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Understanding and managing the interactive impacts of growth in urban land use and climate change on freshwater biota: a case study using the platypus (*Ornithorhynchus anatinus*)

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Abstract

Globally, urban expansion and climate change interact to threaten stream ecosystems and are accelerating the loss of aquatic biodiversity. Waterway managers urgently need tools to understand the potential combined impacts of urbanisation and climate change, and to identify effective mitigating management interventions for protecting freshwater biota. We address this challenge using the semi-aquatic mammal the platypus (*Ornithorhynchus anatinus*) as a focal species. We developed high-resolution environmental spatial data for stream networks and spatially-explicit habitat suitability models to explore the impact of threats, and to identify the combination of management actions most likely to maintain or improve habitat suitability over the next 50 years in greater Melbourne, Australia. We developed and evaluated platypus habitat suitability models (males-and-females and females-only) including validation using an independent environmental DNA (eDNA) dataset. Platypus occurred more commonly in larger, cooler streams with greater catchment-weighted discharge, following periods of greater stream flow. They were positively associated with near-stream forest cover and negatively associated with annual air temperature and urban stormwater runoff. Extensive reductions in suitable platypus habitat are predicted to occur under urbanisation and climate change scenarios, with the greatest threat expected from reduced streamflows. This emphasises the importance of maintaining flow regimes as part of

conserving platypus in the region, however, substantial additional benefit is predicted by concurrent riparian revegetation and urban stormwater management efforts (that also have the potential to contribute to the streamflow objectives). Provision of adequate streamflows in a future with increasing water demands and water security requirements will likely require creative integrated water management (IWM) solutions. Our high-resolution stream network and habitat suitability models have allowed predictions of potential range-shifts due to urban expansion and climate change impacts at management-relevant scales and at the whole-of-landscape scale. This has enabled systematic strategic planning, priority action planning and target setting in strategic policy development.

Keywords

Platypus, *Ornithorhynchus anatinus*, boosted regression trees, climate change, environmental DNA, eDNA, habitat suitability model, species distribution model, urbanization

Introduction

Freshwater systems are amongst the ecosystems considered to be most vulnerable to biodiversity loss worldwide (Dudgeon et al., 2006). This reflects the increasing extent and intensity of human activities, resulting in habitat degradation and fragmentation, altered flow regimes, water pollution, overexploitation of resources and exotic species invasion (Dudgeon et al., 2006; Strayer & Dudgeon, 2010). In Australia, for example, the list of threatened freshwater faunal species in the national *Environment Protection and Biodiversity Conservation Act 1999* includes 38 fish, 41 frogs and 16 invertebrates (www.environment.gov.au ; accessed 14 April 2020). To halt or reverse the decline of biodiversity loss in freshwater ecosystems, waterway managers and the wider community need tools for understanding the threats to biota (the *what*, *where* and *how*) and tools for comparing the management interventions most likely to address those threats. To support the development of a waterway health strategy, co-designed with the catchment community, we developed a suite of habitat suitability models for macroinvertebrate families, native fish species and platypus (Coleman et al., 2018; Chee et al., 2020). Here we use findings for the platypus (*Ornithorhynchus anatinus*) as a case study demonstrating our approach to developing and using spatially-explicit habitat suitability models (HSMs) to understand and communicate the potential interactive impacts of two major threats – urban growth and climate change – on platypus in streams across Melbourne, Australia.

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The platypus is a semi-aquatic mammal that occurs in freshwater systems in eastern and southeastern Australia, including Tasmania (Grant, 1992). It is the only amphibious, egg-laying mammal, and has venomous spurs (in males only) and bill electroreceptors that are believed to be used to detect prey (Grant &Temple-Smith, 2003; Grant & Fanning, 2007). Its diet consists mainly of benthic freshwater invertebrates (Faragher et al., 1979; McLachlan-Troup et al., 2010) and, when not foraging, it rests in burrows adjacent to waterways (e.g. Serena et al., 1998). Platypus are currently listed as Near Threatened by the International Union for Conservation of Nature (IUCN) (Woinarski et al., 2014; Woinarski & Burbidge, 2016), and in 2020 were listed as Vulnerable in the state of Victoria under the *Flora and Fauna Guarantee Act 1988*. Although we lack comprehensive data to properly assess current versus historical distributions of platypus, localised extinctions and range contractions have been reported in the metropolitan areas around Melbourne, Sydney and Brisbane, and the lower reaches of the Murrumbidgee and Murray rivers in New South Wales, Victoria and South Australia (Grant & Temple-Smith, 1998; 2003). Reasons for the decline in platypus distribution and abundance in metropolitan areas are likely to have included the interactive impacts of urban growth, agricultural activities, riparian and instream habitat degradation, water pollution, barriers to movement, changes in flow regimes and introduced noxious species (e.g. Grant & Temple-Smith, 2003; Serena & Pettigrove, 2005; Martin et al., 2014).

Future predictions of global biodiversity loss indicate that changes in land use and climate are of particular concern for freshwater ecosystems (Sala et al., 2000). In Melbourne, human population growth is expected to increase from the current number of approximately five million people to at least eight million by 2050 (Victorian Government, 2018), and the future climate is likely to be hotter and drier. For instance, based on median values from 42 global climate model projections, by 2065 mean daily air temperatures are expected to increase in the greater Melbourne area by around 2.1-2.3 °C and mean annual runoff is expected to decrease by around 16-20% (DELWP, 2016).

Given the projected change in climate, and expansion of urban areas in greater Melbourne, there is an urgent need to understand how these factors will affect freshwater biota in the region and to identify opportunities for management interventions. Earlier modelling work by others highlights the potentially substantial impacts of a warmer climate on the distribution of platypus across its entire range within Australia (Klamt et al., 2011) and impacts of river damming, invasive species, land clearing or droughts (Bino et al., 2020). Using platypus as an example, we describe our process of developing spatially-explicit, quantitative HSMs using more than 20 years of platypus field survey data, and a spatial stream network dataset of ecologically relevant environmental predictors. We evaluate our models using cross-validation and independent validation with an environmental DNA (eDNA) dataset, to assess model predictive accuracy. We then used these models to explore potential impacts of urban growth and climate change scenarios on platypus habitat suitability in the waterways of greater Melbourne, and to identify and support deliberations about the combination of management actions (urban stormwater management, riparian revegetation, streamflow protection) most likely to maintain or improve platypus habitat suitability over the next 50 years.

Maps of scenario predictions were shared at catchment community co-design workshops that took place over multiple workshops in 2017 and 2018. They facilitated knowledge sharing, mutual learning about catchment biodiversity values, the distribution pattern of threats, what was at stake under different plausible scenarios, and discussions about the relative strengths of mitigating actions. We did not quantify comparisons of differences in scenarios beyond the maps which visually depict the difference patterns across the study area. Instead models were used to predict, map and enable stakeholders to visually compare the relative differences associated with plausible scenarios and mitigating actions in isolation and combination. At the catchment-based community workshops conducted for each of the five major catchments, the colour-coded relative performance of mitigating actions for reaches within each catchment was what was of primary interest. The model development, community engagement and strategy development process took place between 2017 and 2018 and contributed to Melbourne's Healthy Waterways Strategy 2018-2028 (https://healthywaterways.com.au/). While this work focuses on platypus, it illustrates a quantitative framework to support management decisions that is transferable to other stream biota.

Materials and methods

Platypus survey data

For model building, we used 2,506 presence-absence records from platypus survey data collected from 609 sites across greater Melbourne from 1995 to 2009 as part of the

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Melbourne Urban Platypus Monitoring Program (**Fig. 1a**). Surveys were conducted (mainly from September to May) by setting two fyke nets at each site (one facing upstream, the other facing downstream) with mesh wings at either side of the net entrance positioned so that the two nets blocked the entire width of the stream channel (Serena & Williams, 2012). Consecutive trapping sites were located approximately 1.1 ± 0.3 km (mean ± SE) apart, which roughly matches the distance that a platypus is expected to travel while foraging overnight (Serena & Pettigrove, 2005). Nets were set in the late afternoon and checked at intervals of four hours or less to remove captured animals until nets were removed from the water the following morning. Platypus sex and age class was assigned based on the presence and morphology of calcaneal spurs, with three male age classes (juvenile ≤ 10 months, sub-adult 11-23 months or adult ≥ 23 months) and two female age classes (juvenile ≤ 10 months or sub-adult/adult > 10 months) recognised (Temple-Smith, 1973; Williams et al., 2013). The 1995-2009 window was chosen to match the period of data capture (and derivation) for the environmental predictors (described below). For model validation, we used presence-absence survey data from 2010-2019 (1,893 records from 254 sites) again collected through the Melbourne Urban Platypus Monitoring Program using fyke nets. We also collected eDNA data at 330 sites (carried out from May to September 2016 and September 2017 to September 2018) (**Fig. 1b**).

Environmental DNA sampling, choice of primers, PCR conditions and laboratory quality control followed the methods of Lugg et al. (2018). Water samples for eDNA analysis were collected in duplicate (2017/18 samples) or triplicate (2016 samples) at each site and filtered on-site by passing between 300-500 ml of water through an enclosed Sterivex® 0.22μM filter (Merck, Germany) using a sterile 60 mL syringe. Filters were placed on ice in the field and transported to the laboratory within 24 hours and stored at −20 °C until DNA extraction. DNA was extracted from filters using a Qiagen DNeasy Blood & Tissue Kit (Qiagen, Hilden, Germany), using the spin column protocol, with slight modifications. Firstly, 540 μL of ATL buffer and 40 μL of proteinase K were added to each filter unit. Each filter was sealed and incubated at 56 C for 3 h with constant agitation. The lysis solution was transferred into new 2 mL tubes, and hereafter the Qiagen DNeasy Blood & Tissue Kit manufacturer’s protocol was followed for the remaining part of the DNA extraction. In every batch of DNA extractions, a negative control for the DNA extraction procedure was also included where the

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same DNA extraction protocol was followed with a sterile Sterivex® filter (for a total of *n* = 12 in 2016 and *n* = 14 in 2017/18 extraction negative controls).

A 57 base pair sequence of the mitochondrial control region was used to target platypus-specific DNA and real-time quantitative Polymerase Chain Reaction (qPCR) TaqMan® assays (Life Technologies, Carlsbad, California) used to amplify and quantify the target DNA. For each sample, three replicate qPCRs were undertaken (total of six or nine per site), and negative and positive controls included in each PCR run. Taking a conservative approach, a site was only considered to have platypus present if at least two of the six or nine qPCRs detected platypus DNA. There was no evidence of eDNA sample contamination from field or laboratory procedures with all controls returning a negative result.

Environmental predictors

We used environmental data from a digital stream network database of 8,233 stream reaches (median length ~0.5 km) representing waterways of the greater Melbourne area (Walsh & Webb, 2014). In this database, descriptors (predictors) for each reach included ecologically relevant aspects of natural variability (e.g. temperature, stream discharge) and human impact variables that reflect mechanisms by which human activities alter the natural environment (e.g. Attenuated Imperviousness—an indicator of urban stormwater runoff and its associated impacts on flow regime and water quality (Walsh & Webb, 2016)). Our candidate set of predictors selected to describe instream habitat suitability for platypus was based on a balance of three considerations: i) ecological relevance (*sensu* Austin, 2002) inferred from knowledge about habitat requirements (e.g. Serena et al., 1998; 2001), mortality factors (Serena & Williams, 2010), and effects of flow and urbanisation on the species (e.g. Martin et al., 2014; Serena et al., 2014; Serena & Grant, 2017); ii) ability to portray management interventions; and iii) availability of spatial data across the region. The rationale was to develop models that would provide region-wide predictions of platypus response to climatic changes, land use changes, mitigating interventions and their interactions. A description of each of the environmental predictors, including broad regional patterns across the study area, is provided in **Table 1**. Maps showing how environmental predictors vary across the entire stream network provided in **Supporting Information Fig. S1**.

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Each platypus presence-absence record was assigned to its corresponding stream reach and the predictor values extracted (Data available from Coleman et al. (2021)). Antecedent Runoff depended on stream reach as well as sample record date (see **Table 1**). Predictors were checked for multicollinearity and those selected for use in model development had pairwise Pearson correlations < 0.80 (e.g. following Dormann et al. (2013)).

Model development

Two separate models were developed—one using all platypus records (i.e. juvenile, sub-adult and adult males and females; hereafter referred to as the 'male-female' model) and one using only sub-adult and adult female data (the 'female-only' model). We quantified female-only habitat relationships separately because they have more stringent habitat requirements for nesting sites and for foraging to support lactation (Serena & Grant, 2017). Martin et al. (2014) also found that adult females are more sensitive than males to impacts caused by urban stormwater runoff.

We selected Boosted Regression Trees (BRT) as our modelling technique because it performs well in comparison with other modelling techniques (Elith et al., 2006), can fit non-linear relationships and naturally model interactions (De'ath, 2007; Elith et al., 2008; Vesk et al., 2010), and can handle outliers and missing data with minimal loss of information (Breiman et al., 1984; Hastie et al., 2009). Additionally, methods are available for estimating the relative importance of predictors, for depicting fitted response curves, detecting interactions amongst environmental descriptors and model evaluation (Elith et al., 2008).

All analyses were carried out in R (R Foundation for Statistical Computing, 2008) using the 'gbm' package (v2.1.3, Ridgeway, 2012) plus additional code written by Elith et al. (2008) (now included in the 'dismo' package v1.1-4 (Hijmans et al., 2017)). Candidate BRT models were fitted using learning rates ranging from 0.005 to 0.0025, and tree complexity ranging from 2 to 5, allowing two to five-way interactions among predictors. We also developed candidate models with various monotone settings (-1, +1) for specific predictors such as Mean Annual Temperature and Mean Annual Discharge Depth (see **Table 1**). We evaluated the response curves and mapped predictions of various combinations of monotone settings and predictors to ensure that the final models were reflective of ecological understanding. To control for overfitting, we used 10-fold cross-validation (CV) for model development and

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automatic selection of the optimal number of trees. In selecting the final models, we set a threshold of a minimum of 1,000 trees to mitigate against unwanted variation between runs of the stochastic modelling process (Elith et al., 2008). We were then guided by predictive performance as measured by the metrics described below.

Model evaluation

Model evaluation was done quantitatively using 'percentage deviance explained' and 'area under the receiver operating characteristics curve' (AUC) as metrics of model performance. Percent deviance explained measures the goodness-of-fit between predicted and observed values, and is expressed as a percentage of the null deviance (i.e. the deviance of a model containing no terms and having a fitted value for all observations equal to the mean probability across the observations). Percentage deviance explained was calculated from 'held-out' data in the cross-validation process. AUC measures a model's ability to discriminate between sites where the species is present and where it is absent. The AUC value is the probability that the prediction for a presence record is greater than the prediction for an absence record. AUC ranges from 0 to 1, where a value of 1 indicates perfect discrimination, and a value of 0.5 implies predictive ability that is no better than a random prediction.

We evaluated the models (built on data from 1995-2009) using i) internal ten-fold cross-validation during the model building process, and ii) independent netting data (collected from 2010-2019) and eDNA datasets (from 2016-2018) (Data available from Coleman et al. (2021)). We computed AUC (using the evaluate function in the 'dismo' package) for both netting and eDNA datasets.

Using just the independent netting dataset, predictive performance was also compared with calibration plots using functions from R package 'PresenceAbsence' (Freeman & Moisen, 2008), which illustrate the congruence (or lack thereof) between predicted probability of occurrence at individual sites with observed rates of occurrence (Pearce & Ferrier, 2000). Calibration plots were produced by aggregating sites into bins based on their predicted values, then for each bin, the proportion of sites where occurrence was observed was plotted (Freeman & Moisen, 2008). Confidence intervals were also calculated. Ideally, in a model with good calibration, one would expect that 80% of sites with a predicted probability of 0.8

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should yield a presence – and so on for other bins – resulting in points being positioned along the 45° (diagonal) line. We did not create a calibration plot from the eDNA dataset because it is a substantively different survey method with different detection ability than the netting data used in model development.

Scenarios

Scenarios were devised to explore the potential impacts of urban growth, climate change, and mitigation interventions on platypus habitat suitability across the Melbourne region (**Table 2**). We used estimates of various predictors as at 2016 to portray the current (CURR) scenario. For the purposes of long-term strategic planning over a nominal 50-year horizon, we developed a business-as-usual future (BAUF) scenario. This scenario focused on important widespread threats of warming, drying and increased impacts of urban stormwater. Using best available estimates in 2017, that were consistent with the Victorian Department of Environment, Land, Water and Planning projections (DELWP, 2016), yet still within the range of conditions of the training data (excluding a part of the Little River system in the Werribee catchment where platypus were not recorded in our netting or eDNA data) used to develop our models, warming was represented by a 1.5 °C increase in Mean Annual Temperature. Drying was represented by a reduction in Mean Annual Runoff Depth equivalent to a 25% reduction in long term mean annual discharge at the mouth of the Yarra River. To represent drier conditions we used monthly discharge estimates from a natural analogue identified by Walsh & Webb (2013)—a 4-year period prior to December 2000 where mean annual discharge was 75% of the long-run average. The spatial extent and specific distribution pattern of future impervious land cover was estimated and mapped by comparing extant impervious land cover against Victoria’s VicMap Planning dataset planning scheme zone data (downloaded Sept 2017 from https://www.data.vic.gov.au/data/dataset/vicmap-planning).

The primary management intervention scenarios considered were (**Table 2**):
1) establishing riparian vegetation to a width of at least 20 m on both banks of all waterway reaches (‘RV20’; Attenuated Forest Cover set to 1 in the model)
2) harvesting, treating and infiltrating (‘disconnecting’) all excess stormwater runoff prior to entering streams (Attenuated Impervious Cover set to 0) from either existing and new urban areas (‘SW1’) or just in new urban areas (‘SW2’)

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3) maintaining current stream flows (Mean Annual Discharge Depth the same as the CURR scenario) despite climate change ('NoDry')

These interventions were considered in isolation and in combination (**Table 2**). There was no consideration of the cost of interventions, nor feasibility under current policy settings, the purpose was to explore the predicted outcome of intervention scenarios if they were implemented (most likely through a range of complementary measures). However, given that the interventions are consistent with current 'best-practice' waterway management, we regard them as plausible with sufficient investment.

Results

Both the male-female and female only platypus occurrence models provided improved predictions relative to the null model. Mean CV percentage deviance explained was 15.68% for the male-female platypus model and 9.62% for the female-only platypus model. Mean AUC scores for both models (0.75 and 0.73, respectively) indicated useful discriminatory ability of sites where platypus are present and where they are absent (**Supporting Information Table S1**). The most influential predictors (in descending order) were Catchment Area, Mean Annual Discharge Depth and Mean Annual Air Temperature in both models (**Figs. 2 and 3**).

Relationships between environmental predictors and probability of platypus occurrence were broadly consistent between the male-female and female-only models (**Figs. 2 and 3**). These models demonstrated a positive stepped relationship between Catchment Area (**Figs. 2a and 3c**), where areas greater than ~800 km^2 and ~1,400 km^2 are more likely to support platypus in the male-female and female-only models, respectively. The probability of occurrence for male-female and female-only platypus increased with Mean Annual Discharge Depth (values >~380 mm more likely to support platypus; **Figs. 2b and 3a**), Antecedent Runoff (values >~-0.75 and >~-0.25 more likely to support platypus, respectively; **Figs. 2e and 3d**), and Attenuated Forest Cover (values >~0.25 and ~0.35 more likely to support platypus, respectively; **Figs. 2g and 3e**). The increase was approximately linear for Mean Annual Discharge Depth, Antecedent Runoff and Attenuated Forest Cover. Conversely, a negative linear relationship between the probability of platypus occurrence in both the male-female and female-only platypus models and Mean Annual Air Temperature was observed (values

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<~13.2 °C more likely to support platypus; **Figs. 2d and 3b**), and a negative, initial steep decline relationship, with Attenuated Imperviousness (values between zero and <~0.05 and <~0.03 more likely to support platypus, respectively; **Figs. 2f and 3f**).

Validation against independent data

The AUC scores for male-female and female-only platypus models computed from our independent netting data (**Figs. 4a and b**) are, as expected, lower than that of the mean CV AUC scores (0.64 vs 0.75, and 0.66 vs 0.73, respectively). However, the AUC computed from the eDNA dataset was 0.83 (**Fig. 4c**), indicating better model discrimination performance of the male-female model than indicated by the mean CV and independent netting AUC scores (0.75 and 0.64 respectively). Overall, the model performance was considered sufficient to support the analysis of future scenarios.

The calibration plot for the male-female platypus model shows a positive bias (i.e. values of observed occurrence versus predicted probability of occurrence tending to sit above the 45^0 line), indicating consistent under prediction of probability of occurrence, especially at lower levels of probability (Fig. 5a). There are also very few data points in the bins for higher predicted probability values (**Fig. 5a**). For the female-only model, the points on the whole are closer to the 45° line, indicating reasonable calibration, but again, there are relatively few data points in the bins associated with higher predicted probabilities of occurrence (**Fig. 5b**).

Model scenarios

The predicted current (CURR) distribution of platypus as at 2016, shows large sections of the Bunyip River and the middle-upper Yarra River, including the mainstem of the Yarra River to the suburbs of Melbourne, where the probability of platypus occurrence (both the male-female and female-only models) is highest (**Fig. 6a, b**). These are stream reaches where Mean Annual Stream Discharge Depth and Attenuated Forest Cover is higher and Mean Annual Air Temperature and Attenuated Imperviousness is lower (**Fig. S1**). The CURR scenario also shows small lengths of stream reaches in the lower and upper Werribee, upper Maribyrnong, upper Dandenong and Westernport catchments where the probability of platypus occurrence is higher. These predictions of current distribution are largely consistent with long-term platypus netting data and recent eDNA survey (**Fig. 1**).

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The business-as-usual future (BAUF) scenario that incorporates warming, drying and increased impervious cover, indicates widespread contraction of suitable platypus habitat in all major river systems in the region. Very few reaches in the Werribee, Maribyrnong and Dandenong catchments are predicted to be suitable for platypus (**Fig. 6 c, d**). The BAUF scenario also suggests substantial contractions in the two current largest areas of suitable platypus habitat, with notable declines in the probability of occurrence throughout much of the upper Bunyip River system and the southern tributaries of the middle Yarra system, including a contraction upstream in the mainstem of the Yarra River.

The likely benefits of management interventions compared to BAUF are depicted by 'difference maps' of probability of occurrence using a diverging blue-white-red colour scale (**Fig. 7** and **Supporting Information Fig. S2)**. For any given management scenario, blue indicates an increase in probability relative to BAUF, red indicates a decrease and white indicates little or no change.

Revegetating all reaches of the stream network to 20 m width on both sides (RV20), produced slight increases in the predicted probability of occurrence of male and female platypus at small lengths across each catchment. The most notable benefit of RV20 is in the Westernport catchment, the middle Yarra tributaries and upper reaches in the Werribee and Maribyrnong catchments using the male-female model, and the mainstem of the middle-upper Yarra River and the mainstems of the Bunyip and Tarago rivers using the female-only model (**Fig. 7a** and **Supporting Information Fig. S2**). While effectively managing urban stormwater in existing and future urban areas (SW1), produced improvements in platypus predicted probability of occurrence in parts of the lower Werribee, lower Yarra, Dandenong and Westernport catchments using the male-female model (**Fig. 7b**) and the mid-lower mainstem of the Yarra River using the female-only model (**Supporting Information Fig. S2**), there were substantially less improvements predicted by either model if urban stormwater is managed only in areas of future urban growth and not in already urbanised areas (SW2) (**Supporting Information Fig. S2**). Maintaining current stream flow regimes under a warmer and drier climate (NoDry), was predicted to produce the most widespread increase in the probability of occurrence (both for male-female and female-only models), most notably in the Yarra, Werribee, upper Maribyrnong and Westernport catchments and small sections of the upper Dandenong catchment using the male-female model, and the Yarra catchment using the female-only model (**Fig. 7c, Supporting Information Fig. S2**).

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While the implementation of management actions in isolation demonstrated some notable benefits with the male-female platypus model (in particular the NoDry and SW1 scenarios), there appeared to be substantially less benefit from single actions with the female-only platypus model. Combining the three management options of RV20, SW1 and NoDry clearly produced the largest benefit in increased probability of male-female or female-only platypus occurrence compared to BAUF (**Fig. 7d** and **Supporting Information Fig. S2**). When management actions were paired, the combination of managing urban stormwater in existing and future urban areas and maintenance of current stream flow regimes under a changing climate (i.e. SW1+NoDry) appears to provide the greatest benefits to platypus using the male-female model. On the other hand, revegetation and maintenance of current stream flow regimes under a changing climate (i.e. RV20+NoDry) appears to provide the greatest benefits to platypus using the female-only model (whilst also showing substantial improvements using the male-female model) (**Supporting Information Fig. S2**). The combination of revegetation and urban stormwater management in both new and existing urban areas (RV20+SW1) also predicts notable benefits using the male-female platypus model. However, as compared to the SW1+NoDry and RV20+NoDry scenarios, benefits appear to be much less widespread and there appears to be little benefit based on the female-only model other than in the Yarra River mainstem (**Supporting Information Fig. S2**).

Discussion

Globally, urban expansion and climate change interact to threaten stream ecosystems and are accelerating the loss of aquatic biodiversity (e.g. Sala et al., 2000). Waterway managers and the wider community urgently need tools to understand the potential combined impacts of urbanisation and climate change, and to identify effective mitigating management interventions for protecting freshwater biota. For example, Maloney et al. (2013) developed species distribution models for several freshwater fish species in Maryland, USA, to understand important environmental drivers of species occurrence, including urbanisation impacts. We addressed this challenge in greater Melbourne, Australia, by developing high-resolution environmental spatial datasets and spatially-explicit habitat suitability models for a suite of in-stream biota and illustrate our approach using the platypus (*Ornithorhynchus anatinus*) as a focal species. Our habitat suitability models enabled managers and community members to explore potential threats to platypus, identify and deliberate about the

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combination of management actions most likely to maintain or improve habitat suitability in the study region over the next 50 years. Our platypus models suggest that climate-change-related drying is likely to compound impacts of forest loss and urban growth on platypus populations, and that effective conservation of the species will require a combination of management actions including revegetation and provision of adequate stream flows.

The influential predictors and their fitted relationships indicate that platypus prefer stream reaches with larger catchment areas and higher mean annual discharge (which in this region is indicative of permanent flow), cooler temperatures, higher forest cover and lower catchment imperviousness (**Figs. 2** and **3**). This is consistent with published accounts of platypus habitat preferences (e.g. Grant & Temple-Smith, 1998; Serena et al., 1998; Serena et al., 2001; Serena & Pettigrove, 2005; Serena et al., 2014; Martin et. al., 2014; Serena & Grant, 2017).

We generated two separate measures of model discrimination performance from two types of independent validation data. Whilst the AUC score computed from fyke netting data suggested moderate model discrimination of the male-female model (0.64), the AUC score computed from eDNA data suggested good model discrimination (0.83). In previous work directly comparing eDNA and fyke-netting survey methods for platypus (based on a subset of the data used in our study), Lugg et al. (2017) found that eDNA surveys may detect platypus more effectively than fyke netting: analysing two eDNA water samples at a site was sufficient to achieve a 95% detection probability, as compared to netting which required 6-10 trapping nights. In other words, absences in our 2010-2019 netting data may not be 'true' absences if there were a low number of repeat site visits during each seasonal sampling campaign. By comparison, the eDNA data, which included duplicate or triplicate sampling during each site visit, may be more likely to indicate 'true' presences and absences. We are encouraged, therefore, by the 0.83 AUC score of the male-female model computed from the eDNA data.

As noted, there was a positive bias in the platypus calibration plot, indicating under prediction of probability of occurrence, especially at lower levels. A possible explanation is that platypus prevalence was higher in the 2010-2019 netting data used for validation as compared to the 1995-2009 netting data used for model-building (0.44 vs. 0.40 respectively). This likely resulted from a shift in intent and purpose in Melbourne Water's platypus netting

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program from broad-scale surveys across the region in 1995-2005 (to ensure most streams had been surveyed), to more spatially focused surveys at sites likely to support platypus (especially from 2013 onwards). This is a limitation of our opportunistic use of the 2010-2019 netting survey data which was not expressly collected for the purpose of model validation.

That both the male-female model (**Figs. 6a**, **6c**) and female-only model (**Figs. 6b**, **6d**) predict extensive contractions in platypus habitat suitability under the BAUF scenario is of major concern. It flags the real possibility of local extinctions occurring in catchments across greater Melbourne, apart from current population strongholds in the middle-upper Yarra and perhaps the upper Bunyip River systems.

Previous studies have demonstrated the importance of riparian vegetation for platypus, highlighting its role in stream bank stabilisation, provision of cover from predators, moderating water temperature to help maintain platypus food resources in the form of aquatic macroinvertebrates, and providing large woody debris and other organic matter for processing by macroinvertebrate prey species (Grant & Temple-Smith, 1998; Serena et al., 1998; Serena et al., 2001). Evidence that the platypus's current distribution across the Melbourne region is directly affected by temperature stress, as suggested by the negative relationship with air temperature in our habitat suitability models, remains uncertain. The platypus has a low resting body temperature (32^{o}C) and functions best when ambient temperatures are less than 29^{o}C (Booth & Connolly, 2008). Nonetheless, the animals are known to occupy rivers located in inland parts of the Murray-Darling Basin and as far north as Cooktown in Queensland (Grant, 1992), presumably as an outcome of their ability to avoid exposure to unsuitable heat by being nocturnally active, feeding in the water and resting in underground burrows. Alternatively, the negative relationship between platypus and air temperature in our study could plausibly reflect the fact that this predictor is broadly correlated with lower rainfall and reduced stream flows that tend to decrease from east to west across the Melbourne study area. The negative associations of platypus occurrence with greater urbanisation and stormwater runoff have also previously been reported (Serena & Pettigrove, 2005; Martin et al., 2014), including 'flashy' stream flows that can be detrimental to reproductive success during the period when juveniles are confined to or first emerging from nesting burrows (Serena et al., 2014). Of the three main forms of intervention, it was NoDry (maintenance of CURR stream flows) that had the largest predicted benefit (**Fig. 7c**).

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These predictions underline the fundamental importance of adequate stream flows in addition to riparian revegetation and stormwater management. For example, a positive relationship between platypus reproductive success and streamflow in the months before breeding has been documented both in streams near Melbourne (Serena et al., 2014) and in a rural river in New South Wales (Serena & Grant, 2017). Specifically, a positive relationship has been identified between antecedent discharge and both the proportion of females that raise young in a given year and mean litter size (Serena & Grant, 2017).

Whilst loss of riparian forest cover and urban stormwater runoff undoubtedly reduce suitability of habitat for platypus, our models predict a likely dominant impact of reduced streamflow on platypus habitat suitability throughout the study area (**Fig. 7**). This prediction forces a rethink regarding the types of interventions that may be required to protect platypus habitat into the future by maintaining the current stream flow regime under future conditions of warming and drying.

Protecting and supplementing stream flows in areas of favourable platypus habitat in the face of a changing climate and a growing population with increasing water demands is a difficult challenge that will require development and testing of systemic and creative integrated water management (IWM) solutions. These includes options such as provision of environmental flows from water storages, revision of rules for stream diversion allocations (particularly minimum flow thresholds), increased infiltration of urban stormwater to restore base flows, and the use of networked real-time monitoring and control technologies to maintain appropriate stream flows through coordinated harvesting and release of urban stormwater using storages on public and private land. Insights from the current modelling work have already galvanised a partnership of researchers, water authorities and councils and informed the development of a real-time monitoring and control pilot project to protect stream flows for the last remaining platypus population in the Dandenong catchment (DELWP, 2018).

Although the platypus habitat suitability models suggested less benefit from riparian revegetation and urban stormwater management actions, we demonstrated the importance of also considering management actions in combination. Urban platypus populations are predicted to benefit substantially if riparian revegetation and stormwater management are undertaken in conjunction with stream flow protection (when compared to the business-as-usual-future scenario – especially for female platypus). While our scenarios are hypothetical,

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large opportunities do exist around Melbourne to implement stormwater management interventions that would keep Attenuated Imperviousness at levels required to protect platypus habitat and other ecological values even under the urban expansion scenario. Finally, the added complementary benefits of riparian revegetation and stormwater management might have been overlooked were it not possible to consider the combined benefits of management actions in our models.

High-resolution, region-wide mapping of predictions arising from scenarios of interest has made it possible to visualise and understand patterns of predicted platypus habitat suitability under a range of plausible climate change and urban growth scenarios. Managers can thereby explore the magnitude and spatial distribution of benefits from a wide range of intervention combinations (**Fig. 7** and **Fig. S2**). These platypus models along with a suite of other models for macroinvertebrate families and native fish species have been used in conjunction with expert and local knowledge to enable systematic strategic planning, identify priority locations and interventions, and set quantitative targets as part of Melbourne's Healthy Waterways Strategy (Coleman et al., 2018; Chee et al., 2020).

As these tools are being applied in practice by the regional catchment management agency (Melbourne Water), it is important to be mindful of their limitations. Firstly, these habitat suitability models are statistical models that quantify relationships between taxa and environmental predictors associated with habitat attributes. They capture correlative associations and patterns but do not describe the processes that determine population viability (e.g. reproduction, survival, mortality and dispersal). Detailed knowledge about these processes may be required for population management and will require tools that complement habitat suitability modelling, such as dynamic population models. While we used the best available information at the time of the development of the Healthy Waterways Strategy for our warming and drying scenarios, we also acknowledge that the magnitude and rates of change of ecologically-relevant climate attributes is rapidly evolving and it will be important to update and incorporate a wider suite of climate change projections to better account for the range of plausible futures as predictions are refined. In particular, the Victorian State government's latest authoritative and up-to-date climate projections were released in 2019 (Clarke et al., 2019). Although this release has application-ready data for mean annual temperature, runoff estimates for our study area are not readily available and will need to be developed.

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The predicted contraction in the distribution of platypus across Melbourne from urban growth and climate change has interesting implications for platypus in other parts of their range – most notably the major cities of Sydney and Brisbane, and urban townships. In the context of the recently revised conservation status of platypus as Near Threatened by the IUCN and Vulnerable in the state of Victoria, applying this modelling approach to other parts of the species' range would contribute to understanding whether further revision of its conservation status is warranted.

Authors Contributions

RAC, CJW, NB and YC conceived the method of ecological model development, including the suite of environmental predictors and management intervention scenarios; RAC consolidated the platypus and environmental predictor data and built the platypus models with support from CJW and YC; YC ran the management intervention scenarios and led model validation with RAC; MS, GAW and JG collected the live-trapping data; JG and AW collected the eDNA data; RAC and YC led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data Accessibility

All live-trapping and eDNA data used to build and validate the platypus models from this study are openly available in figshare at http://doi.org/10.6084/m9.figshare.17085488.

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Figures and Tables

Figure 1 The greater Melbourne area in Victoria, Australia. Major catchment boundaries are (from left to right): Werribee, Maribyrnong, Yarra, Dandenong and Westernport. (a) shows netting sites from 1995-2009 where platypus have been captured (red circles) or not captured (black circles). (b) shows eDNA survey sites 2016-2018 where platypus were detected (red circles) or not detected (black circles). Study area showing predicted probability of occurrence (coloured lines) with the male-female platypus model under the 'CURR' scenario that represents current conditions where all environmental predictors were set to 2016 values.

Figure 2 Fitted response curves for the male-female platypus model and relative percentage contribution in brackets for (a) Catchment Area, (b) Mean Annual Discharge Depth, (c) Antecedent Runoff, (d) Mean Annual Air Temperature, (e) Attenuated Imperviousness and (f) Attenuated Forest Cover.

Figure 3 Fitted female-only platypus model and relative percentage contribution in brackets for (a) Mean Annual Discharge Depth, (b) Mean Annual Air Temperature, (c) Catchment Area, (d) Antecedent Runoff, (e) Attenuated Forest Cover and (f) Attenuated Imperviousness.

Figure 4 Receiver Operating Characteristic (ROC) curves and AUC scores using independent validation data for (a) the male-female platypus model and netting data from 2010-2019, (b) the female-only model and netting data 2010-2019, and (c) the male-female platypus model and eDNA data from 2016-2018.

Figure 5 Calibration plots using the independent netting data from 2010-2019 for (a) the male-female platypus model and (b) the female-only platypus model.

Figure 6 Predicted current distribution of (a) male-female platypus and (b) female-only platypus, and predicted distribution in a more urbanised, drier and warmer future (BAUF) for (c) male-female platypus and (d) female-only platypus.

Figure 7 'Difference maps' of probability of occurrence using a diverging blue-white-red colour scale. For any given management intervention scenario (see Table 2), blue indicates an increase in probability relative to BAUF, red indicates a decrease (no negative values were predicted) and white indicates little or no change. (a) revegetation 20m either side of all

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streams (RV20), (b) disconnection of existing and future urban stormwater (SW1), (c) a warmer but not drier future (NoDry) and (d) revegetation 20m either side of all streams, disconnection of existing and future urban stormwater, and a warmer but not drier future (RV20_SW1_NoDry).

Table 1 Environmental predictors used in the platypus habitat suitability models.

Table 2 Scenarios used to explore the potential impact of urban growth and climate change on platypus distribution, as well as the likely benefit of certain management interventions. All scenarios assess changes relative to business-as-usual future (BAUF) conditions.

Supporting Information

Figure S1 Values for environmental predictors across the stream network that were used to develop the male-female platypus and female only models, excluding Antecedent Runoff. (a) Catchment Area, (b) Mean Annual Discharge Depth, (c) Mean Annual Air Temperature, (d) Attenuated Forest Cover and (e) Attenuated Imperviousness.

Figure S2 'Difference maps' of probability of occurrence using a diverging blue-white-red colour scale) for scenarios not presented in Figure 7 using both the male-female and female only models. For any given management intervention scenario (see Table 2), blue indicates an increase in probability relative to BAUF, red indicates a decrease (no negative values were predicted) and white indicates little or no change.

Table S1 Model summaries and performance metrics for the male-female platypus and female-only platypus presence/absence models.

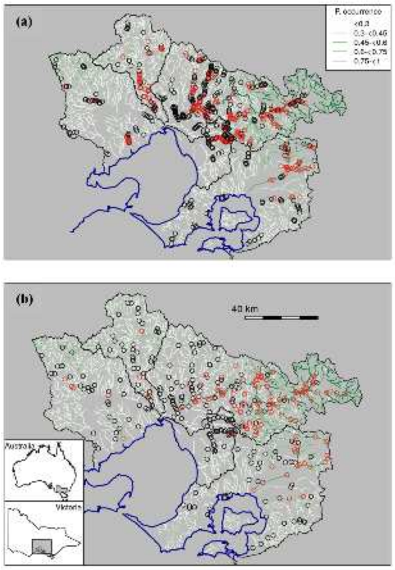
Table 1 Environmental predictors used in the platypus habitat suitability models

Environmental Predictor	Units	Source
Catchment Area	km^2	
Mean Annual Discharge Depth	mm	Gridded (5km by 5km) monthly surface runoff estimates from the Australian Water Availability Project (AWAP; Raupach et al., 2009) for the period from 1900-2017 were used to derive an estimate of mean annual runoff for each grid cell. Grid cells were intersected with sub-catchment boundaries to produce an estimate of runoff for each individual sub-catchment (weighted according to coverage by individual grid cells). Runoff for individual sub-catchments was then averaged over the entire contributing catchment area.
Antecedent Runoff	NA	Calculated from runoff estimates from the Australian Water Availability Project (Raupach et al., 2009) using functions from the SPEI (Standardised Precipitation-Evapotranspiration Index) R package (Beguería & Vincente-Serrano, 2017)
Mean Annual Air Temperature	°C	Derived from STRANNTEMP in Stein et al.'s (2011) Environmental Stream Attributes v1.1 dataset that supplements the Australian Bureau of Meteorology's Geofabric dataset (www.bom.gov.au/water/geofabric/). STRANNTEMP is the average value of BIOCLIM variable 'Annual Mean Temperature' of all grid cells (in the 9" DEM of Australia ver 3 2008) comprising the reach segment and associated valley bottoms.
Attenuated Forest Cover	NA	Walsh & Webb (2014)
Attenuated Imperviousness	NA	Walsh & Webb (2014) and Martin et al. (2014)

Table 2 Scenario descriptions for current conditions (CURR), a business-as-usual-future (BAUF) that includes expected urban growth and climate change, and a range of intervention scenarios (shaded rows) used to explore the likely benefit of certain management interventions on platypus distribution. All intervention scenarios assess changes relative to business-as-usual future (BAUF) conditions.

Scenario Code	**Description**
CURR	Current conditions, all environmental predictors set to 2016 values.
BAUF	Business-as-usual-future, Mean Annual Air Temperature as at 2016 values + 1.5 °C, Mean Annual Discharge Depth (mm) equivalent to a 25% reduction in the long-term mean value at the mouth of the Yarra River, Attenuated Forest Cover set to 2016 values, Attenuated Imperviousness value when all parcels within the region with 'urban' planning scheme zone codes have been developed to their full capacity. The BAUF scenario assumes that future urban areas are drained conventionally, with resulting growth in effective impervious area.
RV20	Like BAUF, but revegetate riparian zones on both stream sides, to 20m width along all streams in the region
SW2	Like BAUF, but treat all future impervious cover such that Attenuated Imperviousness is maintained at 2016 levels
SW1	Like BAUF, but treat all future *and* existing cover such that Attenuated Imperviousness is effectively zero
RV20_SW2	Like BAUF, but revegetate riparian zones on both stream sides, to 20m width along all streams in the region AND treat all future impervious cover such that Attenuated Imperviousness is maintained at 2016 levels
RV20_SW1	Like BAUF, but revegetate riparian zones on both stream sides, to 20m width along all streams in the region AND treat all future *and* existing cover such that Attenuated Imperviousness is effectively zero
BAUF_NoDry	Like BAUF, but set Mean Annual Discharge Depth (mm) to 2016 values
RV20_NoDry	Like BAUF, but revegetate riparian zones on both stream sides, to 20m width along all streams in the region AND set Mean Annual Discharge Depth (mm) to 2016 values

RV20_SW2_NoDry	Like BAUF, but revegetate riparian zones on both stream sides, to 20m width along all streams in the region AND treat all future impervious cover such that Attenuated Imperviousness is maintained at 2016 levels AND set Mean Annual Discharge Depth (mm) to 2016 values
RV20_SW1_NoDry	Like BAUF, but revegetate riparian zones on both stream sides, to 20m width along all streams in the region AND treat all future *and* existing cover such that Attenuated Imperviousness is effectively zero AND set Mean Annual Discharge Depth (mm) to 2016 values



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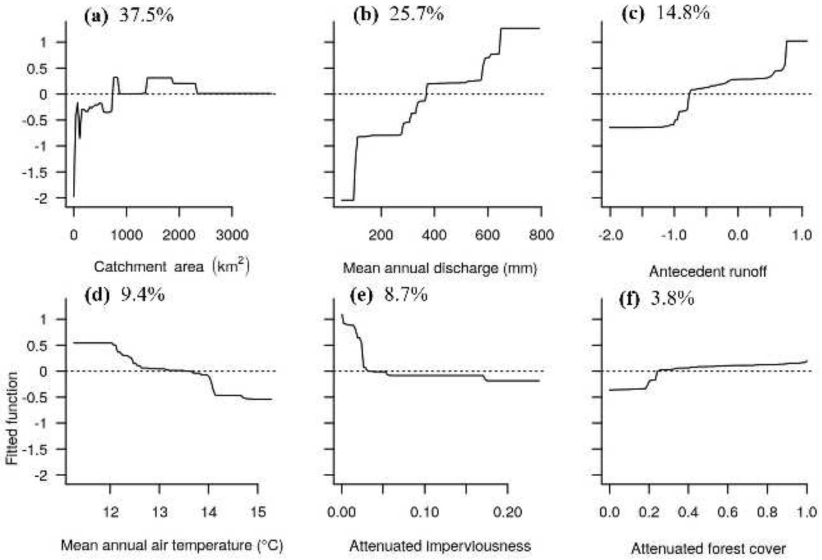

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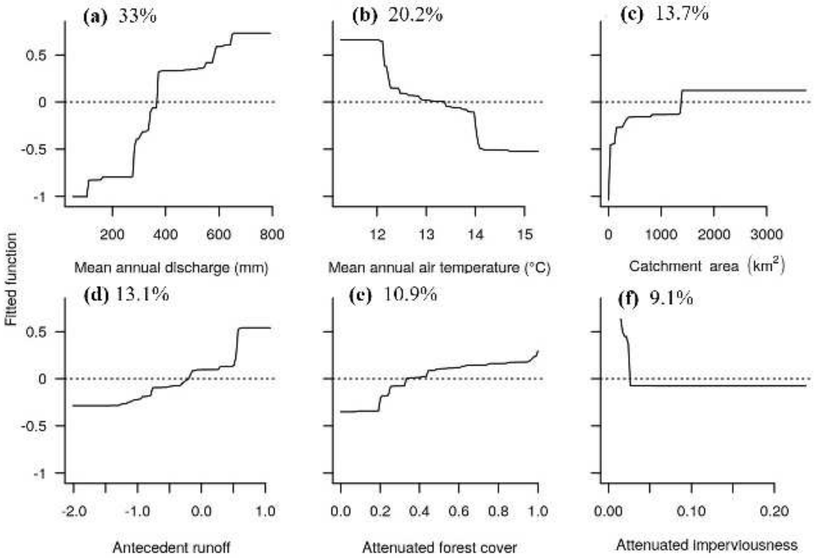

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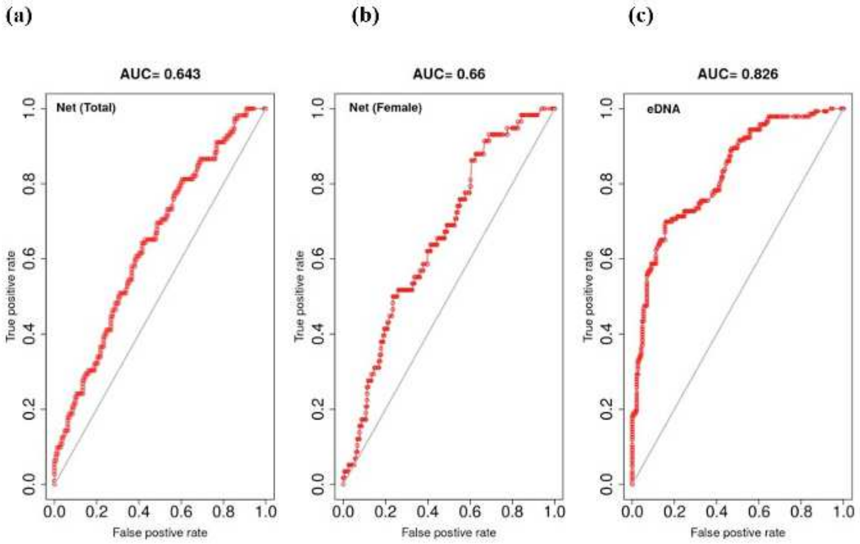

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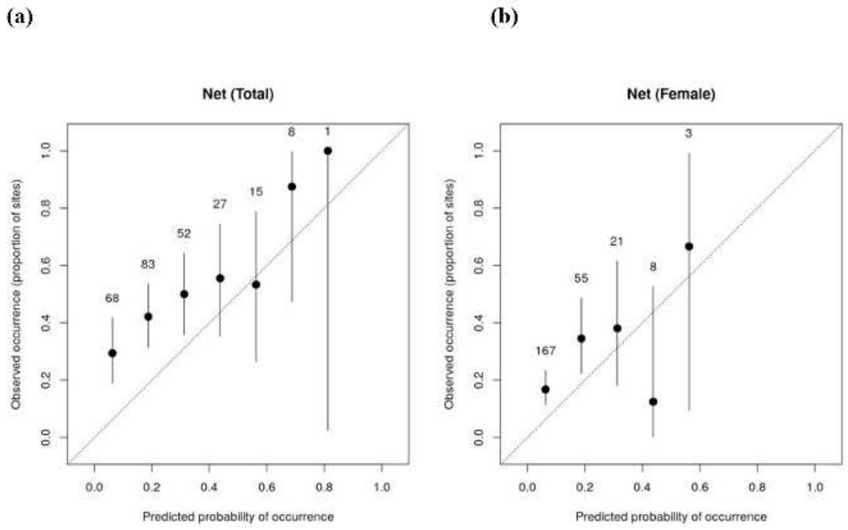

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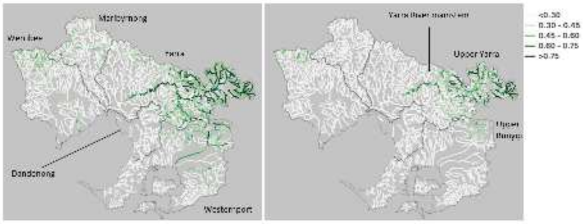
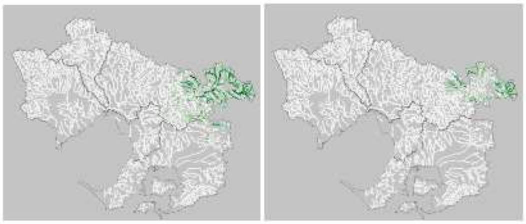

(a) Male-female platypus CURR

(b) Male-female platypus BAUF


(c) Female-only platypus CURR

(d) Female-only platypus BAUF

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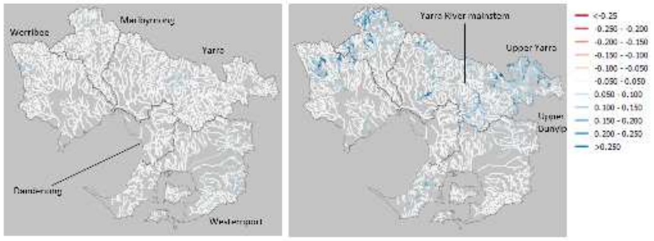
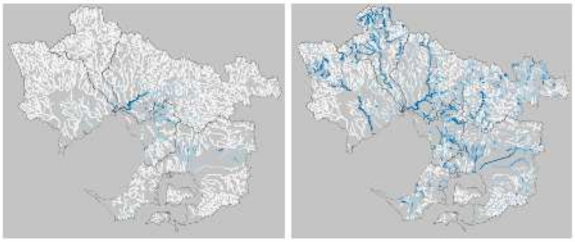
(a) RV20 BAUF **(b)** NoDry BAUF



(c) SW1 BAUF **(d)** RV20_SW1_NoDry BAUF



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