitat models that are robust to the  
467 uncertainties of niche expression in invaded regions. Species-habitat data about optimal and  
468 tolerable environmental ranges can be collected from literature reviews, expert surveys, and field  
469 studies for large spatial-temporal extents and multiple populations. By using the most extreme  
470 bounds (e.g., 90<sup>th</sup> percentile) of environmental tolerance and optimality reported for a species,  
471 this simple assembly method can accommodate the broad range of uncertainty surrounding the  
472 expression of ecological niches at invaded regions (Bates & Bertelsmeier, 2021). This  
473 environmental resistance model is more robust to changes in habitat selection by invasive species  
474 than model assemblies using central tendency metrics (e.g., averaged models), which can fail to  
475 comprehensively represent the broad range of usable geophysical conditions by an invader.

476 By stacking multi-stage intrinsic potential models, our habitat complementation model  
477 integrates critical attributes of landscape complexity to illustrate the probability of the  
478 establishment of invasive populations. Habitat modelling in stream ecosystems requires the  
479 understanding of complex life-history traits, such as the requirement for different critical habitats  
480 for different life stages (Solomon, 1973; Flitcroft et al., 2012, 2014). Thus, multi-stage habitat  
481 models offer a more meaningful quantification of the landscape’s potential to sustain populations  
482 with complex life histories. This approach can also help identify life-stages requiring more  
483 restricted environmental ranges, facilitating the identification of environments where monitoring  
484 and control efforts would be more effective.

485 The ability of this habitat model to integrate diverse sources of information has utility for  
486 case-specific applications in invasion risk assessments. We exemplify this by using land-cover  
487 data to identify environments with low geophysical resistance to invasion. In addition, the  
488 location and intensity of introduction events likely play an important role in the success and  
489 distribution of invasions (e.g., Arismendi et al., 2009). Habitat models compatible with  
490 propagule pressure data improve our ability to map invasion risk for species introduced within

491 large spatial extents. Additional biotic variables (i.e., food, potential competitors, presence of  
492 other invaders, presence/absence of predators) could also be integrated through dynamic models  
493 representing invasion risk in varying scenarios (Buchadas et al., 2017; Soto et al., 2022);  
494 however, this is at the expense of increased complexity of model development and interpretation.  
495 This methodology can also be extended to study the risk of negative interactions between native  
496 and invasive species by assessing the overlap between potential habitats among multiple species  
497 (Jalbert et al., 2021; Manning et al., 2022).

498 We illustrate the advantages of our environmental resistance model to inform decision-  
499 making and resource allocation with applications to three priority species invading a large region  
500 of Patagonia. For North American beaver, the application demonstrates its utility in identifying  
501 overlaps between areas with low environmental resistance and priority management zones (i.e.,  
502 removal and active control zones) that were previously designed by local agencies, suggesting a  
503 high risk of expansion onto the continent where invasion control could become logistically  
504 unfeasible. The study region shows high abundance and connectivity of potential habitats for  
505 invasive Chinook salmon, although with marked patterns of regional heterogeneity that could  
506 inform the management and monitoring of the species. Our findings also illustrate that northern  
507 areas, where there is a concentration of Chinook salmon stakeholders (e.g., Toltén River basin)  
508 have the lowest environmental resistance to salmon invasion. However, this region presents  
509 higher rates of land degradation (e.g., agriculture, forestry, hydropower development) as  
510 compared to more pristine, though less abundant, low-resistance environments in southern  
511 basins. Our model's application to coho salmon exemplifies its potential to inform the research  
512 of invasive species with long-range dispersal capacity, for which risk areas can encompass vast  
513 spatial extents. We identify large areas ( $> 10,000 \text{ km}^2$ ) with high coho salmon invasion risk,  
514 where low resistance systems co-occur with high propagule pressure from net-pen aquaculture  
515 escapes (e.g., Reloncaví, Interior Chiloé, and Melimoyu-Puyuhyapi), and where naturalised coho  
516 salmon have been recently reported (e.g., Górski et al., 2017; Chalde et al., 2019; Maldonado-  
517 Márquez et al., 2020). These results have an immediately useful management application by  
518 aiding in the planning and prioritisation of field monitoring.

519 In conclusion, we contribute to advancing research in the biogeography of invasions with  
520 an environmental resistance model for riverine landscapes. Our habitat intrinsic potential  
521 approach is readily transferable to other widely introduced species as intrinsic potential models  
522 exist for many of them (e.g., rainbow trout, Burnett et al., 2007; northern pike, Jalbert et al.,  
523 2021; brook trout, Manning et al., 2022). Complex and unique relationships between species and  
524 their environments can be assessed using patterns of habitat complementation as critical  
525 determinants of the sustainability of invasive populations. Applications of this flexible and  
526 transferable method may have disproportionately high value when applied to invasions occurring  
527 in data- and resource-poor regions by aiding in the spatial allocation of efforts to monitor the  
528 occurrence, success, and impacts of invasive species on receiving ecosystems.

529

### 530 **Data Availability**

531 The data supporting the findings of this study are publicly available through Dryad  
532 (<https://doi.org/10.5061/dryad.3tx95x6jf>) and the source code through Zenodo  
533 (<https://doi.org/10.5281/zenodo.6618378>).

534

### 535 **References**

536 Abell, R. (2002). Conservation Biology for the Biodiversity Crisis: A Freshwater Follow-up.  
537 *Conservation Biology*, 16(5), 1435–1437. <https://doi.org/10.1046/j.1523-1739.2002.01532.x>

- 538 Acevedo, P., Jiménez-Valverde, A., Aragón, P., & Niamir, A. (2016). New Developments in the Study of  
539 Species Distribution. In R. Mateo, B. Arroyo, & J. T. Garcia (Eds.), *Current Trends in Wildlife*  
540 *Research* (pp. 151–175). Springer International Publishing. [https://doi.org/10.1007/978-3-319-](https://doi.org/10.1007/978-3-319-27912-1_7)  
541 [27912-1\\_7](https://doi.org/10.1007/978-3-319-27912-1_7)
- 542 Agrawal, A., Schick, R. S., Bjorkstedt, E. P., Szerlong, R. G., Goslin, M. N., Spence, B. C., Williams, T.  
543 H., & Burnett, K. M. (2005). *Predicting the potential for historical Coho, Chinook and Steelhead*  
544 *habitat in Northern California* (Technical Memorandum NMFS SWFSC-379). NOAA.
- 545 Alcaraz, C., Vila-Gispert, A., & García-Berthou, E. (2005). Profiling invasive fish species: The  
546 importance of phylogeny and human use. *Diversity and Distributions*, *11*(4), 289–298.  
547 <https://doi.org/10.1111/j.1366-9516.2005.00170.x>
- 548 Alexander, M. D. (1998). *Effects of beaver (Castor canadensis) impoundments on stream temperature*  
549 *and fish community species composition and growth in selected tributaries of Miramichi River,*  
550 *New Brunswick* (Canadian Technical Report of Fisheries and Aquatic Sciences). Department of  
551 Fisheries and Oceans.
- 552 Amigo, J., & Ramírez, C. (1998). A bioclimatic classification of Chile: Woodland communities in the  
553 temperate zone. *Plant Ecology*, *136*(1), 9–26. <https://doi.org/10.1023/A:1009714201917>
- 554 Anderson, C. B., Tagliaferro, M., Fisk, A., Rosemond, A. D., Sanchez, M. L., & Arts, M. T. (2020). Fatty  
555 acids elucidate sub-Antarctic stream benthic food web dynamics invaded by the North American  
556 beaver (*Castor canadensis*). *Polar Biology*, *43*(5), 423–433. [https://doi.org/10.1007/s00300-020-](https://doi.org/10.1007/s00300-020-02644-z)  
557 [02644-z](https://doi.org/10.1007/s00300-020-02644-z)
- 558 Arismendi, I., Penaluna, B. E., Dunham, J. B., De Leaniz, C. G., Soto, D., Fleming, I. A., Gomez-Uchida,  
559 D., Gajardo, G., Vargas, P. V., & León-Munoz, J. (2014). Differential invasion success of  
560 salmonids in southern Chile: Patterns and hypotheses. *Reviews in Fish Biology and Fisheries*,  
561 *24*(3), 919–941.
- 562 Arismendi, I., Penaluna, B. E., & Jara, C. G. (2020). Introduced beaver improve growth of non-native  
563 trout in Tierra del Fuego, South America. *Ecology and Evolution*, *10*(17), 9454–9465.  
564 <https://doi.org/10.1002/ece3.6636>
- 565 Arismendi, I., Soto, D., Penaluna, B., Jara, C., Leal, C., & León-Muñoz, J. (2009). Aquaculture, non-  
566 native salmonid invasions and associated declines of native fishes in Northern Patagonian lakes.  
567 *Freshwater Biology*, *54*(5), 1135–1147.
- 568 Basulto, S. (2003). *El largo viaje de los salmones: Una crónica olvidada: propagación y cultivo de*  
569 *especies acuáticas en Chile* (1st ed., Vol. 1). Maval.
- 570 Bates, O. K., & Bertelsmeier, C. (2021). Climatic niche shifts in introduced species. *Current Biology*,  
571 *31*(19), R1252–R1266. <https://doi.org/10.1016/j.cub.2021.08.035>
- 572 Benda, L., Miller, D., Andras, K., Bigelow, P., Reeves, G., & Michael, D. (2007). NetMap: A New Tool  
573 in Support of Watershed Science and Resource Management. *Forest Science*, *53*(2), 206–219.  
574 <https://doi.org/10.1093/forestscience/53.2.206>
- 575 Benda, L., Poff, N. L., Miller, D., Dunne, T., Reeves, G., Pess, G., & Pollock, M. (2004). The Network  
576 Dynamics Hypothesis: How Channel Networks Structure Riverine Habitats. *BioScience*, *54*(5),  
577 413–427. [https://doi.org/10.1641/0006-3568\(2004\)054\[0413:TNDHHC\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2004)054[0413:TNDHHC]2.0.CO;2)
- 578 Bidlack, A. L., Benda, L. E., Miewald, T., Reeves, G. H., & McMahan, G. (2014). Identifying suitable  
579 habitat for Chinook salmon across a large, glaciated watershed. *Transactions of the American*  
580 *Fisheries Society*, *143*(3), 689–699.
- 581 Börgel, R. (1965). *Mapa geomorfológico de Chile: Descripción geomorfológica del territorio*. Biblioteca  
582 Nacional.
- 583 Brazier, R. E., Puttock, A., Graham, H. A., Auster, R. E., Davies, K. H., & Brown, C. M. L. (2021).  
584 Beaver: Nature’s ecosystem engineers. *WIREs Water*, *8*(1), e1494.  
585 <https://doi.org/10.1002/wat2.1494>
- 586 Brown, K. A., Spector, S., & Wu, W. (2008). Multi-scale analysis of species introductions: Combining  
587 landscape and demographic models to improve management decisions about non-native species.  
588 *Journal of Applied Ecology*, *45*(6), 1639–1648. <https://doi.org/10.1111/j.1365-2664.2008.01550.x>

589 Buchadas, A., Vaz, A. S., Honrado, J. P., Alagador, D., Bastos, R., Cabral, J. A., Santos, M., & Vicente,  
590 J. R. (2017). Dynamic models in research and management of biological invasions. *Journal of*  
591 *Environmental Management*, 196, 594–606. <https://doi.org/10.1016/j.jenvman.2017.03.060>  
592 Burnett, K. M., Reeves, G. H., Miller, D. J., Clarke, S., Vance-Borland, K., & Christiansen, K. (2007).  
593 Distribution of salmon-habitat potential relative to landscape characteristics and implications for  
594 conservation. *Ecological Applications*, 17(1), 66–80.  
595 Busch, D. S., Sheer, M., Burnett, K., McElhany, P., & Cooney, T. (2013). Landscape-level model to  
596 predict spawning habitat for lower Columbia River fall Chinook Salmon (*Oncorhynchus*  
597 *tshawytscha*). *River Research and Applications*, 29(3), 297–312.  
598 Chalde, T., Nardi, C. F., & Fernández, D. A. (2019). Early warning: Detection of exotic coho salmon  
599 (*Oncorhynchus kisutch*) by environmental DNA and evidence of establishment at the extreme  
600 south of Patagonia. *Canadian Journal of Fisheries and Aquatic Sciences*, 76(12), 2343–2349.  
601 Cid-Aguayo, B., Ramirez, A., Sepúlveda, M., & Gomez-Uchida, D. (2021). Invasive Chinook Salmon in  
602 Chile: Stakeholder Perceptions and Management Conflicts around a New Common-use Resource.  
603 *Environmental Management*, 68(6), 814–823. <https://doi.org/10.1007/s00267-021-01528-0>  
604 Clarke, S. E., Burnett, K. M., & Miller, D. J. (2008). Modeling Streams and Hydrogeomorphic Attributes  
605 in Oregon From Digital and Field Data. *JAWRA Journal of the American Water Resources*  
606 *Association*, 44(2), 459–477.  
607 Correa, C., & Moran, P. (2017). Polyphyletic ancestry of expanding Patagonian Chinook salmon  
608 populations. *Scientific Reports*, 7(1), 14338. <https://doi.org/10.1038/s41598-017-14465-y>  
609 Dittbrenner, B. J., Pollock, M. M., Schilling, J. W., Olden, J. D., Lawler, J. J., & Torgersen, C. E. (2018).  
610 Modeling intrinsic potential for beaver (*Castor canadensis*) habitat to inform restoration and  
611 climate change adaptation. *PloS One*, 13(2), e0192538.  
612 Dunning, J. B., Danielson, B. J., & Pulliam, H. R. (1992). Ecological Processes That Affect Populations  
613 in Complex Landscapes. *Oikos*, 65(1), 169–175. <https://doi.org/10.2307/3544901>  
614 Esri. (2022). *ArcGIS Pro* (2.8). Environmental Systems Research Institute.  
615 Fausch, K. D., Torgersen, C. E., Baxter, C. V., & Li, H. W. (2002). Landscapes to riverscapes: Bridging  
616 the gap between research and conservation of stream fishes: a continuous view of the river is  
617 needed to understand how processes interacting among scales set the context for stream fishes  
618 and their habitat. *BioScience*, 52(6), 483–498.  
619 Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for  
620 global land areas. *International Journal of Climatology*, 37(12), 4302–4315.  
621 <https://doi.org/10.1002/joc.5086>  
622 Firman, J. C., Steel, E. A., Jensen, D. W., Burnett, K. M., Christiansen, K., Feist, B. E., Larsen, D. P., &  
623 Anlauf, K. (2011). Landscape Models of Adult Coho Salmon Density Examined at Four Spatial  
624 Extents. *Transactions of the American Fisheries Society*, 140(2), 440–455.  
625 <https://doi.org/10.1080/00028487.2011.567854>  
626 Flitcroft, R. L., Arismendi, I., & Santelmann, M. V. (2019). A review of habitat connectivity research for  
627 Pacific salmon in marine, estuary, and freshwater environments. *JAWRA Journal of the American*  
628 *Water Resources Association*, 55(2), 430–441.  
629 Flitcroft, R. L., Burnett, K. M., Reeves, G. H., & Ganio, L. M. (2012). Do network relationships matter?  
630 Comparing network and instream habitat variables to explain densities of juvenile coho salmon  
631 (*Oncorhynchus kisutch*) in mid-coastal Oregon, USA. *Aquatic Conservation: Marine and*  
632 *Freshwater Ecosystems*, 22(3), 288–302.  
633 Flitcroft, R. L., Burnett, K., Snyder, J., Reeves, G., & Ganio, L. (2014). Riverscape Patterns among Years  
634 of Juvenile Coho Salmon in Midcoastal Oregon: Implications for Conservation. *Transactions of*  
635 *the American Fisheries Society*, 143(1), 26–38. <https://doi.org/10.1080/00028487.2013.824923>  
636 García-Berthou, E. (2007). The characteristics of invasive fishes: What has been learned so far? *Journal*  
637 *of Fish Biology*, 71, 33–55.  
638 Gomez-Uchida, D., Cañas-Rojas, D., Riva-Rossi, C. M., Ciancio, J. E., Pascual, M. A., Ernst, B., Aedo,  
639 E., Musleh, S. S., Valenzuela-Aguayo, F., Quinn, T. P., Seeb, J. E., & Seeb, L. W. (2018).

640 Genetic signals of artificial and natural dispersal linked to colonization of South America by non-  
641 native Chinook salmon (*Oncorhynchus tshawytscha*). *Ecology and Evolution*, 8(12), 6192–6209.  
642 <https://doi.org/10.1002/ece3.4036>

643 Gomez-Uchida, D., Sepúlveda, M., Ernst, B., Contador, T. A., Neira, S., & Harrod, C. (2018). Chile's  
644 salmon escape demands action. *Science*, 361(6405), 857–858.  
645 <https://doi.org/10.1126/science.aau7973>

646 Górski, K., González, J. F., Vivancos, A., Habit, E. M., & Ruzzante, D. E. (2017). Young-of-the-year  
647 Coho Salmon *Oncorhynchus kisutch* recruit in fresh waters of remote Patagonian fjords in  
648 southern Chile (51 S). *Biological Invasions*, 19(4), 1127–1136.

649 Hastings, A., Cuddington, K., Davies, K. F., Dugaw, C. J., Elmendorf, S., Freestone, A., Harrison, S.,  
650 Holland, M., Lambrinos, J., Malvadkar, U., Melbourne, B. A., Moore, K., Taylor, C., &  
651 Thomson, D. (2005). The spatial spread of invasions: New developments in theory and evidence.  
652 *Ecology Letters*, 8(1), 91–101. <https://doi.org/10.1111/j.1461-0248.2004.00687.x>

653 Huertas Herrera, A., Lencinas, M. V., Toro Manríquez, M., Miller, J. A., & Martínez Pastur, G. (2020).  
654 Mapping the status of the North American beaver invasion in the Tierra del Fuego archipelago.  
655 *PLOS ONE*, 15(4), e0232057. <https://doi.org/10.1371/journal.pone.0232057>

656 Huet, M. (1959). Profiles and Biology of Western European Streams as Related to Fish Management.  
657 *Transactions of the American Fisheries Society*, 88(3), 155–163. [https://doi.org/10.1577/1548-8659\(1959\)88\[155:PABOWE\]2.0.CO;2](https://doi.org/10.1577/1548-8659(1959)88[155:PABOWE]2.0.CO;2)

658

659 Humphries, P., Keckeis, H., & Finlayson, B. (2014). The River Wave Concept: Integrating River  
660 Ecosystem Models. *BioScience*, 64(10), 870–882. <https://doi.org/10.1093/biosci/biu130>

661 Jaksic, F. M., & Castro, S. A. (2021). *Biological invasions in the South American Anthropocene: Global*  
662 *Causes and Local Impacts*. Springer Nature. <https://doi.org/10.1007/978-3-030-56379-0>

663 Jalbert, C. S., Falke, J. A., López, J. A., Dunker, K. J., Sepulveda, A. J., & Westley, P. A. H. (2021).  
664 Vulnerability of Pacific salmon to invasion of northern pike (*Esox lucius*) in Southcentral Alaska.  
665 *PLOS ONE*, 16(7), e0254097. <https://doi.org/10.1371/journal.pone.0254097>

666 Jeschke, J. M., & Strayer, D. L. (2008). Usefulness of bioclimatic models for studying climate change and  
667 invasive species. *Annals of the New York Academy of Sciences*, 1134, 1–24.  
668 <https://doi.org/10.1196/annals.1439.002>

669 Jiménez-Valverde, A., Peterson, A. T., Soberón, J., Overton, J. M., Aragón, P., & Lobo, J. M. (2011). Use  
670 of niche models in invasive species risk assessments. *Biological Invasions*, 13(12), 2785–2797.  
671 <https://doi.org/10.1007/s10530-011-9963-4>

672 Karra, K., Kontgis, C., Statman-Weil, Z., Mazzariello, J. C., Mathis, M., & Brumby, S. P. (2021). Global  
673 land use / land cover with Sentinel 2 and deep learning. *2021 IEEE International Geoscience and*  
674 *Remote Sensing Symposium IGARSS*, 4704–4707.  
675 <https://doi.org/10.1109/IGARSS47720.2021.9553499>

676 Kolar, C. S., & Lodge, D. M. (2001). Progress in invasion biology: Predicting invaders. *Trends in*  
677 *Ecology & Evolution*, 16(4), 199–204. [https://doi.org/10.1016/S0169-5347\(01\)02101-2](https://doi.org/10.1016/S0169-5347(01)02101-2)

678 Kuhl, H. (1820). *Beiträge zur Zoologie und vergleichenden Anatomie*. Hermannschen Buchhandlung.

679 Leidholt-Bruner, K., Hibbs, D., & McComb, B. (1992). Beaver Dam Locations and Their Effects on  
680 Distribution and Abundance of Coho Salmon Fry in Two Coastal Oregon Streams. *Northwest*  
681 *Science*, 66.

682 Lockwood, J. L., Hoopes, M. F., & Marchetti, M. P. (2013). *Invasion Ecology*. Wiley-Blackwell.

683 Lokteff, R. L., Roper, B. B., & Wheaton, J. M. (2013). Do Beaver Dams Impede the Movement of Trout?  
684 *Transactions of the American Fisheries Society*, 142(4), 1114–1125.  
685 <https://doi.org/10.1080/00028487.2013.797497>

686 Lunetta, R. S., Cosentino, B. L., Montgomery, D. R., Beamer, E. M., & Beechie, T. J. (1997). GIS-based  
687 evaluation of salmon habitat in the Pacific Northwest. *Photogrammetric Engineering and Remote*  
688 *Sensing*, 63(10), 1219–1229.

689 Maldonado-Márquez, A., Contador, T., Rendoll-Cárcamo, J., Moore, S., Pérez-Troncoso, C., Gomez-  
690 Uchida, D., & Harrod, C. (2020). Southernmost distribution limit for endangered Peladillas

691 (Aplochiton taeniatus) and non-native coho salmon (*Oncorhynchus kisutch*) coexisting within the  
692 Cape Horn biosphere reserve, Chile. *Journal of Fish Biology*, 96(6), 1495–1500.  
693 <https://doi.org/10.1111/jfb.14309>

694 Manning, M. A., Arismendi, I., Olivos, J. A., & Giannico, G. (2022). Assessing Hybridization Risk  
695 Between ESA-Listed Native Bull Trout (*Salvelinus confluentus*) and Introduced Brook Trout (*S.*  
696 *fontinalis*) Using Habitat Modeling. *Frontiers in Environmental Science*, 10.  
697 <https://www.frontiersin.org/article/10.3389/fenvs.2022.834860>

698 Matter, A. N., Falke, J. A., López, J. A., & Savereide, J. W. (2018). A Rapid-Assessment Method to  
699 Estimate the Distribution of Juvenile Chinook Salmon in Tributary Habitats Using eDNA and  
700 Occupancy Estimation. *North American Journal of Fisheries Management*, 38(1), 223–236.

701 Miller, D. J. (2003). *Programs for DEM analysis* (Theory and Technology in Natural Sciences and  
702 Watershed Management, p. 37). Earth Systems Institute.  
703 [https://www.fsl.orst.edu/clams/download/pubs/miller\\_DEM\\_Programs\\_2003.pdf](https://www.fsl.orst.edu/clams/download/pubs/miller_DEM_Programs_2003.pdf)

704 Mitchell, S. C., & Cunjak, R. A. (2007). Stream flow, salmon and beaver dams: Roles in the structuring  
705 of stream fish communities within an anadromous salmon dominated stream. *Journal of Animal*  
706 *Ecology*, 76(6), 1062–1074. <https://doi.org/10.1111/j.1365-2656.2007.01286.x>

707 Montgomery, D. R. (1999). Process domains and the river continuum. *JAWRA Journal of the American*  
708 *Water Resources Association*, 35(2), 397–410.

709 Moyle, P. B., & Light, T. (1996). Biological invasions of fresh water: Empirical rules and assembly  
710 theory. *Biological Conservation*, 78(1), 149–161. [https://doi.org/10.1016/0006-3207\(96\)00024-9](https://doi.org/10.1016/0006-3207(96)00024-9)

711 Naiman, R. J., Bilby, R. E., Schindler, D. E., & Helfield, J. M. (2002). Pacific Salmon, Nutrients, and the  
712 Dynamics of Freshwater and Riparian Ecosystems. *Ecosystems*, 5(4), 399–417.  
713 <https://doi.org/10.1007/s10021-001-0083-3>

714 Naiman, R. J., Johnston, C. A., & Kelley, J. C. (1988). Alteration of North American Streams by Beaver.  
715 *BioScience*, 38(11), 753–762. <https://doi.org/10.2307/1310784>

716 Neira, R., Lhorente, J. P., Newman, S., Yáñez, J. M., Araneda, M., & Filp, M. (2014). Evolution of coho  
717 salmon (*Oncorhynchus kisutch*) breeding programs. *Proceedings, 10th World Congress of*  
718 *Genetics Applied to Livestock Production*.

719 Olden, J. D., Poff, N. L., & Bestgen, K. R. (2006). Life-History Strategies Predict Fish Invasions and  
720 Extirpations in the Colorado River Basin. *Ecological Monographs*, 76(1), 25–40.

721 Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C.,  
722 D'Amico, J. A., Itoua, I., Strand, H. E., Morrison, J. C., Loucks, C. J., Allnutt, T. F., Ricketts, T.  
723 H., Kura, Y., Lamoreux, J. F., Wettengel, W. W., Hedao, P., & Kassem, K. R. (2001). Terrestrial  
724 Ecoregions of the World: A New Map of Life on Earth. *BioScience*, 51(11), 933–938.  
725 [https://doi.org/10.1641/0006-3568\(2001\)051\[0933:TEOTWA\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2)

726 Parkes, J., Paulson, J., Donlan, C., & Campbell, K. (2008). *Control of North American Beavers in Tierra*  
727 *del Fuego: Feasibility of Eradication and Alternative Management Options* (Research Report  
728 LC0708/084; Landcare Research).

729 Penaluna, B. E., Allen, J. M., Arismendi, I., Levi, T., Garcia, T. S., & Walter, J. K. (2021). Better  
730 boundaries: Identifying the upper extent of fish distributions in forested streams using eDNA and  
731 electrofishing. *Ecosphere*, 12(1), e03332. <https://doi.org/10.1002/ecs2.3332>

732 Petro, V. M., Taylor, J. D., Sanchez, D. M., & Burnett, K. M. (2018). Methods to Predict Beaver Dam  
733 Occurrence in Coastal Oregon. *Northwest Science*, 92(4), 278–289.  
734 <https://doi.org/10.3955/046.092.0405>

735 Poff, N. L. (1997). Landscape filters and species traits: Towards mechanistic understanding and  
736 prediction in stream ecology. *Journal of the North American Benthological Society*, 16(2), 391–  
737 409.

738 Pollock, M. M., Pess, G. R., Beechie, T. J., & Montgomery, D. R. (2004). The Importance of Beaver  
739 Ponds to Coho Salmon Production in the Stillaguamish River Basin, Washington, USA. *North*  
740 *American Journal of Fisheries Management*, 24(3), 749–760. <https://doi.org/10.1577/M03-156.1>

- 741 Romey, B. (2018). *Modeling Spawning Habitat Potential for Chum (Onchorhynchus keta) and Pink*  
742 *Salmon (O. gorbuscha) in Relation to Landscape Characteristics in Coastal Southeast Alaska*  
743 [Portland State University]. <https://archives.pdx.edu/ds/psu/26223>.  
744 <https://doi.org/10.15760/etd.6136>
- 745 Schlosser, I. J. (1995a). Critical landscape attributes that influence fish population dynamics in headwater  
746 streams. *Hydrobiologia*, 303(1–3), 71–81.
- 747 Schlosser, I. J. (1995b). Dispersal, Boundary Processes, and Trophic-Level Interactions in Streams  
748 Adjacent to Beaver Ponds. *Ecology*, 76(3), 908–925. <https://doi.org/10.2307/1939356>
- 749 Sepúlveda, M., Arismendi, I., Soto, D., Jara, F., & Farias, F. (2013). Escaped farmed salmon and trout in  
750 Chile: Incidence, impacts, and the need for an ecosystem view. *Aquaculture Environment*  
751 *Interactions*, 4(3), 273–283. <https://doi.org/10.3354/aei00089>
- 752 Skewes, O., Gonzalez, F., Olave, R., Ávila, A., Vargas, V., Paulsen, P., & König, H. E. (2006).  
753 Abundance and distribution of American beaver, *Castor canadensis* (Kuhl 1820), in Tierra del  
754 Fuego and Navarino islands, Chile. *European Journal of Wildlife Research*, 52(4), 292–296.  
755 <https://doi.org/10.1007/s10344-006-0038-2>
- 756 Solomon, D. J. (1973). Evidence for Pheromone-influenced Homing by Migrating Atlantic Salmon,  
757 *Salmo salar* (L.). *Nature*, 244(5413), 231–232. <https://doi.org/10.1038/244231a0>
- 758 Soto, D., Arismendi, I., Olivos, J. A., Canales-Aguirre, C. B., Leon-Muñoz, J., Niklitschek, E. J.,  
759 Sepúlveda, M., Paredes, F., Gomez-Uchida, D., & Soria-Galvarro, Y. (2022). Environmental risk  
760 assessment of non-native salmonid escapes from net pens in the Chilean Patagonia. *Reviews in*  
761 *Aquaculture*, 15(1), 198–219. <https://doi.org/10.1111/raq.12711>
- 762 Soto, D., Jara, F., & Moreno, C. (2001). Escaped salmon in the inner seas, southern Chile: Facing  
763 ecological and social conflicts. *Ecological Applications*, 11(6), 1750–1762.
- 764 Strayer, D. L. (2010). Alien species in fresh waters: Ecological effects, interactions with other stressors,  
765 and prospects for the future. *Freshwater Biology*, 55, 152–174.
- 766 Suzuki, N., & McComb, W. C. (1998). Habitat classification models for beaver (*Castor canadensis*) in the  
767 streams of the central Oregon coast range. *Northwest Science*, 72(2), 102–110.
- 768 Vannote, R. L., Minshall, G. W., Cummins, K. W., Sedell, J. R., & Cushing, C. E. (1980). The River  
769 Continuum Concept. *Canadian Journal of Fisheries and Aquatic Sciences*, 37(1), 130–137.  
770 <https://doi.org/10.1139/f80-017>
- 771 Vicente, J. R., Kueffer, C., Richardson, D. M., Vaz, A. S., Cabral, J. A., Hui, C., Araújo, M. B., Kühn, I.,  
772 Kull, C. A., Verburg, P. H., Marchante, E., & Honrado, J. P. (2019). Different environmental  
773 drivers of alien tree invasion affect different life-stages and operate at different spatial scales.  
774 *Forest Ecology and Management*, 433, 263–275. <https://doi.org/10.1016/j.foreco.2018.10.065>
- 775 Virbickas, T., Stakėnas, S., & Steponėnas, A. (2015). Impact of Beaver Dams on Abundance and  
776 Distribution of Anadromous Salmonids in Two Lowland Streams in Lithuania. *PLOS ONE*,  
777 10(4), e0123107. <https://doi.org/10.1371/journal.pone.0123107>
- 778 Walbaum, J. J. (1792). *Petri Artedi renovati: Bibliotheca et philosophia ichthyologica*. Ant. Ferdin. Röse.
- 779 Ward, J. V. (1989). The Four-Dimensional Nature of Lotic Ecosystems. *Journal of the North American*  
780 *Benthological Society*, 8(1), 2–8. <https://doi.org/10.2307/1467397>
- 781 Ward, J. V. (1998). Riverine landscapes: Biodiversity patterns, disturbance regimes, and aquatic  
782 conservation. *Biological Conservation*, 83(3), 269–278. [https://doi.org/10.1016/S0006-](https://doi.org/10.1016/S0006-3207(97)00083-9)  
783 [3207\(97\)00083-9](https://doi.org/10.1016/S0006-3207(97)00083-9)
- 784 White, S. M., Giannico, G., & Li, H. (2014). A ‘behaviorscape’ perspective on stream fish ecology and  
785 conservation: Linking fish behavior to riverscapes. *WIREs Water*, 1(4), 385–400.  
786 <https://doi.org/10.1002/wat2.1033>
- 787 Wiens, J. A. (2002). Riverine landscapes: Taking landscape ecology into the water. *Freshwater Biology*,  
788 47(4), 501–515. <https://doi.org/10.1046/j.1365-2427.2002.00887.x>

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## 790 Conflict of Interest

791 The authors declare no conflicts of interest.

792

793 **Biosketch**

794 **J. Andres Olivos** is interested in the landscape ecology of aquatic biodiversity and gives  
795 emphasis on the effects of climate and land-use changes, hydrological disturbances, and  
796 biological invasions, as the most pressing issues for sustainability and conservation. This article  
797 is a coproduction with a multi-disciplinary research team working on the management and  
798 conservation of fish and wildlife at broad spatiotemporal scales.

799

800 **Authors contributions**

801 **J.A.O.** led the conceptualization, data collection, geospatial modelling, analysis, elaboration of  
802 figures, and writing of the manuscript. **I. A.** and **B. P.** provided critical guidance in the  
803 conceptualization and writing of the manuscript. **R. F.** and **G. G.:** provided extensive feedback  
804 and guidance. **A. H. H.,** and **J. F.:** provided comprehensive datasets for the development and  
805 validation of habitat models. All authors reviewed, edited, and approved the submission of the  
806 manuscript.