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Resistance of Australian fish communities to drought and flood: implications for climate change and adaptations

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Climate change-induced extreme weather and related drought and flood conditions are heterogeneous across space and time. The variability in location, timing, and magnitude of rainfall can alter how species respond to the drought and flood disturbances. To further complicate this matter, when droughts end they are often followed by extreme flooding, which are rarely considered as a disturbance (Humphries et al. 2024), let alone assessed with its own heterogeneity. Consequently, it is difficult to quantify impacts on ecological communities across large spatiotemporal scales without considering flood-drought disturbance characteristics in sequence (Burton et al. 2020). We hypothesized that native organisms have evolved resistance to withstand repeated cycles of drought-flood disturbances, and that established non-native species have adapted to persist in novel conditions. To test this, we fit spatiotemporal models of species occurrence with local rainfall patterns as covariates in the drought and flood impacted Murray-Darling basin in Australia during the decade long Millenium Drought, and its recovery period. During these drought conditions, river-floodplain organisms in the Murray-Darling became localized in refugia that limited longitudinal and lateral connectivity (Bond et al. 2008), and following flooding the same organisms were exposed to dispersal and recruitment opportunities (Humphries et al. 2020), as well as to hypoxic blackwater events that lead to the mortality of aquatic organisms (Small et al. 2014). At the basin-scale we found that the range size of most native and non-native fishes were highly resistant to the extreme drought and post-flood conditions. At local scales, species richness, or detection, actually increased under drought conditions. Both findings highlight the resistance of species to climate change driven extreme weather, which opens new questions on community adaptations.

Keywords: adaptive potential, climate change, extreme weather, invasive species, range expansion

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Introduction

Australia's climate is characterized by extreme drought and flood, which are increasing due to climate change (Head et al. 2014). The Millenium Drought (2001–2009) is often considered the worst drought in south-east Australia's recorded history. A combination of El Niño conditions and climate change caused major rainfall deficits throughout the decade, and degraded ecosystems, in particular the Murray-Darling River basin (van Dijk et al. 2013, Cai et al. 2014). As the rainfall returned post-2010, instances of extreme flooding events were widespread. Despite more rainfall, certain areas within the basin fell short of long-term rainfall deficits (Heberger 2011). To better understand the spatial heterogeneity of drought and flood first requires local-scale species occurrence data, and a modelling framework that accounts for spatial autocorrelation.

The Sustainable River Audit (SRA), a riverscape-scale monitoring program, measured the ecosystem health for the basin during this time period (Murray-Darling Basin Authority 2019). It provided a relatively high resolution riverscape-scale view of the core fish community (19 of 64 species; Supporting information) extent of occurrence (EOO) across space and time. By geo-referencing point-based

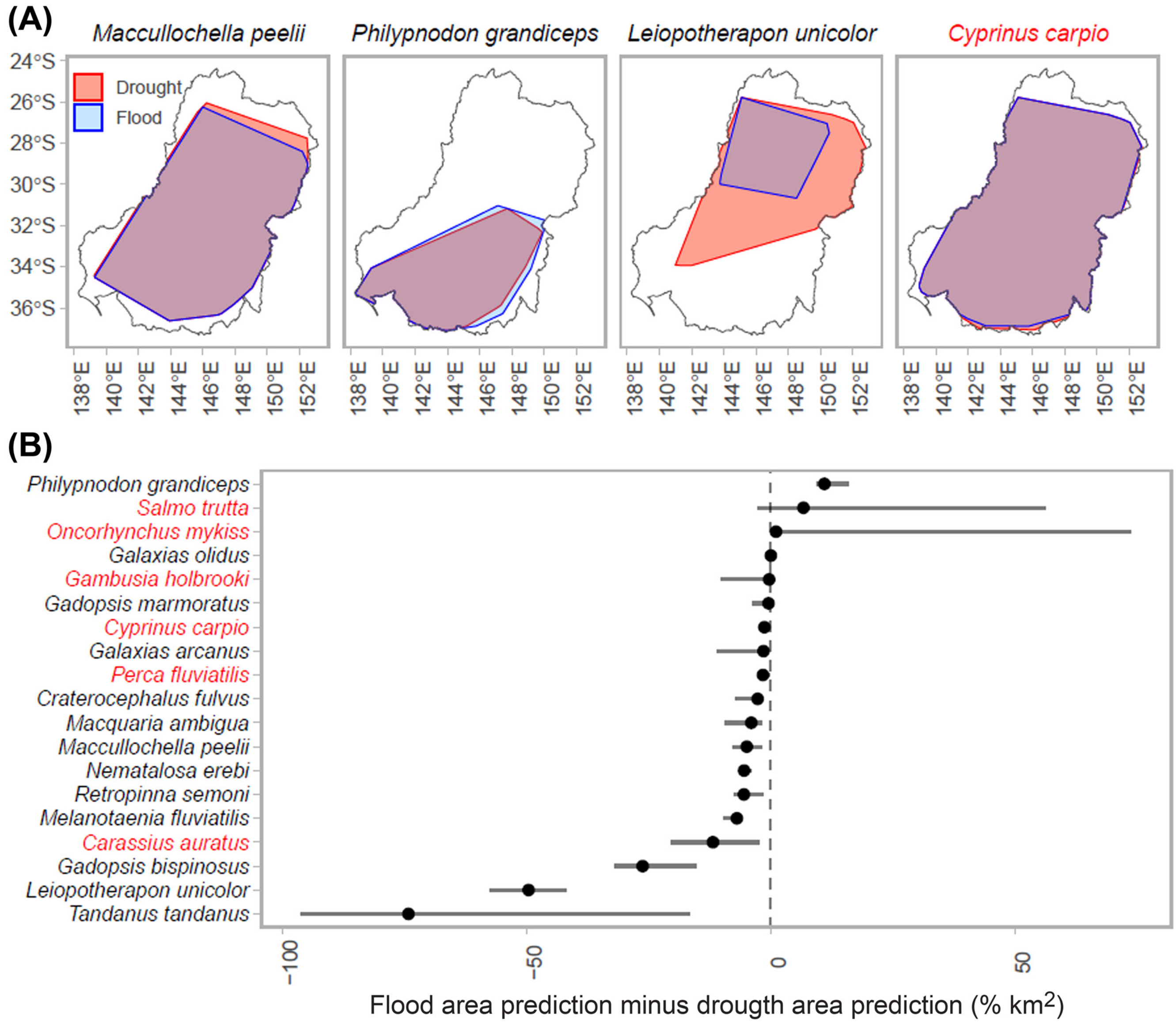

Figure 1. Estimated effect of extreme drought followed by extreme flood on Murray-Darling Basin core community fish ranges. (A) Four examples of individual species response where each range is the extent of occurrence (EOO) area. Red polygon indicates EOO during drought, blue polygon indicates EOO during flood, purple indicates overlap. (B) Median point interval plots of flood EOO area minus drought EOO area for all core community fish in the Murray Darling Basin. Intervals correspond to the 5–95 percentile of EOOs ranging from occurrence thresholds of 0.01–0.15 (n = 15) (Supporting information). Fish with negative values favor drought conditions, where fish with positive values favor flood conditions. Non-native fish are indicated in red italics.

monthly rainfall for all SRA observations (2005–2013) we linked the spatial and temporal dynamics of the meteorological drought and flood processes with the EOO for the core fish community (i.e. species that are detected every year) using a spatially explicit generalized linear mixed model with Gaussian Markov random fields using the stochastic partial differential equation (SPDE) approach (Lindgren et al. 2011, Anderson et al. 2024). This approach provides a way to link the rainfall measurements to locally observed fish occurrence data while also accounting for spatially correlated latent effects. With the models we predict site-level spatial occurrence of each species under drought and flood conditions, and aggregate those over the entire watershed. Simulating the net effect of drought and then flood is accomplished by taking the difference in predicted ranges.

Our models estimated that the range of most native and non-native fishes was highly resistant to drought and flood. Native species, ranging from large predators such as *Maccullochella peelii* (Fig. 1A), to small-bodied species such as *Philypnodon grandiceps* were well-adapted to Australia's climate extremes. Some native species, such as *Leiopotherapon unicolor*, expanded southward under drought conditions, while introduced species typically showed no difference or expanded during floods (Fig. 1B). The number of sites with an occurrence increased during drought conditions for some native fishes, but this did not correspond to an EOO increase (Supporting information). Expansion of native fish ranges during drought could be related to enhanced detectability or an example of adaptations to warmer temperatures, low dissolved oxygen, and dispersal responses (Peniston et al. 2023) prior to becoming isolated in refugia. More recently established non-native species like *Cyprinus carpio* were also highly resistant to flood and drought. The pace at which introduced species can develop adaptations to withstand both disturbances, and also become dominant and cause adverse effects on native communities (Kopf et al. 2019), is an important topic as extreme weather becomes more pervasive. Despite being introduced in the 19th century, *C. carpio* only proliferated widely in the Murray-Darling following very large floods in the 1970s (Shearer and Mulley 1978). Underlying causes of these dynamics and the success of non-native species may be tied to the magnitude, frequency, or the timing of the disturbance (Commander and White 2020, Cinto Mejía and Wetzel 2023).

River fish communities' resistance to drought and flood in Australia are consistent with the relatively high degree of adaptive potential expected for biota on Earth's driest inhabited continent (Morrongiello et al. 2011). Although these results provide some optimism in light of current climate change, our analyses did not consider physiological tolerances or the combined effects of other anthropogenic pressures. The combined impacts of other anthropogenic pressures with altered temperature and hydrology are likely to cause important local shifts in freshwater fish distributions and population sizes (Bond et al. 2011, Morrongiello et al. 2011). The implications of our study underscore the need to uncover mechanisms enabling adaptations under climate change and extreme weather disturbances.

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Author contributions

Henry H. Hansen: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (equal); Validation (equal); Visualization (equal); Writing – original draft (lead); Writing – review and editing (equal). **Eva Bergman**: Funding acquisition (lead); Project administration (lead); Supervision (equal); Validation (supporting); Writing – original draft (supporting); Writing – review and editing (lead). **Keller Kopf**: Conceptualization (supporting); Data curation (supporting); Formal analysis (supporting); Investigation (supporting); Methodology (supporting); Validation (lead); Visualization (supporting); Writing – original draft (equal); Writing – review and editing (equal). **Max Lindmark**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Supervision (equal); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal).

Transparent peer review

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.2547d7x05 (Hansen et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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