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Running head. Fish population persistence in dryland rivers

Title: Fish population persistence in hydrologically variable landscapes.

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18 **Abstract**

19 Forecasting population persistence in environments subjected to periodic disturbances
 20 represents a general challenge for ecologists. In arid and semi-arid regions, climate change
 21 and human water use present significant threats to the future persistence of aquatic biota
 22 whose populations typically depend on permanent refuge waterholes for their viability, as
 23 such habitats are increasingly being lost as a result of decreasing runoff and increased water
 24 extraction. We constructed a spatially explicit population model for golden perch *Macquaria*
 25 *ambigua* (Richardson), a native freshwater fish in the Murray-Darling Basin, eastern
 26 Australia. We then used the model to examine the effects of increased aridity, increased
 27 drought frequency, and localized human water extraction on population viability. Consistent
 28 with current observations, the model predicted golden perch population persistence under the
 29 current climate and levels of water use. Modeled increases in local water extraction greatly
 30 increased the risk of population decline, while scenarios of increased aridity and drought
 31 frequency were associated with only minor increase in this risk. We conclude that natural
 32 variability in abundances and high turnover rates (extinction / recolonization) of local
 33 populations dictate the importance of spatial connectivity and periodic cycles of population
 34 growth. Our study also demonstrates an effective way to examine population persistence in
 35 intermittent and ephemeral river systems by integrating spatial and temporal dynamics of
 36 waterhole persistence with demographic processes (survival, recruitment and dispersal)
 37 within a stochastic modeling framework. The approach can be used to help understand the
 38 impacts of natural and anthropogenic drivers, including water resource development, on the
 39 viability of biota inhabiting highly dynamic environments.

40

41 **Keywords**

- 42 climate change, drought, dryland rivers, golden perch, intermittent streams, metapopulation,
43 population viability analysis, water planning

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44 **Introduction**

45 Understanding the persistence of populations in patchy and variable environments is a key
 46 challenge for both basic and applied ecology – both in terms of understanding the processes
 47 that promote persistence, but also the likely impacts of changing disturbance regimes.
 48 Dryland rivers, (i.e. those flowing through arid and semi-arid regions), are among the most
 49 variable environments in the world, drain roughly 40% of the global land-mass and
 50 experience only intermittent runoff (Puckridge et al. 2000, Walker et al. 2006, Falke et al.
 51 2010). Such rivers are thus highly variable in terms of discharge, and frequently contract to
 52 isolated waterholes which become critical refuges for aquatic biota (Puckridge et al. 1998).
 53 The ability for species to persist in these rivers can depend strongly on their ability to tolerate
 54 harsh environmental conditions within isolated refuges, coupled with high fecundity and
 55 dispersal rates to facilitate recolonization during periods of connectivity (e.g. Magoulick and
 56 Kobza 2003, Crook et al. 2010).

57
 58 Increasingly, however, the persistence of dryland river biota is being threatened by the
 59 growing issue of water scarcity (Falke et al. 2010). In many regions, human water demands,
 60 especially for irrigation, have given rise to high levels of water extraction from rivers and
 61 groundwater sources in dryland regions (Sheldon et al. 2002). At a global scale, climate-
 62 change induced intensification of the hydrologic cycle is further expected to increase aridity
 63 in many dryland ecosystems, and droughts are expected to become more frequent (Dai 2011).

64
 65 Estimating the impacts of hydrologic changes on biota is made difficult by the fact that many
 66 taxa persist within regional metapopulations, where persistence is governed by links between

67 local populations via dispersal (Labbe and Fausch 2000, Perry and Bond 2009). Such spatial
 68 population structuring can easily give rise to highly non-linear population dynamics, making
 69 it difficult to foresee potentially critical thresholds of habitat loss or isolation (Wilcox et al.
 70 2006).

71
 72 Dryland rivers are common within the inland catchments of Australia, and are recognized as
 73 having some of the most variable flow regimes in the world (Puckridge et al. 1998).
 74 Associated with this are plant and animal assemblages that rely heavily on refuge waterholes
 75 to persist during extended dry periods, and which are renowned for their ‘boom and bust’
 76 cycles (Arthington et al. 2005, Sternberg et al. 2011). Waterholes in most of these rivers are
 77 subjected to water extraction (via pumping), sometimes for irrigation, but more often to
 78 supply water for stock and domestic use (CSIRO 2008b).

79
 80 In the present study, we developed a spatially explicit population model to examine the
 81 impacts of changing water availability on the population dynamics and persistence of a native
 82 fish species. We focused on golden perch, *Macquaria ambigua* (Richardson, 1845), in the
 83 Moonie River in the northern Murray-Darling Basin. Golden perch is a large native
 84 percichthyid fish that is common and widespread in the northern Murray-Darling and
 85 neighboring Lake Eyre Basin systems. Golden perch is the primary apex fish predator in the
 86 region, and frequently accounts for a large proportion of the overall fish biomass in refuge
 87 waterholes (Balcombe et al. 2006). Recent genetic studies of golden perch in the Moonie
 88 River reveal high levels of population connectivity punctuated by frequent population
 89 bottlenecks, suggesting dispersal among local populations helps regulate long-term
 90 persistence of the regional population (Huey et al. 2011).

91

92 In developing the model, we draw on several recent empirical datasets describing the
93 movement and demographics of golden perch in the Moonie River and the influence of flow
94 variability on the size and persistence of refuge waterholes. We then use the model to
95 examine three potential threats to waterhole persistence: (i) regional increases in the extent of
96 annual drying (aridity); (ii) increases in the frequency of extreme dry years (droughts); and
97 (iii) threats associated with localized waterhole drying from both excessive pumping for
98 irrigation and the taking of water for stock and domestic purposes. As well as providing
99 useful information on population viability for this system, our work serves to demonstrate a
100 modeling approach that could readily be applied to a range of other questions (or taxa)
101 regarding population persistence in desert rivers, as well as contributing to our broader
102 understanding of the role that disturbance regimes play in regulating metapopulation
103 persistence in highly dynamic landscapes (e.g. Wilcox et al. 2006, Elkin and Possingham
104 2008).

105

106 **Methods**

107 **Study area**

108 The Moonie River catchment is located in the north of the Murray-Darling Basin and drains
109 an area of c. 14,870 km² (Figure 1). The catchment experiences low annual rainfall (500–600
110 mm pa), high inter-annual rainfall variability, and high evaporative losses (1800–2200 mm
111 pa) (CSIRO 2008b). This climate gives rise to highly intermittent stream flow characterized
112 by long periods with no flow (mean ± se of 198 ± 14 days; max 701 days; Figure 2). Periodic
113 drought cycles further add to the extremes in flow intermittency, and for most of the year the

114 river exists as a series of isolated waterholes that act as refuges for aquatic biota. The location
 115 and bathymetry of waterholes in some sections of the Moonie River have been mapped using
 116 a mix of aerial mapping and boat-surveys. Where waterhole data was incomplete, either due
 117 to lack of any survey, or emphasis on mapping larger waterholes only, data from surveyed
 118 sections was used to generate semi-random waterhole locations (including their size and
 119 depths) such that the un-surveyed reaches shared the same longitudinal distribution and size-
 120 frequency structure of waterholes as for the surveyed reaches (Queensland Government,
 121 unpubl. data). In total there were 77 waterholes in the modeled river network, 32 of which
 122 were considered “shallow” and therefore were expected to dry out during drought years (see
 123 methods for details on how “shallow” and “deep” waterholes were each affected by the
 124 different disturbances).

125
 Figure 1 and Figure 2 about here

126 **Modeling approach**

127 We developed a spatial population model in which individual waterholes were treated as
 128 local populations. The dynamics of each local population were modeled using a female-only
 129 stochastic age-structured matrix model (reflecting survival (S) and fecundity (F)). Local
 130 populations were connected by dispersal to account for immigration and emigration into and
 131 away from individual waterholes during the wet season. Dispersal rates were modeled as a
 132 function of waterhole isolation. The local carrying capacity (k) of individual populations was
 133 varied spatially and temporally as a function of waterhole size. The model further accounted
 134 for variation in vital rates (S, F) and carrying capacity (k) due to the effects of both
 135 background environmental fluctuations (normal inter-annual hydrologic variability), and
 136 local and regional disturbances from waterhole pumping and drought, respectively.

137 The model was constructed using RAMAS Metapop (Akçakaya 2005), which has been

138 widely used to model metapopulation dynamics in terrestrial and aquatic ecosystems (Root
 139 1998, Akçakaya *et al.* 1999, 2003). RAMAS has the capacity to include the effects of various
 140 disturbance regimes (referred to as catastrophes within the RAMAS framework). We
 141 included both local (waterhole pumping) and regional (drought) catastrophes in the model, as
 142 well as the effects of increasing aridity.

143 The effect of each scenario on golden perch populations was assessed by considering three
 144 primary population measures: (a) the median metapopulation size under each scenario; (b)
 145 average patch occupancy (number of waterholes occupied), which would likely fall if
 146 dispersal and recolonization rates and local recruitment were insufficient to balance rates of
 147 local population loss (e.g. from waterhole pumping); and (c) quasi-extinction risk (arbitrarily
 148 set at the whole metapopulation falling below 100 individuals within the modeled time
 149 interval).

150 **Demographic parameters**

151 Golden perch are both highly fecund and highly mobile (Pusey *et al.* 2004). Floods appear to
 152 enhance survival and growth of young fish but are not required for spawning (Balcombe *et al.*
 153 2006, Sternberg *et al.* 2011). The stage matrices employed in the present analysis assumed
 154 similar fecundity patterns across all years.

155 *Vital rates*

156 Demographic parameter estimates were derived from an analysis of length-frequency data for
 157 golden perch collected from the Moonie River during the austral spring from 2006-2010,
 158 using three fyke nets per site (Huey *et al.* 2011, Sternberg *et al.* 2011). These data were
 159 converted to age-frequency data on the basis of a regression of age against length from a
 160 subset of fish collected as part of another study in an adjacent tributary of the Darling, from
 161 which otoliths were removed and aged (N Menke *et al.*, unpublished data; equation 1).

162 Because fish are not always sexed during these surveys male and female growth and survival
 163 rates were presumed equal in this analysis. We then based the model structure on the
 164 observed age distribution, with 7 age classes and maturity reached in the 3+ age class (Figure
 165 3; Pusey et al. 2004).

166

167
$$\text{age (days)} = 94.252 \times e^{\text{length(mm)} \times 0.0105} \quad (\text{eq. 1})$$

168

169 Survival rates were calculated by regressing $\ln(\text{abundance}) \sim \text{age}$ for each survey year. All
 170 slopes were linear, suggesting constant survival rates across age classes during the 2006-2010
 171 surveys ($S = 0.53 \pm 0.10$). Per capita net reproduction was estimated from the ratio of (pre-
 172 spawning) 0+ abundances relative to those of reproductive adult females in the previous year
 173 ($F = 6.60 \pm 1.64$). Reproductive individuals were restricted to 3+ age classes (Pusey et al.
 174 2004), and reproductive output was assumed equal across all age classes. In reality fecundity
 175 will vary with the size of the individual, but by how much is not certain from available data.
 176 However, the similar mortality rate across age-classes helped reduce the sensitivity of the
 177 results to this simplification.

178

179 *Dispersal*

180 Dispersal rates were derived from acoustic tracking of juvenile and adult fish movement over
 181 the 2007/8 and 2008/2009 wet seasons. A total of 80 golden perch were tagged with acoustic
 182 tags (V7-4L-69KHz, Vemco, Nova Scotia, Canada), and their movements recorded using a
 183 network of 17 listening stations (VR2W, Vemco, Nova Scotia, Canada) installed throughout
 184 a ~85 km reach of the Moonie River, which encompassed 15 semi-permanent waterholes.

185 Dispersal in the model refers to the proportion of a population in one waterhole taking up
 186 residence in a different waterhole in the next year. The flow patterns of the survey years from
 187 2007 to 2010 displayed contrasting event numbers and seasonality of flows, so that dispersal
 188 parameters were calculated based on the maximum distance of movements of identified fish
 189 during a single flow event between waterholes. These generally occurred on the first flow
 190 events of a season. Tag loss rates were highest in the month after tagging, generally before a
 191 flow event, and individuals disappearing from the pool of tagged fish were not included in
 192 the calculation of dispersal rate. Mortality was assumed equal for moving and resident fish.
 193 Return migrations were observed, but appeared to be contingent on suitable late season or
 194 winter flow events, and were not modeled as independent dispersal events. Instead it was
 195 assumed that the maximum distance travelled from the waterhole of origin was the most
 196 likely indicator of waterhole re-colonization potential and gene flow between populations (J.
 197 M. et al., unpublished data). The acoustic tracking data suggested fish moved in an upstream
 198 and downstream direction at approximately equal rates, with the frequency of movement of
 199 individual fish decaying exponentially as a function of distance from the tagging location
 200 (Fig 3.). The proportion of individuals dispersing between each population pair (M_{ij}) was
 201 estimated on the basis of an exponential (stream) distance decay function, with an additional
 202 constraint on maximum dispersal distance (D_{max} ; see eq. 2).

203
$$M_{ij}=a \cdot \exp(-D_{ij}^c/b), \quad \text{if } D \leq D_{max} \quad \text{eq. 2}$$

204
$$M_{ij}=0, \quad \text{if } D > D_{max}$$

205

206 Specific parameter values for the fitted curve (Figure 3) were $a = 0.6$, $b = 20$, $c = 1.0$, $D_{max} =$
 207 80. Dispersal rates were allowed to randomly fluctuate by setting the CV for dispersal
 208 parameter equal to 0.20. There was no density dependent constraint on dispersal because

209 opportunities for movement between waterholes only occurred during high flow events when
 210 density dependent factors are unlikely to be important (Arthington and Balcombe 2011). One
 211 aspect of dispersal that we do not additionally consider is the potential movement of larvae
 212 away from their natal site. Golden perch larvae are known to drift downstream, however we
 213 have little information on the distances travelled, nor any evidence to suggest such
 214 movements lead to widespread mixing and/or recolonization of isolated waterholes. We thus
 215 focus on adult movement, which is well documented and occurs over larger scales than is
 216 likely for larval drift.

217

Figure 3 about here

218 *Carrying capacity*

219 Carrying capacity of individual waterholes is primarily a function of their size, which can
 220 fluctuate by orders of magnitude (and fall to zero) in successive years. While other factors
 221 such as rates of primary and secondary production, prey accessibility and habitat quality, may
 222 also vary (Arthington and Balcombe 2011), these were all considered subordinate to the
 223 effects of hydrologic variability, and were not considered in the model. There are no
 224 experimental field data to indicate carrying capacity of these waterholes, but golden perch are
 225 widely stocked in impoundments and farm dams. We therefore used recommended maximum
 226 stocking rates for golden perch as a guide to carrying capacity; approximately 500 kg ha⁻¹
 227 (Boyd 2006), which equates to ~0.05 fish m⁻² given an average weight of 1 kg. This density
 228 is consistent with maximum densities of ~ 1000 kg ha⁻¹ of mature fish observed after
 229 extended periods of flooding and recruitment in several neighboring arid-zone rivers
 230 (Balcombe et al. 2007, Sternberg et al. 2011). The effect of density dependence on local
 231 populations was modeled as a simple ceiling function, in which vital rates were modified

232 only once k was reached. Because of their small size, 0+ fish were excluded from population
 233 size estimates for the purposes of determining when to invoke density dependence in the
 234 model.

235
 236 Assessing which vital rates (mortality, fecundity or dispersal) are influenced by density
 237 dependence was another key step in developing the model. Sternberg *et al.* (2011) found
 238 only minor inter-annual variation in body condition of fish caught in the same fyke net
 239 surveys used here, and suggested that survival rates rather than fecundity are the primary
 240 factor affected by hydrology. However, fish densities during these surveys were well below
 241 the estimated carrying capacity, and survival was relatively stable across age classes. In
 242 addition, the interpretation made by Sternberg *et al.* (2011) arguably pertains more to the
 243 absence of a boom in post-flood recruitment when resource availability is high, than to the
 244 likely effects of resource limitation. There are also no published examples in which
 245 crowding (i.e. density-dependent) effects have been linked to the mortality of this species,
 246 suggesting the response to crowding may also be subtle. We therefore hypothesized instead
 247 that declines in body condition from crowding would be more likely to affect reproductive
 248 investment than the survival of adults. Thus, density dependence was modeled to reduce
 249 fecundity only.

250

251 **Environmental stochasticity**

252 *Inter-annual variability*

253 The volume of waterholes varies in two important ways. First, individual waterholes differ
 254 substantially in their volume when full, and hence, in their maximum carrying capacity k_{max} .
 255 Second, differences in the depth of each waterhole affect the rate at which they dry, and how
 256 long they persist. Fifteen depth loggers installed in waterholes in the Moonie River from

257 2004-2006 showed that water loss rates (corresponding to ca 0.01 mday⁻¹) are relatively
 258 constant throughout the dry season and among waterholes (Queensland Government
 259 unpublished data). From this, a sequence of minimum annual waterhole volumes (and
 260 proportional habitat loss) was calculated on the basis of dry season duration and estimated
 261 reduction of waterhole area. This provided a sequence of annual k values for each waterhole,
 262 which we based on the assumed carrying capacity of 0.05 fish m⁻², from which waterhole
 263 specific values for k_{avg} and k_{sd} could be calculated. Because inter-annual hydrologic
 264 variability tends to affect all waterholes similarly, k -values were modeled as being strongly
 265 correlated within each time step ($r^2=0.8$). The correlation among individual k -values was still
 266 set at $r^2 < 1.0$ to reflect the likely influence of local shading, waterhole shape, soil conditions
 267 etc. on local habitat quality and hence carrying capacity.

268
 269 *Extended dry periods (regional catastrophes)*

270 Extreme dry spells – here termed droughts - were modeled as regional catastrophes within
 271 RAMAS. We used the frequency of droughts (identified as extreme dry spells) in the
 272 historical record as a basis for their frequency in the model. Droughts were modeled to occur
 273 randomly with a probability of 0.05 in the baseline scenario (i.e. with an average return
 274 interval of 20 years, as per the historical flow sequence; Figure 2). Droughts directly affected
 275 population abundances by killing all fish in shallow waterholes, which dry out in drought
 276 years. In contrast, deep waterholes (~30% by number) persist even during drought, and were
 277 modeled as resistant to drought impacts. Local populations within deep waterholes were
 278 affected only by inter-annual variability in k , which for these habitats never approached zero.

279
 280 **Scenarios**

281 Several scenarios of altered runoff and threats to waterhole persistence from local pumping

282 were explored. These focused on changes in carrying capacity caused by increased drought
 283 frequency (2 scenarios), reduced runoff (3 scenarios), and increased pumping (3 scenarios)
 284 from permanent waterholes. These three factors were examined in a factorial design ($n=24$
 285 scenarios in total; Table 1).

286
 Table 1 about here

287 While there remains considerable uncertainty about future runoff trends in this region, we
 288 envisage these 24 scenarios effectively bracket the range of possible futures that might arise.
 289 They therefore help gauge potential threats to long-term population viability of golden perch
 290 that might arise as a result of changes in disturbance regimes (e.g. regional versus local
 291 events), and thus help to inform long-term management strategies.

292
 293 *Altered drought frequency*

294 Droughts are expected to become more frequent in the Murray-Darling Basin due to climate
 295 change, although the exact changes in frequency and intensity are difficult to predict (CSIRO
 296 2008a). Here, drought frequency was arbitrarily doubled from its historical frequency to
 297 occur, on average, once every 10 years (i.e. with a probability of 0.10 in any single time step;
 298 Table 1). This increase was intentionally set slightly higher than the 80% increase in drought
 299 frequency for the east coast by 2070 predicted by Mpelasoka et al. (2008) to provide a
 300 conservative test of population sensitivity to changing drought frequency.

301
 302 *Decreased runoff and sedimentation*

303 Rainfall runoff modeling suggests future runoff in the Moonie River catchment will decline
 304 by ~10% (median), with worst case scenarios closer to a 20% reduction (CSIRO 2008b).

305 Decreased runoff will increase the average period without flow each year, which will reduce

306 the average carrying capacity of waterholes. However, because much of the runoff in the
 307 Moonie River occurs during floods, the predicted 20% reduction in runoff volume is unlikely
 308 to result in such marked increases in cease to flow spell durations. Thus, two scenarios were
 309 examined; a +5% and +10% increase in cease to flow spell duration. For each scenario the
 310 change in carrying capacity was estimated on the basis of average changes in waterhole
 311 volume at the end of the shortened dry spell (Table 1).

312

313 *Local pumping*

314 In contrast to climatic influences on waterhole persistence, the effects of pumping are
 315 primarily localized to individual waterholes, and are actually more likely to affect large
 316 permanent waterholes than smaller ones that persist only in some years. The threats from
 317 local water extraction were modeled as the probability of individual waterholes being
 318 pumped dry (“pumping likelihood”, $Pr = 0.01, 0.05$ and 0.10 ; Table 1). This refers to the risk
 319 that water extraction by pumps from isolated waterholes for irrigation or stock and domestic
 320 use could lead to the waterhole contracting substantially in size. Stock and domestic water
 321 use is a riparian land right in Queensland and pumps for this use tend to be much more
 322 common along waterholes known to persist during droughts, and while extraction for other
 323 purposes is regulated, the risks of over-extraction (whether intentionally or from pumps
 324 accidentally being left on) are a concern. The effects of local and regional disturbances are
 325 thus orthogonal to one another in their impacts on deep versus shallow waterholes.

326

327 **Initial abundances and age-structure**

328 Initial abundances and age-structure were estimated on the basis of average densities and
 329 size/age-frequencies observed in field surveys over the period 2006-2009 (S. Balcombe
 330 *unpublished data*). However, to avoid any bias associated with these initial conditions, the

331 first 10 years were treated as a burn-in period when running the models and ignored in the
332 results.

333 **Model-runs**

334 Population outcomes were examined over a 100-year time horizon. Each scenario was
335 replicated 1000 times to establish the effects of demographic and environmental stochasticity.
336 Vital rate parameters were sampled from a log-normal distribution and S , F and K were
337 correlated at each time-step. Model runs were described on the basis of average
338 metapopulation abundance, terminal patch-occupancy rates, and cumulative extinction risk
339 over the 100-year time horizon.

340

341 **Sensitivity analyses**

342 The sensitivity of the model to uncertainty in the various input parameters was assessed using
343 a simple perturbation analysis (Regan *et al.* 2003), in which the model was rerun with each of
344 the model parameters adjusted independently by $\pm 10\%$ of the starting value. Sensitivity was
345 quantified in terms of the relative effects of each of these changes on each of the summary
346 statistics. This approach highlights influential variables rather than trying to model the actual
347 risks to populations that might arise if all values were adjusted simultaneously (e.g. from
348 coincident reductions in survival and fecundity; Akçakaya *et al.* 2003).

349

350 **Results**

351 **Population viability and model sensitivity**

352 Modeled population sizes varied dramatically through time in response to demographic and
353 environmental stochasticity, but in spite of this temporal variability under baseline (current)
354 conditions population sizes never fell below the quasi-extinction threshold over the modeled

355 time horizon, and can be considered dynamic but stable over long time-scales.

356

357 Sensitivity analysis showed survival rates to have the greatest effect overall on abundances
 358 (relative influence of 0.91), followed by mean fecundity (0.34) and carrying capacity (0.22;
 359 Table 2). Uncertainty in these (and other) parameters had a much greater influence on
 360 abundance than on patch occupancy and extinction risk (Table 2). The influence of dispersal
 361 and spatial correlation structure were relatively weak within the bounds of the model (Table
 362 2).

363

Table 2 about here

364 **Scenario impacts**

365 Population viability was largely unaffected by the decreases in carrying capacity associated
 366 with increased aridity, with only small changes in population size and patch occupancy, and
 367 extinction risk largely unchanged (~ 0.114 ; Figure 4). In contrast, the effect of increased
 368 drought frequency was severe, with extinction risk doubled to 0.24, and average population
 369 size nearly halved from 5578 to 3004 (Figure 4).

370

Figure 4 about here

371 Local pumping scenarios also had a strong influence on population viability. At pumping
 372 likelihoods of ≥ 0.05 the population went extinct in nearly 50% ($Pr \geq 0.452$) of the model runs
 373 (Figure 4). The effect of pumping was exacerbated even further by increased drought
 374 frequency. For example, a pumping likelihood of 0.01 under the baseline model was
 375 associated with a $Pr(\text{extinction})$ of 0.162, up from 0.114 under baseline climate conditions.
 376 With more frequent droughts however, this level of pumping more than doubled extinction
 377 risk to 0.313. At higher levels of pumping ($Pr = 0.05$ and 0.10), population extinction risk

378 became increasingly certain, particularly when combined with more frequent droughts
 379 (Figure 4).

380

381 **Discussion**

382 The metapopulation concept has attracted considerable interest from stream ecologists
 383 working in hydrologically variable river systems (e.g. Gotelli and Taylor 1999, Fagan 2002,
 384 Magoulick and Kobza 2003). In dryland rivers in particular, the patchy and dynamic nature
 385 of refuge habitats, and the role of dispersal have become central questions relating to
 386 population persistence (Labbe and Fausch 2000, Falke et al. 2010, Huey et al. 2011).

387 However, most studies exploring the impacts of changing river flows on population viability
 388 in dryland rivers have sought to model habitat dynamics as a proxy for population dynamics -
 389 as has been the case for environmental flow studies more generally (Jager and Smith 2008,
 390 Shenton et al. 2012). These habitat models do not capture the interactions between habitat
 391 loss and changing demographic rates, nor internal demographic feedbacks, even though such
 392 dynamics can strongly influence regional persistence (Hanski 1998). The modeling
 393 presented here is a tractable means of assessing the effects, not only of more frequent and
 394 intense disturbances, but also the effects of a novel disturbance (i.e. the periodic loss of
 395 individual refuges). It is also one of the few studies exploring the combined effects of
 396 disturbance frequency and intensity on population and landscape dynamics in real-world
 397 systems.

398

399 **Baseline predictions and model sensitivity**

400 One of the most striking features of dryland rivers is the role of temporal environmental
 401 variability in driving habitat availability and hence survival rates (Bunn et al. 2006). Indeed,
 402 survival rates were observed to exert more than twice the influence of any other variable in

403 terms of model sensitivity (Table 2), largely because of high mortality associated with dry
 404 years. In particular, stochastic sequences of dry years in which droughts occurred in quick
 405 succession reduced population sizes to low numbers, at which point they became exposed to
 406 demographic uncertainty and potential Allee effects. In general, although extinction risk
 407 under baseline conditions was low, the model predicted that successive drought sequences
 408 could still give rise to population extinction. Conversely, high abundances were predicted to
 409 occur following successive wet years, with these periods of growth effectively buffering the
 410 population during periods of drought.

411

412 Connectivity among refuges also plays a critical role in sustaining populations in fragmented
 413 landscapes (Hanski 1998), including for desert fishes (Meffe and Vrijenhoek 1988,
 414 Vrijenhoek 1998). In a recent study of the genetic structure of fish populations in the Moonie
 415 River, Huey et al (2011) concluded that, overall, golden perch populations are highly
 416 connected by dispersal, but that periodic bottlenecks from waterhole drying have imparted
 417 some spatial genetic structure via drift. They were unable to determine the means by which
 418 gene-flow occurs – whether by stepping-stone or long-distance dispersal – due to the absence
 419 of migration-drift equilibrium, which is required for making such inferences.

420

421 In contrast, direct observation of fish movement rates revealed a rapid decline in colonization
 422 rates as a function of distance from the source population (Figure 3), suggesting that
 423 connectivity of relatively isolated populations is likely to arise via intermediate ‘stepping
 424 stones’ – a pattern of movement that once again is widely observed among fish populations
 425 (Johnston 2000, Jackson et al. 2001). An implication of this is that successful colonization
 426 events will become less likely, and (presumably therefore) extirpation rates will increase as
 427 pools become more isolated, for example due to local habitat loss or increased aridity.

428

429 **Scenario outcomes**

430 Comparisons among the different scenarios revealed two important findings. First, localized
 431 loss of normally permanent refuge habitats would appear to pose a significant threat to
 432 population viability even when some refuges persist in every year. This result reflects a
 433 classic situation arising in unstable metapopulations, where rates of local recolonization are
 434 insufficient to keep pace with rates of local extinction, which eventually leads to extinction of
 435 the regional population (Hanski 1998). A critical observation is that in many model runs,
 436 populations continued to persist for a considerable period of time even when pumping rates
 437 were high (Figure 5). This means that long-term extinction risk may be very hard to discern
 438 from short-term monitoring programs. For example, even under the most extreme scenarios
 439 modeled (high frequency and intensity of local and regional disturbances), populations still
 440 continued to persist (on average) for 50+ years, and in reality long-term declines would be
 441 further masked by high inter-annual variability. Collectively these results suggest that
 442 extinction debt (*sensu* Tilman et al. 1994), in which extinction is time-delayed but
 443 deterministic, may be high for desert fishes.

444

445 We also found that the effect of frequent local disturbances was high relative to that from
 446 regional disturbances. In a theoretical study Wilcox et al (2006) found varying effects of
 447 frequency and intensity, depending on synchrony of patch dynamics. It is thus likely that our
 448 findings reflect the higher modeled intensity of local disturbances relative to regional
 449 disturbance, and thus would be expected to vary among systems based on the nature of the
 450 disturbance regime and related patch dynamics (Wilcox et al. 2006).

451

452 The second key finding from the scenario comparisons was that even a relatively minor

453 increase in the likelihood of local disturbance caused a large increase in extinction risk, and
454 this response was strongly non-linear as the likelihood of local disturbances was increased.
455 This result is not in itself entirely surprising, and indeed there are many examples from both
456 theoretical and empirical research in which populations display strongly non-linear dynamics
457 in response to changes in vital rates and connectivity among habitat patches (e.g. May 1974,
458 Hanski 1998). The important take home message is that even seemingly stable populations
459 may reach previously unidentified tipping points along gradients of disturbance frequency,
460 beyond which extinction risk becomes very high (Wilcox *et al.* 2006).

461

462 **Management implications**

463 There has been a long standing awareness of the threats to desert fishes from water resource
464 development and other anthropogenic pressures, but also of the difficulties in trying to
465 predict extinction risks among species for whom habitats periodically expand and contract
466 (Minckley and Deacon 1968). Over the last decade threats from increasing aridity and water
467 resource development have generated renewed interest at a global scale (e.g. see the UN
468 ‘Decade for Deserts and Desertification’ program, 2010-2020; <http://unddd.unccd.int/>).
469 Impacts from anthropogenic pressures on desert rivers, and fishes in particular, have received
470 greatest attention in areas such central and south-western USA (Meffe and Vrijenhoek 1988,
471 Fagan *et al.* 2005), south-western Europe (Magalhães *et al.* 2002), and Australia (Unmack
472 2001, Balcombe *et al.* 2006). However, despite this increased focus, a challenge for
473 evaluating longer-term sustainability issues is that much of the existing research on these
474 ecosystems is observational or relatively short-term, and there are few examples in which
475 explicit predictions have been (or can be) been made regarding the likely long-term
476 consequences of altered disturbance regimes. As our research shows, this represents a critical
477 knowledge gap for the management and conservation of dryland rivers (Propst *et al.* 2008).

478

479 Persistence of fish in our study system depends on the presence of deep refuge waterholes
 480 that persist even during severe droughts. Such habitats are prone to surface and groundwater
 481 extraction (e.g. Bunn et al. 2006, Falke et al. 2010), and indeed water resource development
 482 could pose a significant threat to longer-term population viability of fishes in this system if
 483 not adequately managed. Potential strategies to alleviate these risks are to firstly limit the
 484 number of waterholes exposed to additional anthropogenic drawdown. We assumed that
 485 pools are not fed by near-surface groundwater, and thus that the effects of local pumping
 486 remain localized. In areas with highly connected surface-groundwater systems, this
 487 assumption may not hold (e.g. Labbe and Fausch 2000). Understanding the influence of
 488 water-resource development on coupled surface-groundwater systems, and the role of these
 489 interactions in maintaining aquatic refuges remains a poorly studied area of research (Fausch
 490 et al. 2002). While there are some examples in which detailed water-balance models have
 491 been developed for specific planning areas (e.g. Falke et al. 2010), it may be necessary to
 492 also consider proxy methods for predicting waterhole persistence when working over much
 493 larger spatial scales (e.g. see Hermoso et al. 2012).

494

495 An important question is how our work on this single species system can inform the
 496 management of other species, including those for which there are limited data? Perhaps the
 497 first point is to emphasize the heuristic value of PVA models in identifying and beginning to
 498 quantify the sorts of threats that might previously have been overlooked, even for well-
 499 studied species. Secondly, the PVA process provides a structured way of organizing
 500 information that can aid in framing problems and system understanding (‘the ‘facilitator’)
 501 and in helping to compare risks (‘the stockbroker’; Burgman and Possingham 2000). Equally
 502 important is to recognize the risks of over-reliance on PVA as a sole decision making tool

503 ('the loaded gun' ; Burgman and Possingham 2000). Where limited information is available
 504 for particular species, it may still be possible to gather sufficient data to develop models
 505 capable of distinguishing the potential response of species with different life-histories (e.g.
 506 Yen et al. 2013), and to use those models to develop testable hypotheses that can help fill
 507 specific knowledge gaps. For example, above all else our work on golden perch highlights
 508 the potential for extinction debt to mask seemingly certain extinction from this system under
 509 some scenarios, thereby highlighting the importance of considering persistence over
 510 relatively longer time scales than can typically be achieved as part of isolated field studies,
 511 and to think carefully about management actions that influence the historic disturbance
 512 regime.

513
 514 In summary, while a number of studies have highlighted threats to dryland and desert river
 515 fishes from anthropogenic pressures (e.g. Oakes et al. 2005, Bunn et al. 2006, Falke et al.
 516 2010), these primarily describe hydrologic changes or expected distribution patterns, rather
 517 than modeling the actual mechanisms that regulate fish abundances, such as survival and
 518 movement (Oakes et al. 2005). This study helps address this important knowledge gap using
 519 a large-bodied apex fish predator, golden perch, as a model species. The study both highlights
 520 the potential threat from anthropogenic influences to the viability of this species in the study
 521 system, and also demonstrates a novel application of population viability modeling to
 522 examine the effects of changing landscape dynamics (i.e. refuge habitat availability) on
 523 population persistence in dryland rivers. Such an approach could readily be applied to biota
 524 inhabiting highly dynamic environments in other parts of the world.

525

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663 effective water-management strategies in variable climates using population dynamics
664 models. *Journal of Applied Ecology* 50:691–701.

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667 Table 1. Summary of the scenarios examined, including the parameter values and their
 668 associated effects within the model

Scenario	Scenario	Values	Effect
Disturbance	affects		
Drought frequency	Frequency of	0.05	Shallow waterholes: $k=0$
	regional catastrophes	0.10	Deep waterholes: <i>no effect</i>
Aridity (Δ CTF)	Cease to flow	Baseline	Causes a proportional
	duration	+5% +10%	reduction in k (<i>mean, sd</i>)
Local pumping	Likelihood of	0	Shallow waterholes: <i>no effect</i>
	local	0.01	Deep waterholes: $k=0$
	catastrophes	0.05	
		0.10	

669

670

671

672 Table 2. Sensitivity analysis results. The relative influence of varying each parameter on

673 the three summary metrics describes the largest effect after adjusting each of

674 the model input parameters by $\pm 10\%$. Direction indicates the direction of

675 change that had the larger effect (i.e. '+' or '-'), and the ranks are those relative

676 to all other variables in the model. The top 3 ranked parameters are shown in

677 bold

Parameter Group	Parameter	Direction	Relative influence			
			Average Rank	Relative Abundance	Patch Occupancy	Extinction Risk
Carrying Capacity	K_{mean}	-	3	0.22	0.09	0.02
	K_{sd}	-	6	0.31	0.07	0.01
Survivorship	S_{mean}	-	1	0.91	0.66	0.22
	S_{sd}	-	9	0.07	0.02	0.01
Fecundity	F_{mean}	-	2	0.34	0.12	0.02
	F_{sd}	-	7	0.07	0.01	0.01
Dispersal	a	-	12	0.04	0.00	0.01
	b	-	11	0.04	0.00	0.01
	c	-	7	0.09	0.04	0.01
	D	-	9	0.07	0.01	0.01
	CV	-	9	0.10	0.05	0.00
Vital rates						
sample distribution	EV.norm		8	0.08	0.01	0.01
Correlation	FSK		10	0.03	0.01	0.01
Structure	uncorrelated					
	No Spatial		8	0.12	0.03	0.00

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681 Figure Captions

682 Figure 1. Map of the Moonie river catchment showing the location of major waterholes
 683 and their approximate maximum carrying capacity (k_{max}). The inset map
 684 shows the location of the Moonie catchment relative to the Murray-Darling
 685 Basin and the Australian continent.

686

687 Figure 2. Summary of streamflow patterns (a) daily streamflow time-series and (b)
 688 frequency distribution of the longest cease to flow spell at the Nindigully gauge
 689 (Gauge No. 417201B). Note that some spells extend for more than 365 days.

690

691 Figure 3. Plot showing the proportion of tagged fish that moved upstream and
 692 downstream separately and when combined. The dispersal kernel fit to the data
 693 is indicated by the solid black line.

694

695 Figure 4. Bar-graphs summarising scenario outcomes in terms of (a) terminal population
 696 size, (b) terminal patch occupancy, and (c) cumulative extinction risk.

697 Individual scenarios are indicated by the boxes at the top of the diagram (top;
 698 drought frequency; bottom row, drying extent) and individual bars (pumping
 699 likelihood). Error bars represent (a, b) +1 standard deviation and (c) upper 95th
 700 percentile.

701

702 Figure 5. Time series illustrating the average population trajectory under each of the
703 modelled scenarios. Individual plots represent separate drought/aridity
704 scenarios, with individual lines on each plot showing the effects of local
705 disturbance through pumping.

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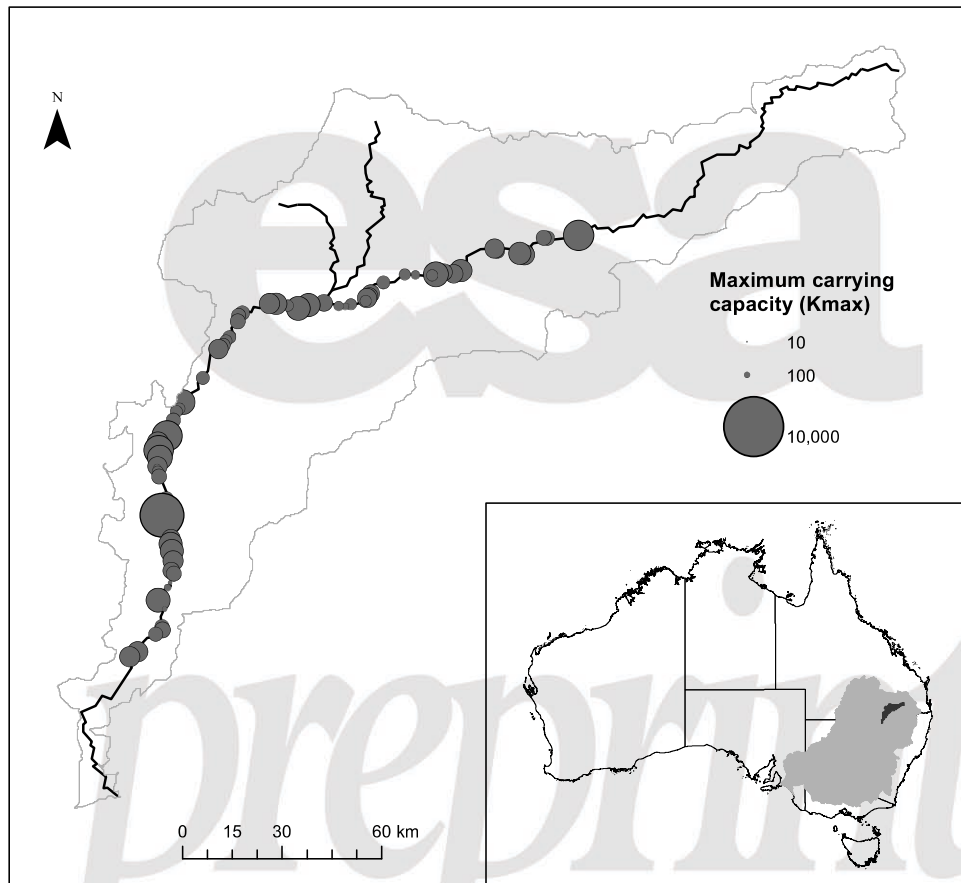


Figure 1

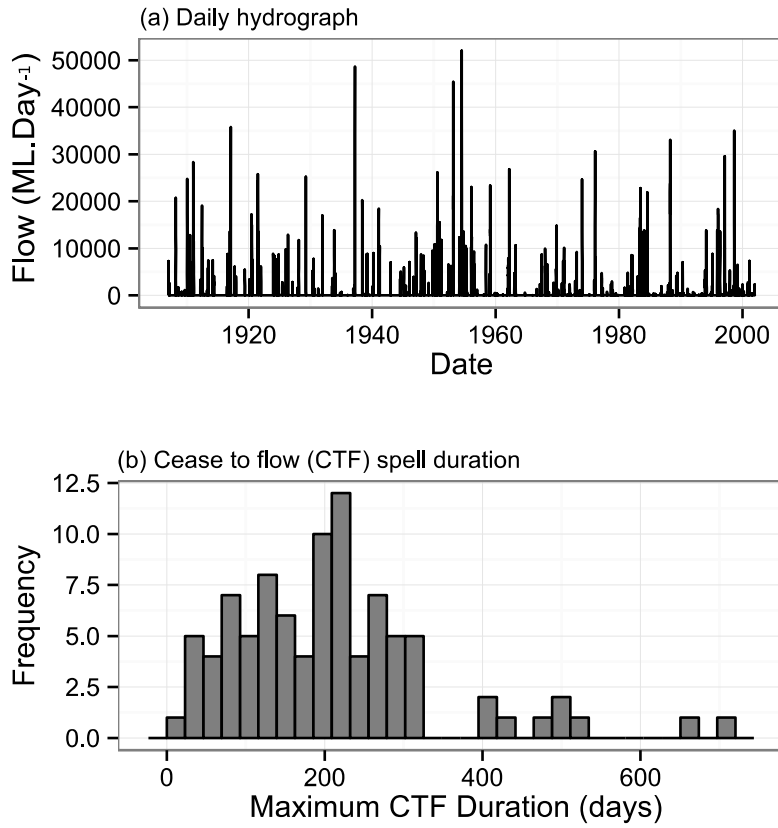


Figure 2

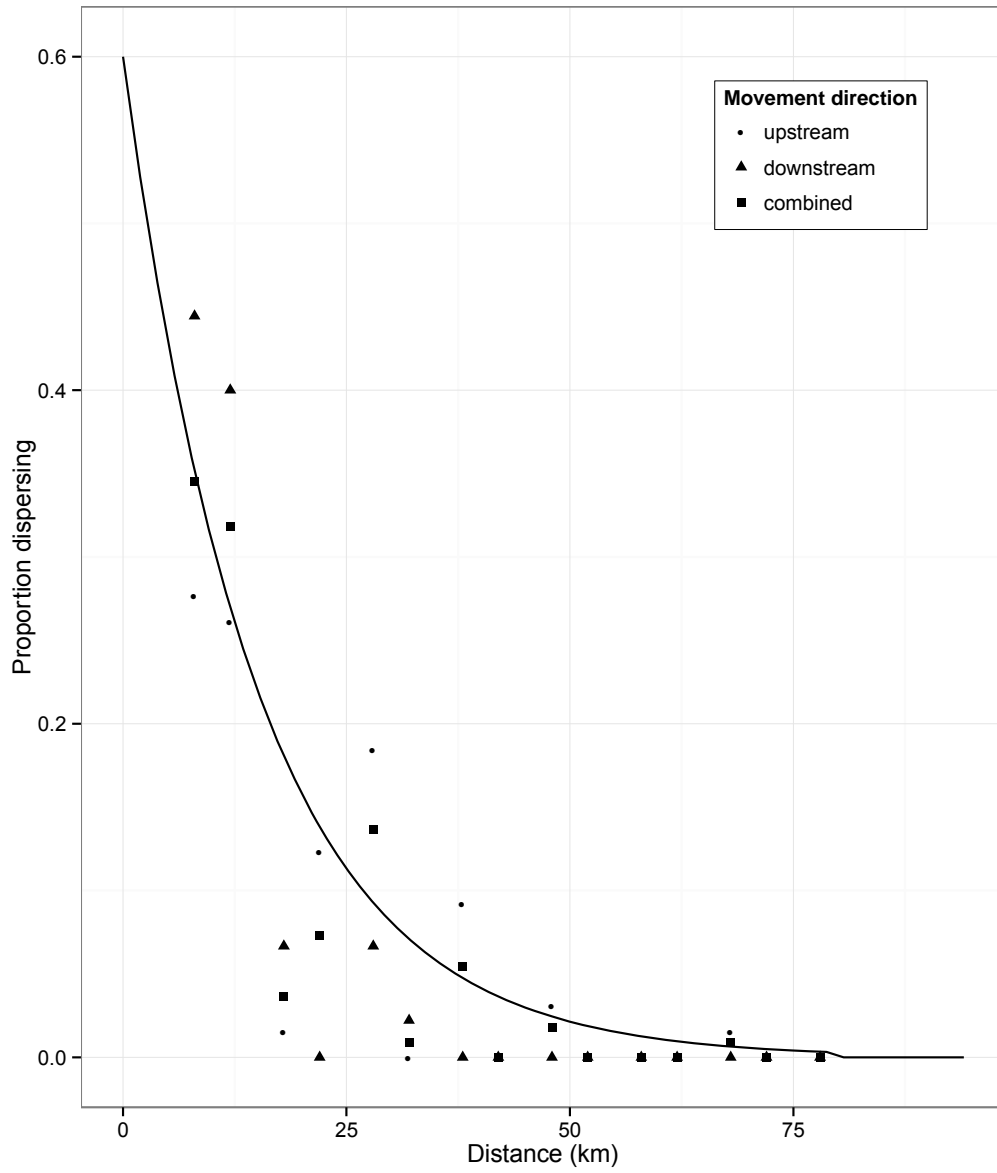


Figure 3

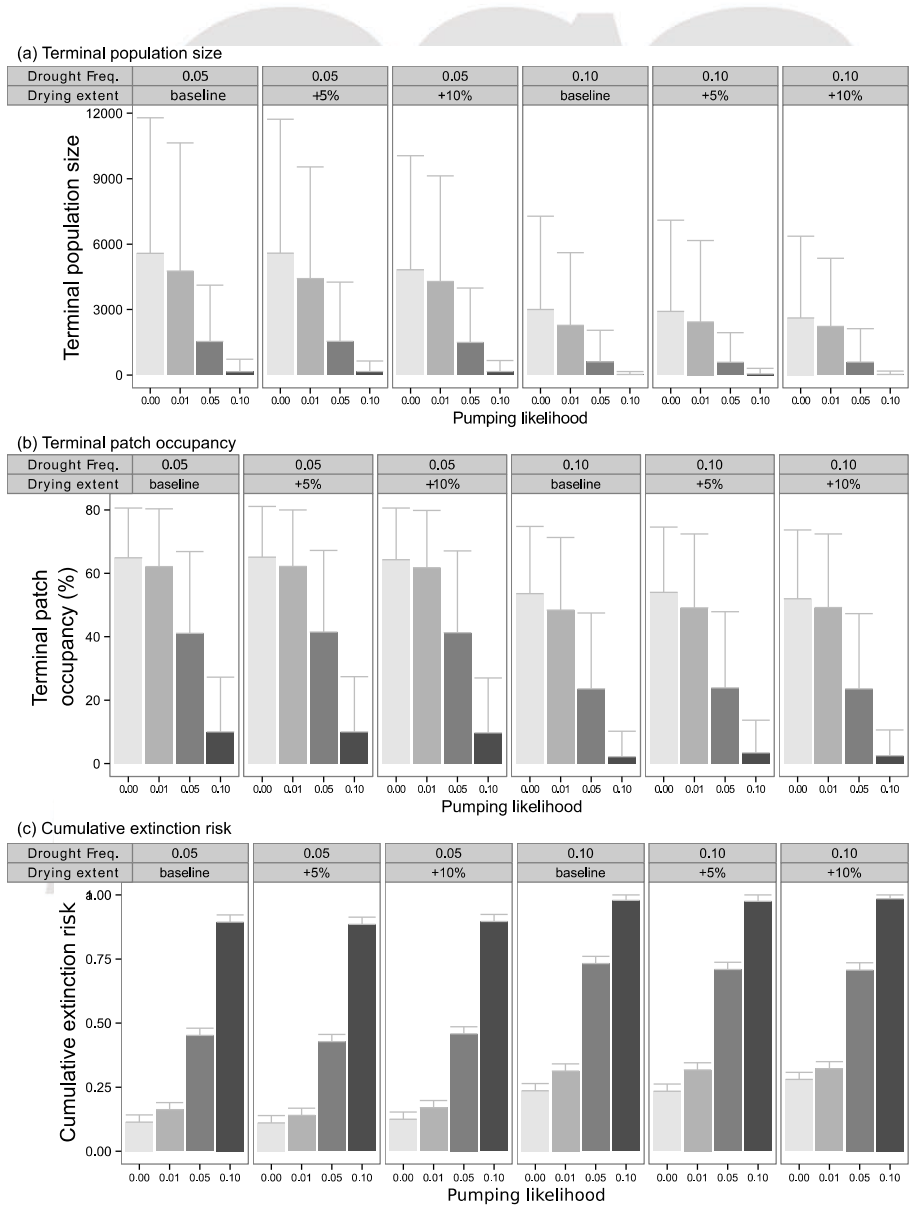


Figure 4

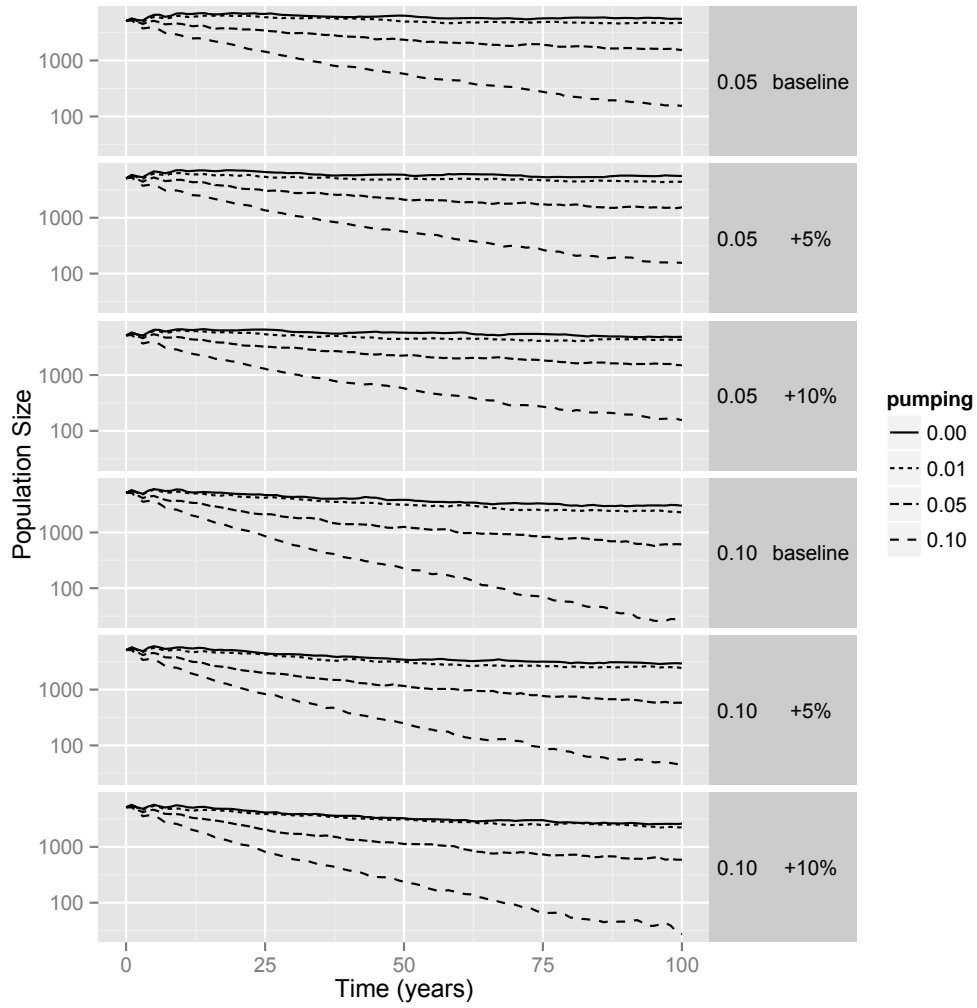


Figure 5