

# Using species distribution models to infer potential climate change-induced range shifts of freshwater fish in south-eastern Australia

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**Abstract.** There are few quantitative predictions for the impacts of climate change on freshwater fish in Australia. We developed species distribution models (SDMs) linking historical fish distributions for 43 species from Victorian streams to a suite of hydro-climatic and catchment predictors, and applied these models to explore predicted range shifts under future climate-change scenarios. Here, we present summary results for the 43 species, together with a more detailed analysis for a subset of species with distinct distributions in relation to temperature and hydrology. Range shifts increased from the lower to upper climate-change scenarios, with most species predicted to undergo some degree of range shift. Changes in total occupancy ranged from –38% to +63% under the lower climate-change scenario to –47% to +182% under the upper climate-change scenario. We do, however, caution that range expansions are more putative than range contractions, because the effects of barriers, limited dispersal and potential life-history factors are likely to exclude some areas from being colonised. As well as potentially informing more mechanistic modelling approaches, quantitative predictions such as these should be seen as representing hypotheses to be tested and discussed, and should be valuable for informing long-term strategies to protect aquatic biota.

**Additional keywords:** bioclimatic model, conservation planning, environmental filters, hydrology, prediction, validation.

## Introduction

With anticipated changes in climate regime, including changes in temperature, rainfall and runoff, there is an increasing emphasis on understanding how species distribution patterns may change, and how to incorporate this information into conservation and restoration planning (Thuiller 2007; Palmer *et al.* 2007). This has stimulated considerable debate about how best to predict potential distributional shifts, and, in particular, whether correlative species distribution models (SDMs) are appropriate for predicting range shifts, or whether more mechanistic approaches are required (Heikkinen *et al.* 2006; Thuiller 2007; Kearney and Porter 2009; Elith *et al.* 2010; Sinclair *et al.* 2010).

Whereas much of this debate pits correlative and mechanistic approaches against one another, an alternative view sees correlative models as a valuable means of establishing hypotheses and identifying important processes to consider when developing mechanistic models for unstudied organisms (Buckley *et al.* 2010). Befitting this view is the recent trend

towards statistical-modelling techniques based on information theory (such as neural networks, regression trees and random forests). These approaches rely less on an underlying model structure than do traditional modelling tools and are well suited to capturing non-linear relationships and interactions among predictors, therefore lending themselves to generating novel insights into species–environment relationships (Olden *et al.* 2008; Elith and Leathwick 2009). Despite the fact that evidence for climate-change impacts on fish species distributions is still rare (Booth *et al.* 2011), recent application of SDM approaches suggests that future range shifts of freshwater biota may be substantial (e.g. Buisson and Grenouillet 2010; Elith *et al.* 2010; Lyons *et al.* 2010).

Climate and hydrologic regimes have long been recognised as important environmental filters operating on aquatic ecosystems. Numerous studies have demonstrated predictable relationships between hydro-climatic conditions and the distribution patterns of freshwater biota – especially fish and

macroinvertebrates (e.g. Poff and Allan 1995; Leathwick *et al.* 2005; Grown and West 2008). In rivers, patterns of flow variability are a major driver of ecosystem structure and function, and thus changes in flow can have a strong impact on species occurrence patterns (e.g. Kennard *et al.* 2007; Bond *et al.* 2010). Studies examining the effects of climate change on patterns of stream flow (e.g. Poff *et al.* 1996; Gibson *et al.* 2005; CSIRO 2008) suggest potential for substantial changes not just in average runoff but also in the occurrence, frequency and timing of ecologically relevant flows such as cease-to-flow periods and overbank flows that inundate floodplain areas. There is thus a need to try and capture these aspects of hydrology in examining climate-change impacts in aquatic ecosystems and to provide robust predictions of changes in species distribution.

Here, we examine potential range shifts of freshwater fish species in Victoria in south-eastern Australia under a range of climate scenarios, and explore species–environment relationships to help elucidate important hydro-climatic drivers. We developed SDMs linking contemporary species distributions to average contemporary climatic, hydrologic and physiographic characteristics, and combined the resultant models with scenarios of drought and climate change to explore the likely long-term impacts of different climate scenarios on species distributions. We developed models for 43 freshwater species and explored the impacts of three (low, median and high temperature) scenarios for 2030.

As well as summarising the overall changes in distribution patterns of the 43 species, we also present more detailed results for three native species, namely river blackfish (*Gadopsis marmoratus* Richardson, 1848), golden perch (*Macquaria ambigua* Richardson, 1845) and flathead gudgeon (*Philypnodon grandiceps* (Krefft, 1864)), and one introduced species, brown trout (*Salmo trutta* Linnaeus, 1758), with the aim of highlighting the types of response functions displayed to strong hydro-climatic drivers for each species, and illustrating the geographic range shifts that may occur. These species occupy a range of habitats from cool-water perennial streams through to intermittent lowland streams and large floodplain rivers, and are thus illustrative of the types of responses displayed by other species. There are varying levels of existing information on physiological tolerances and traits of each species; in particular, there is much detailed work on the physiological tolerances of brown trout against which to contrast the observed associations arising from our correlative models.

## Materials and methods

### *Fish distribution data*

Survey records detailing species distribution data were drawn from the Victorian Department of Sustainability and Environment's Aquatic Fauna Database (AFD), which holds records from sites across Victoria as far back as the late 1800s. We restricted our analysis to 3708 sites surveyed between 1980 and 2000 for which reliable location and sampling information were available, overcoming some of the problems associated with the reliability of (particularly early) records in these sorts of databases. AFD data were supplemented by more recent data collected between 2004 and 2006 from 769 sites across Victoria that were surveyed as part of the Murray–Darling Basin

Sustainable Rivers Audit (SRA) and the Southern Basins Audit (SBA). SRA and SBA surveys used electrofishing (backpack-, bank- and/or boat-mounted units), whereas the AFD database records involved a range of methods, including electrofishing, nets and piscicides. Sites below large impoundments were excluded from our analyses because such reaches tend to hold fish communities that are markedly atypical of those expected on the basis of natural climate and hydrology (e.g. Pollino *et al.* 2004; Quist *et al.* 2005), which could lead to misleading modelled relationships. We also excluded sites for which the spatial coordinates could not be reconciled against other information such as stream name and other site information, indicating potential errors in location details. All data were converted to presence/absence for the modelling, and in total, 43 species were represented (Table 1). This included several estuarine species frequently encountered in freshwater environments, but did not distinguish between some taxa for which taxonomic uncertainties remain, including the *Hypseleotris* species complex (including *H. klunzingeri* and several undescribed species) and *Galaxias olidus*, which also consists of several as yet undescribed species.

### *Environmental data*

The major source of environmental data was a digital elevation model (DEM)-derived stream network linked to a set of summary statistics on climate and catchment characteristics associated with each reach (Stein 2006). The stream network is derived from a 9'' DEM and includes more than 45 000 reaches across Victoria. Catchment and climate datasets linked to the stream network are described in more detail by (Stein 2006; Walsh *et al.* 2007), and indicators of catchment disturbance in Stein *et al.* (2002). Variables used in the modelling are summarised in Table 2.

As with similar studies, we attempted to restrict the set of environmental predictors used in the modelling to those for which a mechanistic link with fish occurrence could be identified (e.g. Leathwick *et al.* 2005), and further sought to focus on climate-related predictors to maximise model sensitivity to climate-change scenarios. A comparison of model structures did, however, show that the inclusion of elevation improved the fit of the models for a small number of species (especially estuarine taxa), while having very minor impacts on predictions and scenarios for other species. There was also a weaker than expected correlation between temperature and elevation ( $r = 0.65$ ), and here we present results from models that include elevation.

### *Hydrologic data*

Given the recognised importance of hydrology as an environmental filter on biotic distributions in south-eastern Australia (e.g. Grown and West 2008; Bond *et al.* 2010), information on the hydrologic regime of individual river reaches was seen as a key component of the environmental-data requirements for modelling climate-change impacts. Although there is an increasing emphasis on ecologically relevant aspects of the flow regime in studies of climate-change impacts on runoff (e.g. Gibson *et al.* 2005; CSIRO 2008), most such studies are based on summarising results from calibrated rainfall–runoff models,

**Table 1. Fish species for which species distribution models were constructed and model fit based on area under the receiver operator-characteristic curve (AUC)**

Conservation status under the federal *Environmental Protection and Biodiversity Conservation (EPBC) Act* and state *Flora and Fauna Guarantee (FFG) Act*. Listings include vulnerable (VU), near threatened (NT), endangered (EN), listed (L)

Scientific name	Common name	Conservation status		Model fit	
		EPBC	FFG	AUC (naïve)	AUC (bootstrap)
<i>Acanthopagrus butcheri</i>	Black bream			1.00	0.99
<i>Aldrichetta forsteri</i>	Yelloweye mullet			1.00	1.00
<i>Anguilla australis</i>	Short-finned eel			0.95	0.94
<i>Anguilla reinhardtii</i>	Marbled eel			0.98	0.99
<i>Atherinosoma microstoma</i>	Small-mouth hardyhead			1.00	1.00
<i>Bidyanus bidyanus</i>	Silver perch		L	0.50	0.50
<i>Craterocephalus stercusmuscarum fulvus</i>	Fly-specked hardyhead		L	0.93	0.89
<i>Gadopsis bispinosus</i>	Two-spined blackfish			1.00	0.99
<i>Gadopsis marmoratus</i>	River blackfish			0.95	0.93
<i>Galaxias brevipinnis</i>	Climbing galaxias			0.98	0.97
<i>Galaxias fuscus</i>	Barred galaxias	EN	L	0.92	0.88
<i>Galaxias maculatus</i>	Common jollytail			0.95	0.95
<i>Galaxias olidus</i>	Mountain galaxias			0.99	–
<i>Galaxias truttaceus</i>	Spotted galaxias			0.91	0.89
<i>Galaxiella pusilla</i>	Eastern little galaxias	VU	L	0.87	0.84
<i>Geotria australis</i>	Pouched lamprey			1.00	0.94
<i>Gobiomorphus australis</i>	Striped gudgeon	NT		0.97	0.91
<i>Hypseleotris klunzingeri</i>	Western carp gudgeon			0.92	0.85
<i>Maccullochella macquariensis</i>	Trout cod	EN	L	0.98	1.00
<i>Maccullochella peelii peelii</i>	Murray cod	VU	L	0.99	1.00
<i>Macquaria ambigua</i>	Golden perch			0.99	0.96
<i>Macquaria australasica</i>	Macquarie perch	EN	L	1.00	0.96
<i>Macquaria colonorum</i>	Estuary perch			1.00	0.97
<i>Macquaria novemaculeata</i>	Australian Bass			1.00	0.97
<i>Melanotaenia fluviatilis</i>	Australian rainbowfish		L	0.99	0.85
<i>Mordacia mordax</i>	Short-headed lamprey			1.00	1.00
<i>Nannoperca australis</i>	Southern pygmy perch			0.99	0.99
<i>Nannoperca obscura</i>	Yarra pygmy perch	VU	L	1.00	0.95
<i>Nannoperca variegata</i>	Ewen pygmy perch	VU	L	0.99	0.98
<i>Philypnodon grandiceps</i>	Flathead gudgeon			0.96	0.97
<i>Prototroctes maraena</i>	Australian grayling	VU	L	1.00	0.98
<i>Pseudaphritis urvillii</i>	Congolli			1.00	0.99
<i>Retropinna semoni</i>	Australian smelt			0.89	0.86
<i>Tetractenos glaber</i>	Smooth toadfish			0.93	0.92
<i>Carassius auratus</i>	Goldfish	Introduced		0.90	0.86
<i>Cyprinus carpio</i>	Common carp	Introduced		0.93	0.91
<i>Gambusia holbrooki</i>	Mosquitofish	Introduced		0.97	0.95
<i>Misgurnus anguillicaudatus</i>	Weatherloach	Introduced		0.95	0.97
<i>Oncorhynchus mykiss</i>	Rainbow trout	Introduced		0.88	0.88
<i>Perca fluviatilis</i>	Redfin perch	Introduced		0.99	0.84
<i>Rutilus rutilus</i>	Roach	Introduced		0.91	0.91
<i>Salmo trutta</i>	Brown trout	Introduced		1.00	1.00
<i>Tinca tinca</i>	Tench	Introduced		0.99	0.95

which can realistically only be calibrated for specific nodes in a river network, generally at gauged sites where calibration data are available. Although this approach produces detailed time-series of runoff, logistically it is not feasible to build these models at a density capable of representing hydrologic characteristics of the entire river network. An alternative approach is to develop regression models relating flow characteristics (flow indices) measured at a gauge with climate and upstream catchment characteristics, and to use these models to extrapolate hydrologic indices to other parts of the river network (Sinclair

Knight Merz 2005; Sanborn and Bledsoe 2006). This approach provides insights into long-term stream-flow characteristics that can be combined with other catchment attribute data to develop SDMs (Lyons *et al.* 2010). Gauge data for use in the hydrologic modelling were drawn from 120 unregulated sites distributed across Victoria (see Kennard *et al.* 2010b, for gauge locations), with sufficient record length to adequately quantify hydrologic regimes – in this case more than 15 years (Kennard *et al.* 2010a). A small set of hydrologic indices, including mean daily flow, daily and annual coefficient of variation in flow volumes (daily

**Table 2. Environmental predictors used in modelling hydrologic regimes and fish-occurrence patterns**

Variable	Description	Unit	Included in models	
			Hydrology	Fish
TEMPHOTQ	Average daily temp in hottest 13 weeks	°C	✓	✓
TEMPCOLDQ	Average daily temp in coldest 13 weeks	°C	✓	✓
SOLRAD	Local annual mean solar radiation	MJ m <sup>-2</sup> day <sup>-1</sup>	✓	✓
RAIN (MONTHLY)	Average rainfall in each month (Jan.–Dec.)	mm	✓	
RAIN_ANN	Average annual rainfall	mm	✓	✓
TMAX (MONTHLY)	Average maximum daily temperature in each month	°C	✓	
TMAX_ANN	Annual mean maximum temperature	°C	✓	✓
TMIN (MONTHLY)	Average minimum daily temperature in each month	°C	✓	
TMIN_ANN	Annual mean minimum temperature	°C	✓	✓
APET (MONTHLY)	Monthly areal potential evapotranspiration (Jan.–Dec.)	mm	✓	
APET_ANN	Annual areal potential evapotranspiration	mm	✓	✓
SOLPAWHC	Solum plant-available water holding capacity	mm	✓	
A_KSAT	Saturated hydraulic conductivity	mm h <sup>-1</sup>	✓	
Trees	Tree cover	%	✓	
GRASSES	Grass cover	%	✓	
OTHER	Shrublands and other vegetation types	%	✓	
CATRELIEF	(Mean upstream elevation – pour point elevation)/(max upstream elevation – pour point elevation)	%	✓	
RCHELEMEAN	Mean reach elevation	m	✓	✓
RCHELEMIN	Minimum reach elevation	m	✓	
RCHELEMAX	Maximum reach elevation	m	✓	
SUBELEMEAN	Mean subcatchment elevation	m	✓	
SUBELEMIN	Minimum subcatchment elevation	m	✓	
SUBELEMAX	Maximum subcatchment elevation	m	✓	
CATELEMAX	Maximum upstream elevation	m	✓	
CATELEMEAN	Mean upstream elevation	m	✓	
SUBAREA	Subcatchment area	km <sup>2</sup>	✓	
RCHLEN	Reach length	km	✓	
CONFINEMEN	Indicator of valley confinement (RCHCONF)	%	✓	✓
CATAREA	Catchment area	km <sup>2</sup>	✓	✓
STRAHLER	Strahler stream order		✓	
UPSDIST	Upstream distance	km	✓	
VALLEYSLOP	Valley slope	%	✓	
CATSLOPE	Catchment slope	%	✓	
SUBSLOPE	Subcatchment slope	%	✓	
ASPECT	Local aspect	%	✓	
CDI	Catchment disturbance		✓	✓
SCDI	Subcatchment disturbance		✓	✓
LUF	Subcatchment land-use		✓	
IF	Subcatchment infrastructure Development		✓	✓
EF	Subcatchment point sources of pollution		✓	✓
SF	Subcatchment urbanisation		✓	✓
RDI	Overall disturbance		✓	✓
STRDENS	Stream density	km km <sup>-2</sup>	✓	
STRFREQ	Stream frequency	no. streams km <sup>-2</sup>	✓	
COASTAL	Inland v. coastal drainages			✓
MDF	Mean daily runoff	ML		✓
CV_Daily	Variability in daily flows			✓
CV_Ann	Variability in annual runoff			✓
Q90	Low-flow discharge 90th percentile	ML		✓
ZFD	Number of zero flow days	Days		✓

and annual CVs), daily 10th (daily Q10) and 90th (daily Q90) percentile flows, and mean annual number of zero-flow days were included in the predictive modelling. As with the species distribution models themselves, hydrologic indices were modelled as a function of climate and catchment attributes in the catchment above each gauge (Table 2). As summarised in the

results section, high flow events could not be modelled with sufficient reliability to be included in the fish predictive models. Clearly, this removes our capacity to identify the impact of altered high flow regimes on species distributions; however, this is partially offset by the fact that changes in low flow characteristics are critical hydrologic filters affecting in-channel

riverine species distributions (Balcombe *et al.* 2011; Pratchett *et al.* 2011).

#### Climate scenarios

We examined the impacts of three climate-change scenarios (consisting of changes ( $\delta$ ) in temperature (T), precipitation (P) and evapotranspiration (Etw)). Scenarios corresponded to the low, median and high estimates of  $\delta T$  (+0.54°C, +0.85°C and +1.24°C) for 2030 from the SRES marker scenarios of IPCC (2001). Estimates of changes in P and Etw were drawn from a spreadsheet model accompanying Jones and Durack (2005), which presented lower, median and upper estimates of  $\delta P$  (-1.1%, -3.3%, -6.0%) and  $\delta Etw$  (+2.0%, +3.1%, +4.6%) in catchments across Victoria from 10 climate models scaled to the low, median and upper IPCC temperature scenarios. Changes in T, P and Etw were applied to baseline climate characteristics from the climate atlas of Australia (Bureau of Meteorology 2002).

The effects of climate change on species distributions were modelled by first running the statistical hydrology models to derive predicted hydrologic characteristics for each reach under each of the three scenarios. These derived hydrologic data were then combined with scenario climate data and fixed catchment attributes as input to the statistical models built using the historical climate and species-distribution data.

#### Statistical modelling

Statistical models for both hydrology and fish were built using boosted regression trees (BRTs; Elith *et al.* 2008). BRTs represent a form of model averaging, in which multiple models are combined for prediction and inference, thereby accounting for uncertainty in model structure. The BRT method combines large numbers of relatively simple regression-tree models in an adaptive fitting process (Friedman 2001). BRTs have strong predictive performance, are well suited to identifying important predictor variables, and capture non-linearity in the response to individual predictors, and interactions among predictors (Elith *et al.* 2008). BRT models were built using the *gbm* package (Ridgeway 2007) in R (R Development Core Team 2009), with the default shrinkage ('learning rate' in Elith *et al.* 2008) value of 0.001 and the maximum interaction depth ('tree complexity') set to 5. Initial BRT models were based on 4000 trees, and the out-of-bag (OOB) estimate of predictive performance was used to select the optimal number of trees for each species. OOB estimates of error rate are based on bootstrap sampling using a random subset of records (50%) as training data for each iteration.

Model fit was assessed on the basis of the residual error ( $R^2$ ) in the case of continuous response variables, and on the basis of the area under receiver operator-characteristic curves (area-under-curve; AUC) for binomial variables. The receiver operator curves indicate the relative proportions of correctly and incorrectly classified predictions over a wide range of probability threshold levels, and are therefore independent of the (arbitrary) choice of a threshold probability to determine whether or not a site is predicted to be occupied (Burgman 2005). AUC values are also largely independent of species prevalence (Pearce and Ferrier 2000). AUC values  $>0.7$  are generally

deemed to indicate adequate discrimination for occupancy models, whereas AUC values  $>0.9$  indicate excellent discrimination (Pearce and Ferrier 2000). Additional cross-validation of the model predictions included bootstrap validation, by which an estimate of a 'naïve' models optimism is derived from simulations of model building and model testing performed on bootstrap samples (samples drawn with replacement from the model-building data). We used the '.632 + bootstrap' method (Efron and Tibshirani 1997) with 50 bootstrap samples, to calculate adjusted validation statistics for each species. At each bootstrap iteration, we built new hydrology models, based on bootstrap samples of the flow data, so that uncertainties associated with hydrological models were propagated into bootstrap estimates. In addition, we examined predictive performance when models were built using only AFD or SRA and SBA datasets and tested against the other independent dataset, and found results similar to those from combining the two datasets and using a cross-validation approach. Only results from the cross-validation are reported here.

Measures of uncertainty in the predictions associated with each stream reach were also generated for 4 of the 43 species for the median climate-change scenario, by taking repeated bootstrap samples of the biological datasets ( $n = 50$ ), deriving flow and fish BRT models at each iteration, and using these to produce predictions for all reaches in the environmental dataset. Lower and upper bounds (5th- and 95th-percentile values) from this set of predictions were used as an estimate of the confidence interval for each reach. Here, we simply summarise these by using the average interval range for each species across all reaches.

The influence of individual predictor variables was examined with reference to relative influence (RI) statistics and partial-dependence plots. RI statistics are based on the number of times a variable is selected for splitting each regression tree, weighted by the squared improvement to the model as a result of each split, and averaged over all trees (Elith *et al.* 2008). Values are scaled to sum to 100, with higher values indicating stronger influence on the response. Partial-dependence plots indicate how occurrence probabilities change in response to variation in individual predictor variables, after accounting for the average effect of all other variables included in the models (Elith *et al.* 2008). In this instance, the 'effect' (represented on the *y*-axis) is the log-odds ratio; the log of the ratio of the probability of fish being present or being absent, which varies in response to the value of the predictor (represented on the *x*-axis). The shape of the relationship in the partial-dependence plot therefore indicates how relative-occurrence patterns change as one moves along environmental gradients.

## Results

### Hydrology

Of the hydrologic indices examined for inclusion in SDM models, only five (MDF, DailyCV, ZFLOWS, Q90, AnnualCV) could be predicted with a sufficiently high degree of confidence to be of use in subsequent species modelling. Bootstrap  $R^2$ -values for these predictors were 0.64, 0.69, 0.5, 0.40 and 0.67, respectively. Results for high-flow characteristics were generally poor ( $R^2 < 0.4$ ), most likely because the monthly averages

**Table 3. Summary of the relative influence of individual predictors in the final boosted regression tree (BRT) models for the 43 fish species**  
Abbreviations as in Table 2

Variable	Mean	Median	Max.	Min.
TEMPHOTQ	10.96	5.40	50.49	0.88
TEMPCOLDQ	6.35	4.44	41.33	0.00
SOLRAD	3.91	3.59	14.00	0.29
RAIN_ANN	5.16	3.06	24.15	0.07
TMAX_ANN	4.29	3.08	31.34	0.03
TMIN_ANN	4.50	3.87	15.70	0.00
APET_ANN	4.67	3.48	28.61	0.06
RCHELEMEAN	11.27	5.74	46.79	0.00
CONFINEMEN	2.74	2.38	7.61	0.00
CATAREA	4.90	3.33	17.91	0.00
SCDI	4.85	3.84	31.22	0.00
EF	0.17	0.00	1.46	0.00
IF	2.53	2.50	6.93	0.00
SF	3.10	1.88	18.42	0.00
CDI	4.59	3.76	16.53	0.00
RDI	4.63	3.70	18.38	0.00
COASTAL	3.46	0.08	55.07	0.00
MDF	3.01	2.56	9.00	0.00
CV_Daily	3.55	2.80	14.24	0.00
CV_Ann	3.68	2.96	13.06	0.00
Q90	3.21	3.08	11.01	0.00
ZFD	4.46	3.36	26.62	0.01

in T, P and Etw are poor predictors of individual storm events that drive high-flow characteristics. Importantly, as for climate and physiographic variables, hydrologic characteristics displayed a high degree of spatial variation, thereby providing strong gradients in hydrologic filters across the state.

#### Fish SDMs

Overall, BRT models were highly successful in predicting the contemporary (current) distributions of most species, with models for 41 species having bootstrap AUC values of >0.80 (Table 1), and the only two poorly predicted species (*Bidyanus bidyanus* and *Galaxias fuscus*) being very rare in the AFD and SRA datasets, the latter having so few records that bootstrap AUC values could not be calculated.

Overall, influential predictors consisted of a broad mix of climatic-, hydrologic-, physiographic- and human-disturbance indicators (Table 3). The variables TEMPHOTQ, TEMP-COLDQ, TMAX\_ANN, RCHELEMEAN, SCDI, COASTAL and ZFD had the strongest influence on distribution patterns for any single species. Among the four species for which detailed response functions are discussed, the relative influence of individual predictors differed greatly, although in all cases, temperature (either maximum or minimum temperature or both) and hydrologic variables were ranked highly. Measures of catchment disturbance and catchment physiography were less important except RCHELEMEAN and COASTAL, which stood out for *G. marmoratus*, and RCHELEMEAN, which was influential for *P. grandiceps* and *S. trutta* (Fig. 1a–d). Partial-response functions for individual predictors were frequently non-linear, with species detection probabilities increasing or

decreasing sharply along important environmental gradients. Examples include the dramatic decrease in occupancy of *G. marmoratus* and *S. trutta* at sites with non-perennial flow, and a relatively narrow band of minimum and maximum temperatures (Fig. 1a, d).

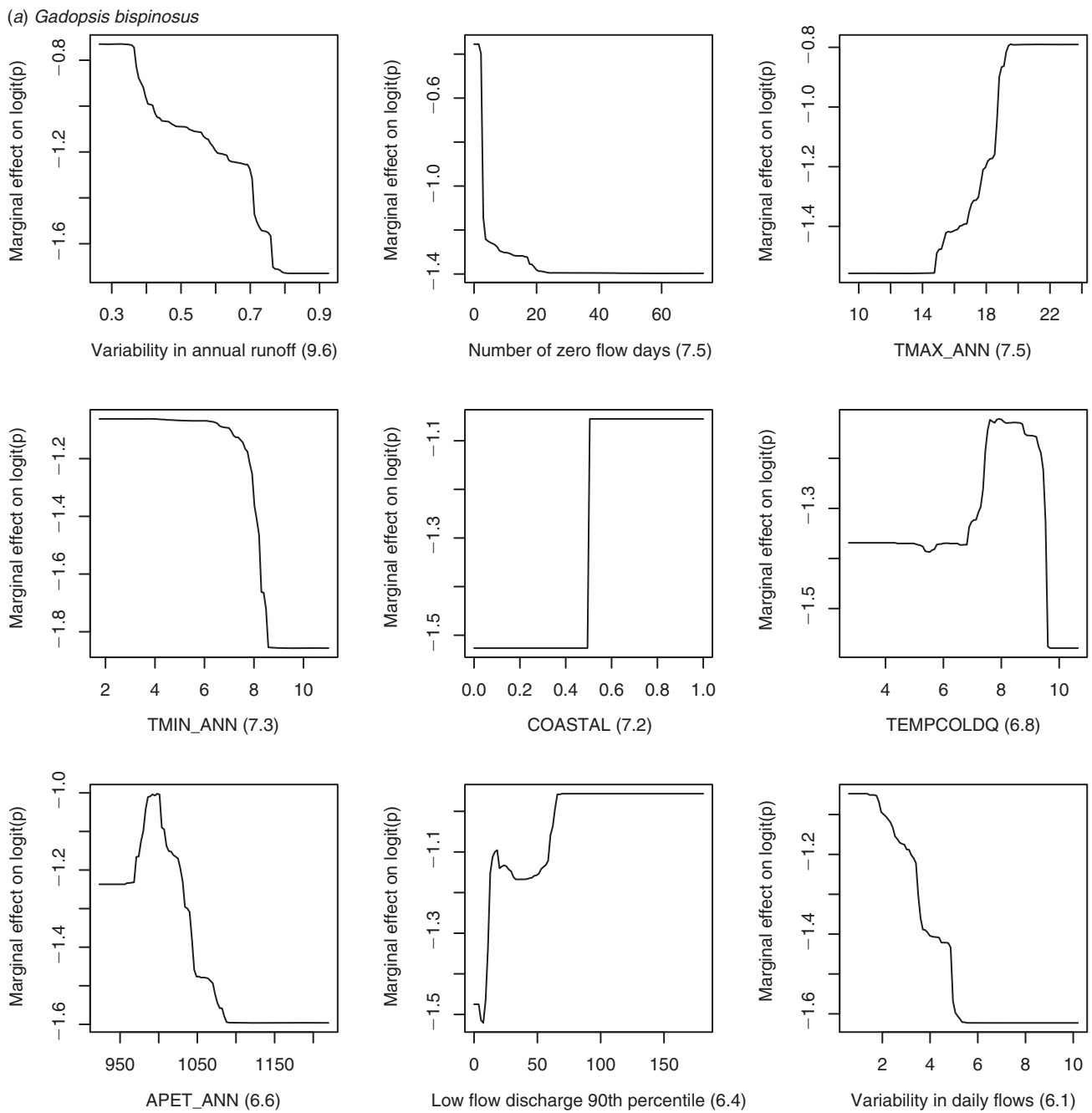
#### Scenario predictions

The models predicted responses by most species to each of the three climate-change scenarios, with range contractions and range expansions as well as overall range shifts (i.e. balanced contraction and expansions; Table 4) for both native and exotic species. Results differed depending on the approach to summarising range shifts. For example, some species showed consistent changes in both total occupied stream length and changes in the length of stream having high rates of occurrence ( $Pr > 0.5$ ). Species showing strong and consistent range contractions included *Gadopsis bispinosus* and *Gadopsis marmoratus*, and the exotic species *Salmo trutta* and *Oncorhynchus mykiss*. Species showing predicted range expansions included *Macquaria ambigua*, and several diadromous and estuarine species often encountered in the lower reaches of coastal rivers, as well as several exotic species, including *Gambusia holbrooki* and *Misgurnus anguillicaudatus*. A larger group of species showed inconsistent trends, with some showing range increases overall, but substantial declines in the length of stream with high occurrence probabilities (e.g. *Nannoperca variegata* and *Philypnodon grandiceps*) or *vice versa*. The direction of response by such species also tended to vary with each climate scenario (Table 4). These various patterns of losses and gains from reaches with historically low, moderate and high occurrence probabilities are represented by changes in the occurrence of *G. marmoratus*, *M. ambigua*, *P. grandiceps* and *S. trutta* (Fig. 2), as are the resultant range shifts based on comparisons of historical and median climate change-predicted distribution maps (Fig. 3a–d). Confidence intervals for individual scenarios (baseline and median climate change) for these four species were also relatively narrow, as were those for relative changes in predicted occupancy under the median climate-change scenario, which ranged from  $\pm \sim 3\%$  for *S. trutta* to approximately  $\pm \sim 15\%$  for *M. ambigua* (Table 5).

## Discussion

### Predicted 'baseline' distributions

We developed SDMs to describe the historic distributions of 43 species of freshwater fish in Victoria, south-eastern Australia. Together with detailed response functions for influential predictor variables, the resultant maps provide a useful approach for examining predicted range shifts as well as the utility of SDMs in generating information that can be used to guide the development of mechanistic models. An important strength of BRTs is their capacity to fit non-linear response functions that more adequately describe species responses to environmental gradients than is possible with traditional modelling approaches such as linear regression. Such utility is associated with an increasing array of modelling tools (Elith *et al.* 2010). Importantly, our analyses suggest such non-linear associations with hydro-climatic variables are common.



**Fig. 1.** (a–d) Plots showing the detailed response functions for each of the nine most influential predictor variables for each species. The y-axis reflects changes in log-odds ratios as one moves along each of the environmental gradients depicted in the figures. Values in parentheses in the x-axis labels are ‘relative influence’ (RI) values, which indicate the relative contribution of each variable to predicting the response.

For example, the species for which we presented detailed analyses of environmental drivers, all showed strong threshold relationships to at least some of the predictor variables, especially temperature and the occurrence of cease-to-flow spells, a feature of the hydrologic regime that is frequently regarded as an important threshold in flowing waters (Boulton and Hancock 2006). Thus, although correlative approaches such as this cannot demonstrate causality, nor elucidate specific mechanisms (Sinclair *et al.* 2010), the results strongly concord with expectations derived

from other independent sources of information, and could help devise quantitative and testable hypotheses.

In more general terms, the models also help provide a clear narrative describing the types of environment in which each of these species is most commonly encountered. For example, the models predict that river blackfish (*G. marmoratus*) occurs primarily in perennial streams with annual maximum and minimum temperatures in the range of ~8–15°C and relatively stable annual and daily flow volumes. Similarly, *S. trutta* mostly

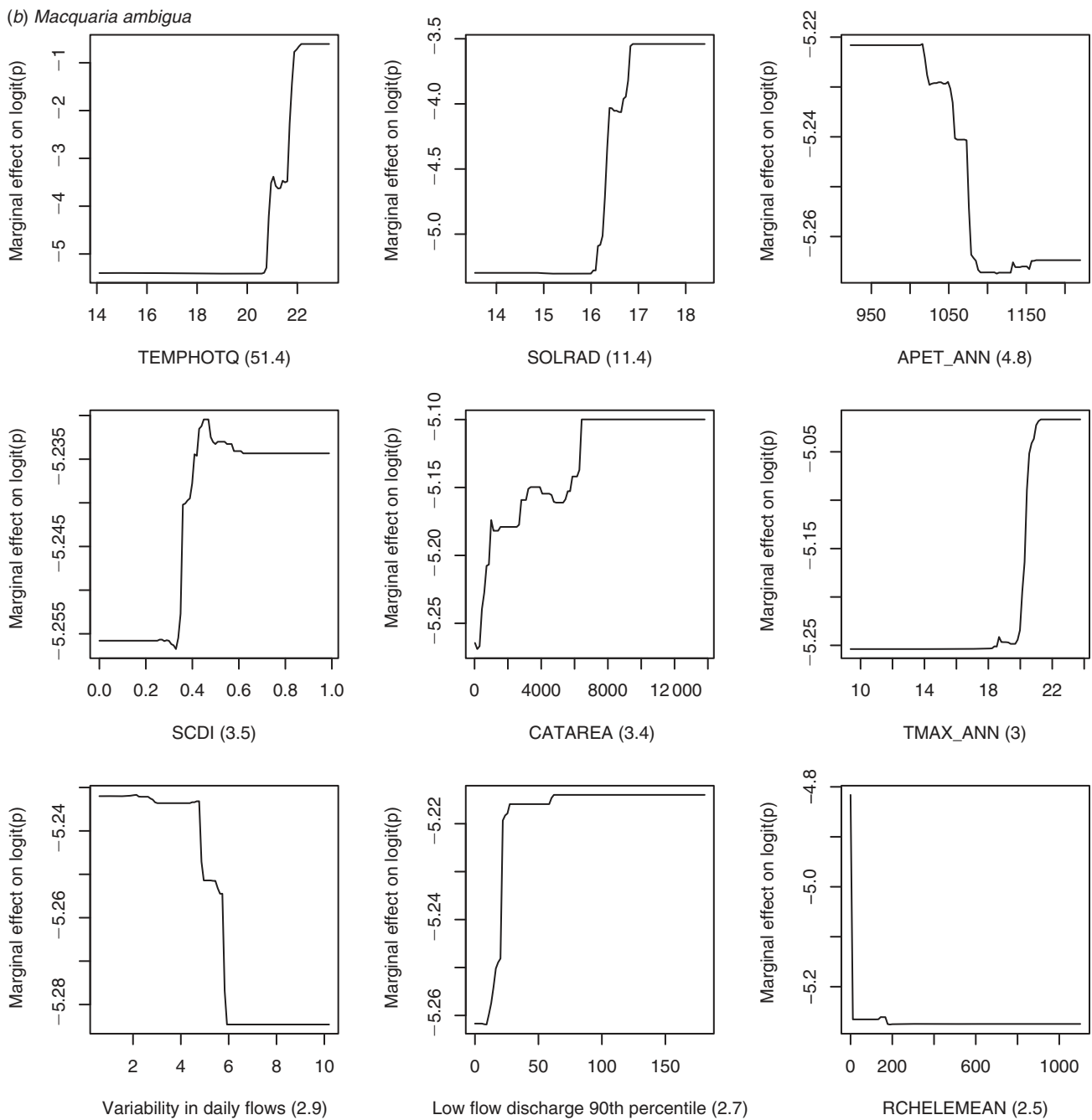


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occupy small, perennial streams at higher altitudes (above ~200 m) with high baseflow, catchment rainfall exceeding ~1000 mm year<sup>-1</sup>, and annual average maximum temperatures not exceeding ~18°C. Reported critical thermal maxima for *S. trutta* range between 23.5–26.7°C, with optimal water temperatures in the range of 8–17°C (Barton 1996). Given that our data are based on average maximum air temperatures, this suggests a reasonably high level of concordance, although more accurate reconciliation of these different measures of temperature would require further work. In contrast, *M. ambigua* are

clearly restricted to larger lowland rivers (large catchment area and baseflow volumes). Further, *M. ambigua* was more prevalent in regions with summer air temperatures >20°C and high inputs of solar radiation, whereas *P. grandiceps* appears to occupy primarily intermittent streams, including those with smaller catchments than those where *M. ambigua* was observed. These descriptions are derived directly from an examination of the partial plots for influential predictors (Fig. 1a–c), but (reassuringly) are largely consistent with the types of qualitative habitat descriptions in many texts (e.g. Merrick and



(c) *Philypnodon grandiceps*

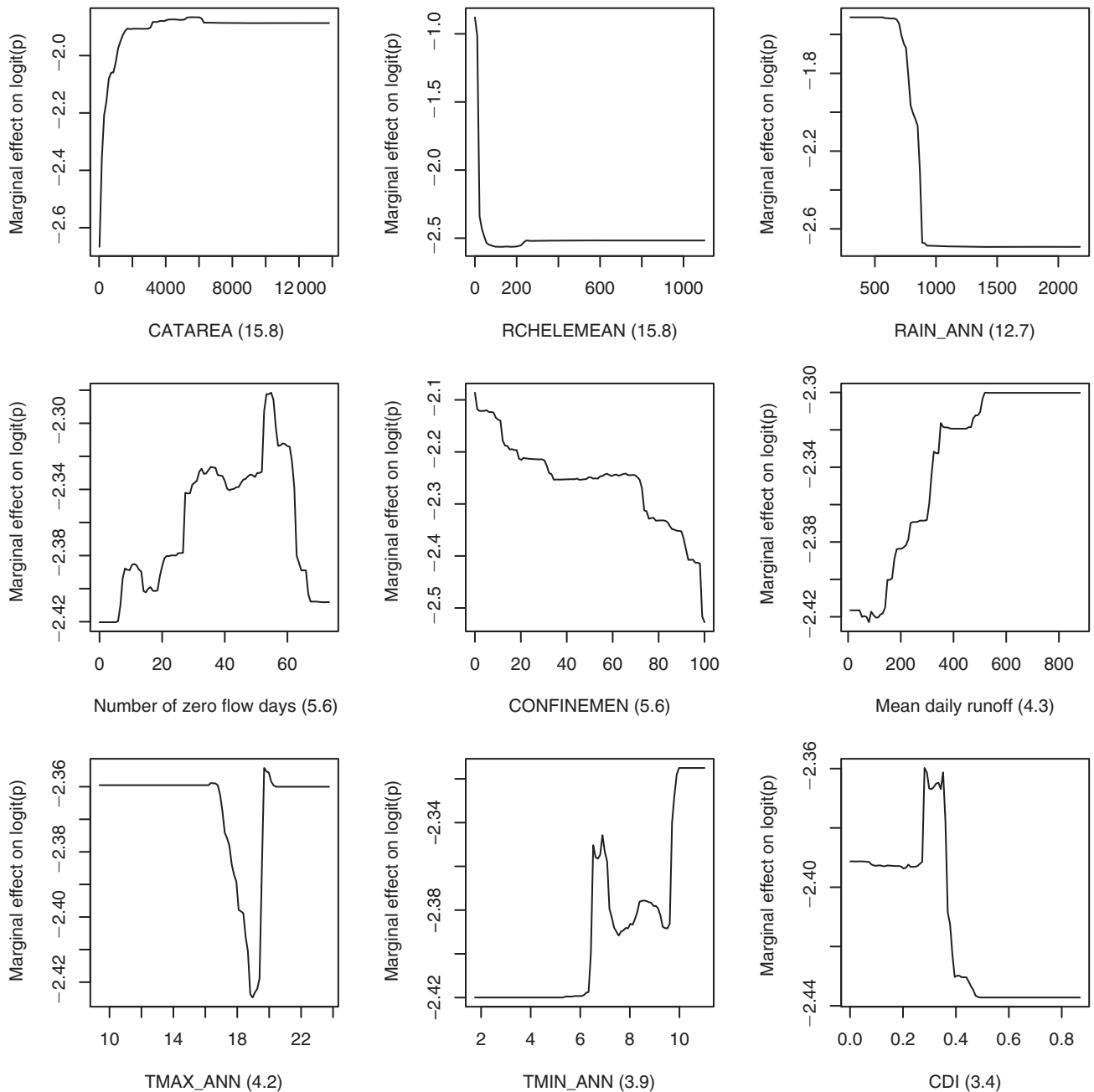


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Schmida 1984; Koehn and O'Connor 1990), but with additional quantitative support drawn from a data-driven assessment of important predictors. Occasionally, the partial plots identify inexplicable patterns, such as the sharp downward trend in occupancy for *P. grandiceps* at  $\sim 18^{\circ}\text{C}$  (average annual maximum temperature). These anomalies can reflect biases in the distribution of sampling locations, with respect to environmental predictors. Our approach was to remove or modify (by making monotonic) such anomalous relationships if they had a large influence on the model predictions (note that TMAX\_ANN had a

very low influence, Fig. 1c), and to focus on the more influential variables for inference. An alternative approach recently advocated by Elith *et al.* (2010) is to simplify tree complexity during the model-building process, which has the effect of smoothing the response functions.

*Predicted climate change-induced range shifts*

When combined with future climate scenarios, our models predicted potentially severe impacts of climate change for some species, including potential losses of populations from entire

(d) *Salmo trutta*

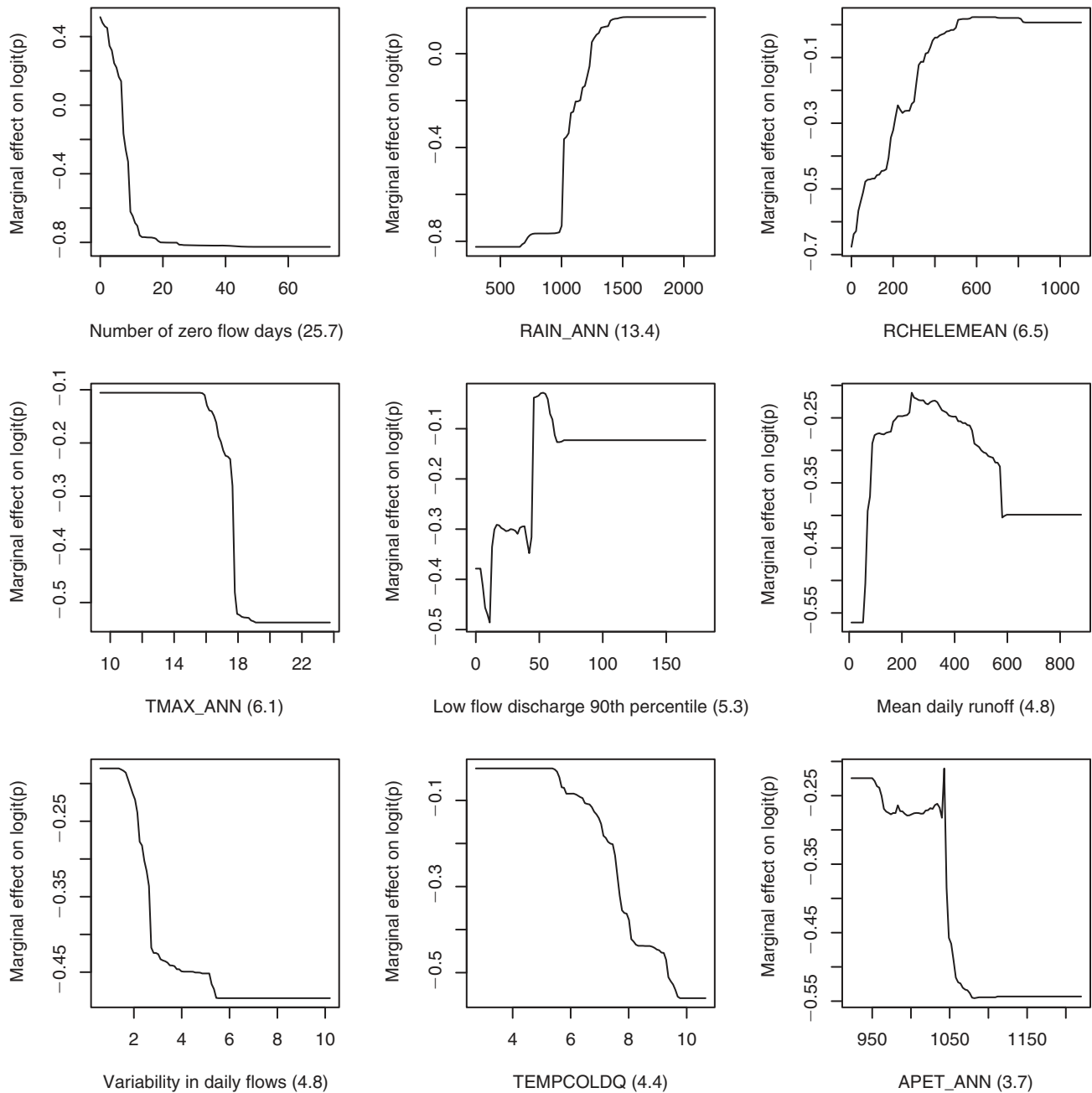


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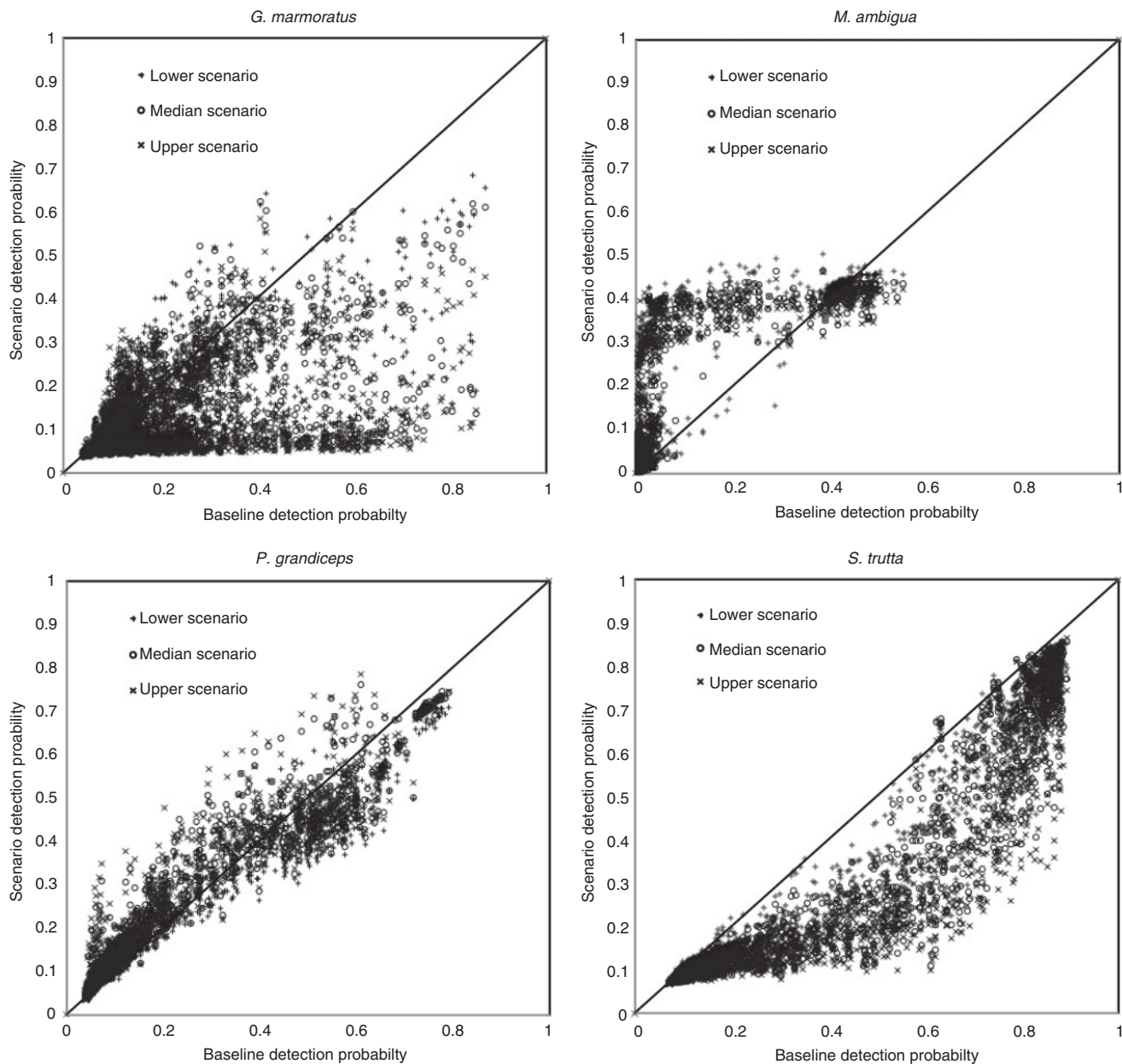
catchments. For example, the models predicted almost a complete loss of river blackfish (*G. marmoratus*) from some north-flowing drainages in Victoria, an area where the species has already undergone substantial range contractions and population declines as a result of anthropogenic disturbances (Trueman 2007). The predicted contractions for this species in terms of the types of habitats affected are also consistent with observed declines in South Australia (Dale McNeil, pers. comm.) and in parts of the Loddon and Goulburn catchments in north-central Victoria during recent drought (N. Bond, unpubl. data). At the

same time, however, whereas some range contractions have been consistent with recent drought impacts, the same cannot be said for range expansions, with as yet limited evidence to suggest that any of the species predicted to increase their range (such as *M. ambigua* and *G. holbrooki*) have done so, despite overall warmer (+0.8°C) and drier (-15% rainfall) conditions across Victoria over the past 10 years (Bond *et al.* 2008). On the one hand, such expansions may have occurred, but are yet to be documented. On the other hand, there is a suite of reasons why range expansions may not occur, or may occur more slowly than

**Table 4. Summary of distributional changes for each species under low, median and high climate-change scenarios expressed as  $\Sigma(\text{reach length} \times \text{Pr}(\text{occurrence}))$  and  $\Sigma(\text{reach length} \times \text{Pr}(\text{occurrence}))|\text{Pr}(\text{occupancy}) > 0.5$**

Maps are provided for species in bold

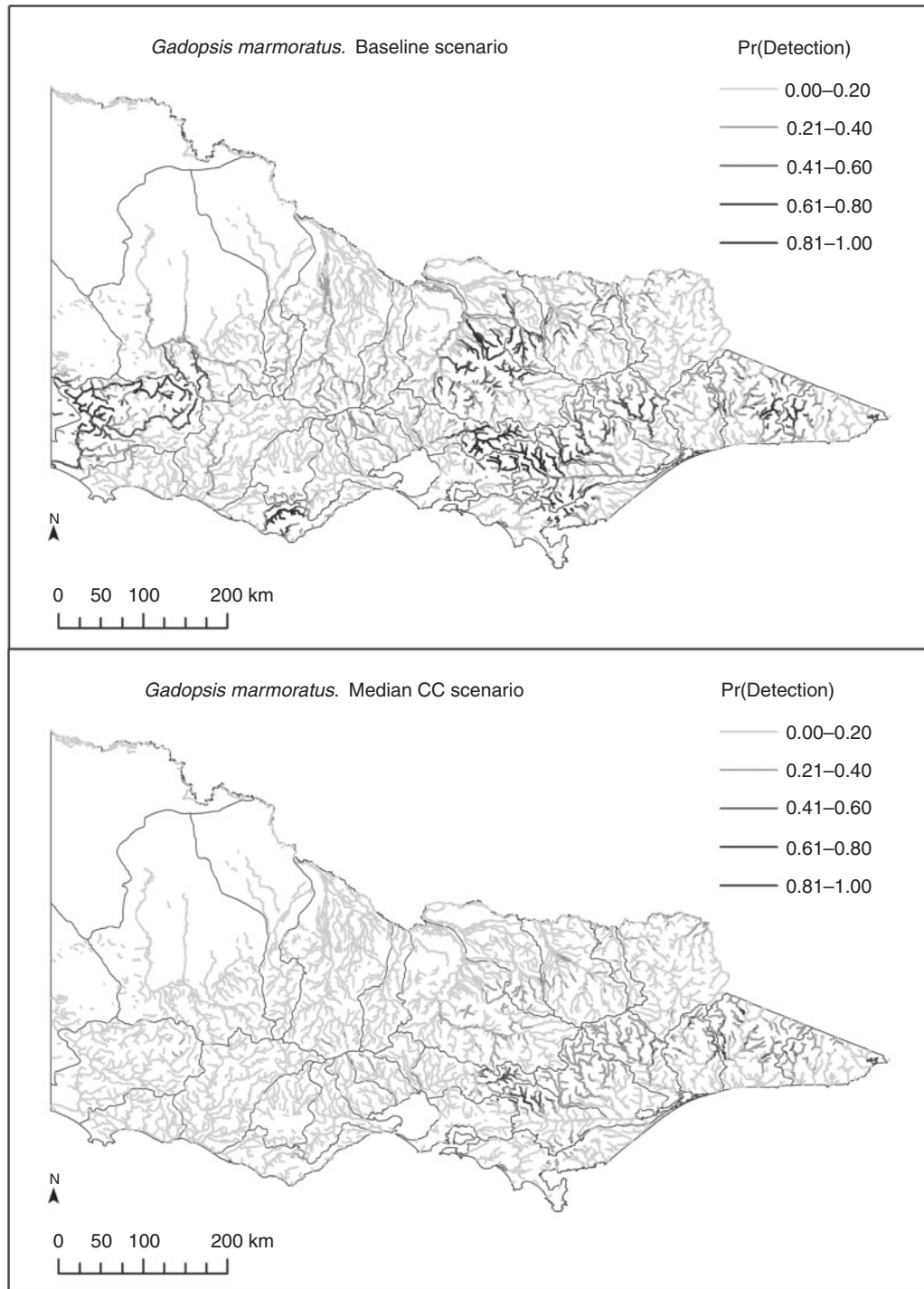
Species	Baseline			Low climate-change scenario			Median climate-change scenario			High climate-change scenario		
	Length $\times$ Pr(Occ)	Length $\times$ Pr(Occ)   Pr(Occ) > 0.5	%Change	Length $\times$ Pr(Occ)	Length $\times$ Pr(Occ)   Pr(Occ) > 0.5	%Change	Length $\times$ Pr(Occ)	Length $\times$ Pr(Occ)   Pr(Occ) > 0.5	%Change	Length $\times$ Pr(Occ)	Length $\times$ Pr(Occ)   Pr(Occ) > 0.5	%Change
<i>Acanthopagrus butcheri</i>	1570	895	4	1636	708	-21	1649	5	-28	1782	14	683
<i>Aldrichetta forsteri</i>	1534	607	36	2093	694	14	2512	64	34	2902	89	843
<i>Anguilla australis</i>	11 211	8638	-2	10 991	8132	-6	10 686	-5	-15	10 073	-10	6134
<i>Anguilla reinhardtii</i>	2558	756	-1	2535	504	-33	2685	5	-32	2717	6	502
<i>Atherinoma microstoma</i>	1181	336	52	1797	556	65	1980	68	65	2724	131	666
<i>Bidyanus bidyanus</i>	27	0	2	28	0	-	28	2	-	27	1	0
<i>Craterocephalus stercusmuscarum</i>	950	0	53	1456	0	-	1863	96	-	1811	91	0
<i>Gadopsis bispinosus</i>	2535	1184	-38	1571	189	-84	1524	-40	-89	1557	-39	166
<b><i>Gadopsis marmoratus</i></b>	<b>7298</b>	<b>1812</b>	<b>-36</b>	<b>4703</b>	<b>198</b>	<b>-89</b>	<b>4285</b>	<b>-41</b>	<b>-92</b>	<b>3855</b>	<b>-47</b>	<b>37</b>
<i>Galaxias brevipinnis</i>	2000	57	43	2870	60	4	3031	52	9	3001	50	100
<i>Galaxias fuscus</i>	26	0	0	26	0	-	26	0	-	26	0	0
<i>Galaxias maculatus</i>	7259	2027	7	7777	1909	-6	7973	10	-12	8183	13	1738
<i>Galaxias olidus</i>	6499	204	4	6748	236	16	6547	1	38	6279	-3	62
<i>Galaxias truttaeae</i>	1802	106	54	2776	86	-19	3328	85	-16	4279	137	138
<i>Galaxiella pusilla</i>	933	0	18	1102	0	-	1197	28	-	1266	36	0
<i>Geotria australis</i>	638	5	10	703	0	-100	795	25	-100	946	48	0
<i>Gobiomorphus australis</i>	1169	0	78	2082	0	-	2485	113	-	3292	182	0
<i>Hypseleotris</i> spp.	4102	360	24	5079	134	-63	5361	31	-36	5938	45	268
<i>Maccullochella macquariensis</i>	1728	35	25	2167	6	-82	2342	35	-76	2634	52	14
<i>Maccullochella peelii peelii</i>	1969	205	30	2562	105	-49	2680	36	-58	3236	64	153
<b><i>Macquaria ambigua</i></b>	<b>3895</b>	<b>121</b>	<b>27</b>	<b>4952</b>	<b>39</b>	<b>-68</b>	<b>5077</b>	<b>30</b>	<b>-100</b>	<b>5457</b>	<b>40</b>	<b>0</b>
<i>Macquaria australasica</i>	718	9	-10	645	0	-100	633	-12	-100	636	-11	0
<i>Macquaria colonorum</i>	1350	313	12	1517	270	-14	1698	26	-1	1822	35	288
<i>Macquaria novemaculeata</i>	1000	82	-12	877	7	-92	906	-9	-95	984	-2	0
<i>Melanotaenia fluviatilis</i>	606	0	40	849	0	-	888	47	-	1064	76	0
<i>Nannoperca australis</i>	2068	137	-17	1706	0	-100	1793	-13	-100	1737	-16	0
<i>Nannoperca obscura</i>	7170	1114	-11	6397	57	-95	6006	-16	-99	5641	-21	0
<i>Nannoperca variegata</i>	1931	113	62	3121	4	-97	3739	94	-100	5039	161	0
<b><i>Philypnodon grandiceps</i></b>	<b>787</b>	<b>132</b>	<b>-19</b>	<b>637</b>	<b>0</b>	<b>-100</b>	<b>736</b>	<b>-6</b>	<b>-100</b>	<b>841</b>	<b>7</b>	<b>0</b>
<i>Protooctes maraena</i>	8244	3616	-1	8179	1778	-51	8997	9	-33	9120	11	2710
<i>Pseudaphritis urvillii</i>	1216	28	-14	1040	0	-100	1029	-15	-100	1133	-7	0
<i>Retroptima senoni</i>	4917	747	7	5274	726	-3	5457	11	2	5514	12	715
<i>Tetractenos glaber</i>	9970	1486	5	10510	1027	-31	10425	5	-49	10212	2	375
<i>Carassius auratus</i>	787	126	46	1150	162	28	1472	87	16	1515	92	101
<i>Cyprinus carpio</i>	5532	169	28	7078	204	21	7838	42	27	8237	49	149
<i>Gambusia holbrooki</i>	7670	3755	2	7803	2265	-40	8019	5	-39	7839	2	1652
<i>Misgurnus anguillicaudatus</i>	7316	939	23	8971	1305	39	10252	40	96	11215	53	2753
<i>Oncorhynchus mykiss</i>	1258	61	62	2033	62	1	2479	97	18	2976	137	62
<i>Percia fluviatilis</i>	3166	890	-32	2158	33	-96	2166	-32	-94	2112	-33	19
<i>Rutilus rutilus</i>	8280	884	1	8374	518	-41	8669	5	-35	8510	3	278
<i>Salmo trutta</i>	890	113	-13	772	5	-96	812	-9	-99	838	-6	3
<b><i>Salmo trutta</i></b>	<b>11 545</b>	<b>6522</b>	<b>-22</b>	<b>9006</b>	<b>4235</b>	<b>-35</b>	<b>8397</b>	<b>-27</b>	<b>-44</b>	<b>7801</b>	<b>-32</b>	<b>3249</b>
<i>Tinca tinca</i>	1760	339	-15	1503	183	-46	1450	-18	-62	1396	-21	77



**Fig. 2.** Scatterplots of baseline-occupancy values against those under low, median and high climate-change scenarios for the four species discussed. These plots are based on results for a random subset ( $n = 2000$ ) of the 16 000 reaches for which predictions were generated to allow points from each scenario to be depicted.

species are extirpated, including physical and biological constraints on dispersal (e.g. barriers, sedentary behaviour), and the influence of important local drivers such as physical habitat features, short-term hydrologic events, food availability or biotic interactions, which may constrain species expansions – many of the factors that have led some authors to caution on the use of SDMs in predicting range shifts (Guisan and Thuiller 2005; Sinclair *et al.* 2010). Our view is that predictions arising from these models are a useful step forward in framing discussions about such limitations, and hence are a useful tool in advancing our general understanding of climate-change impacts, even where the initial model predictions may be

questioned – a conclusion shared by Araújo *et al.* (2005). This can also lead to the identification of critical knowledge and data gaps. For example, an obvious shortcoming identified in the present study for which a statistical work-around was required was the lack of spatially distributed information on both current and potential future hydrologic characteristics of rivers, a gap that reflects the difficulty in modelling hydrology at high spatial and temporal resolutions, particularly in more intermittent systems (Smakhtin 2001). This data gap is likely to continue to hamper our ability to refine predictions of ecological change in response to shifting environmental conditions in ungauged catchments.

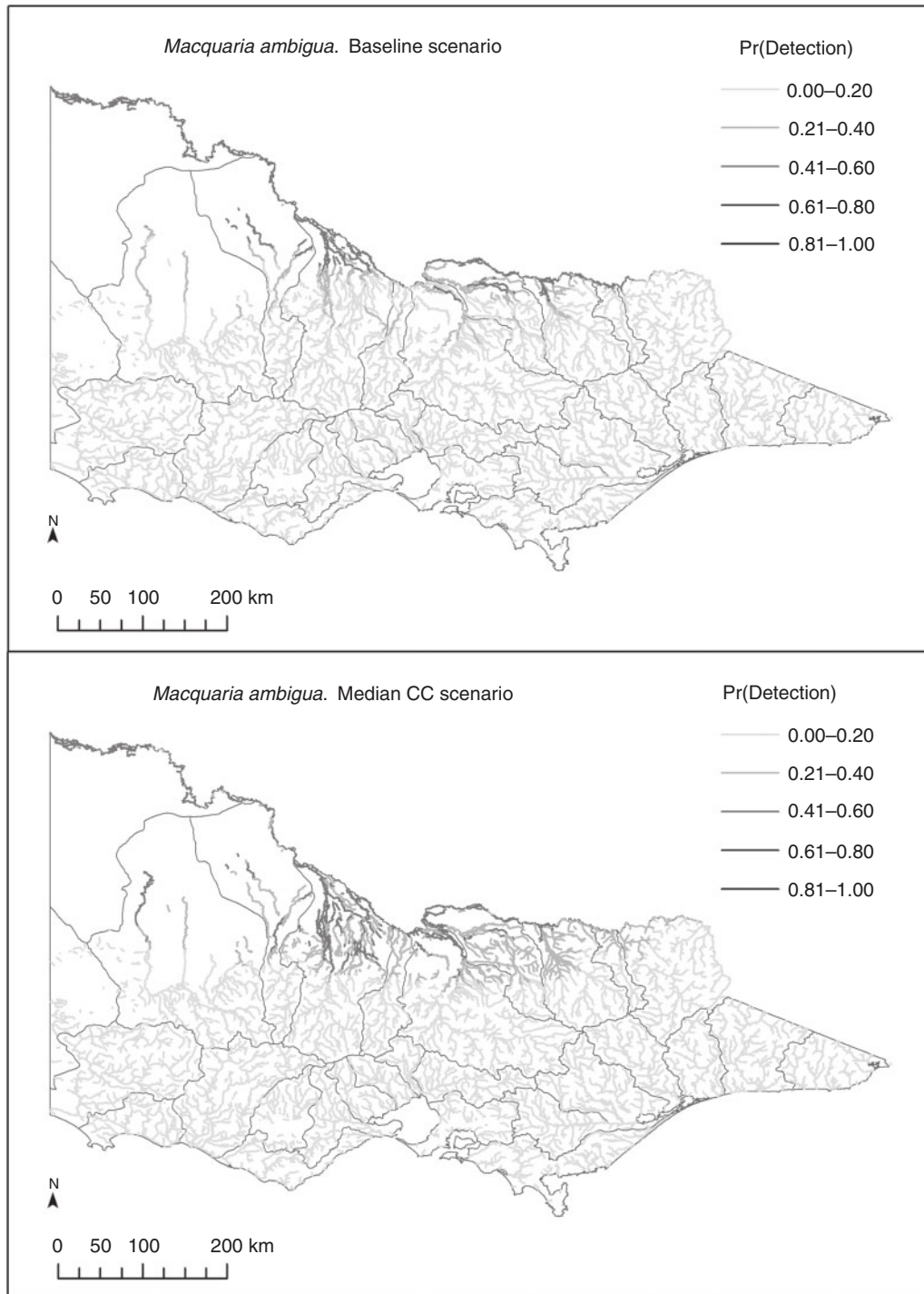


**Figs 3.** Maps showing predicted historic (baseline) and median climate change-scenario predictions for (a) *Gadopsis marmoratus*, (b) *Macquaria ambigua*, (c) *Philypnodon grandiceps* and (d) *Salmo trutta*.

*Uncertainty in range-shift forecasts*

We attempted to capture some indication of the uncertainty in the model predictions for some species, although these are expressed here only in tabular form (Table 5), and are restricted to uncertainty associated with the SDMs themselves under each

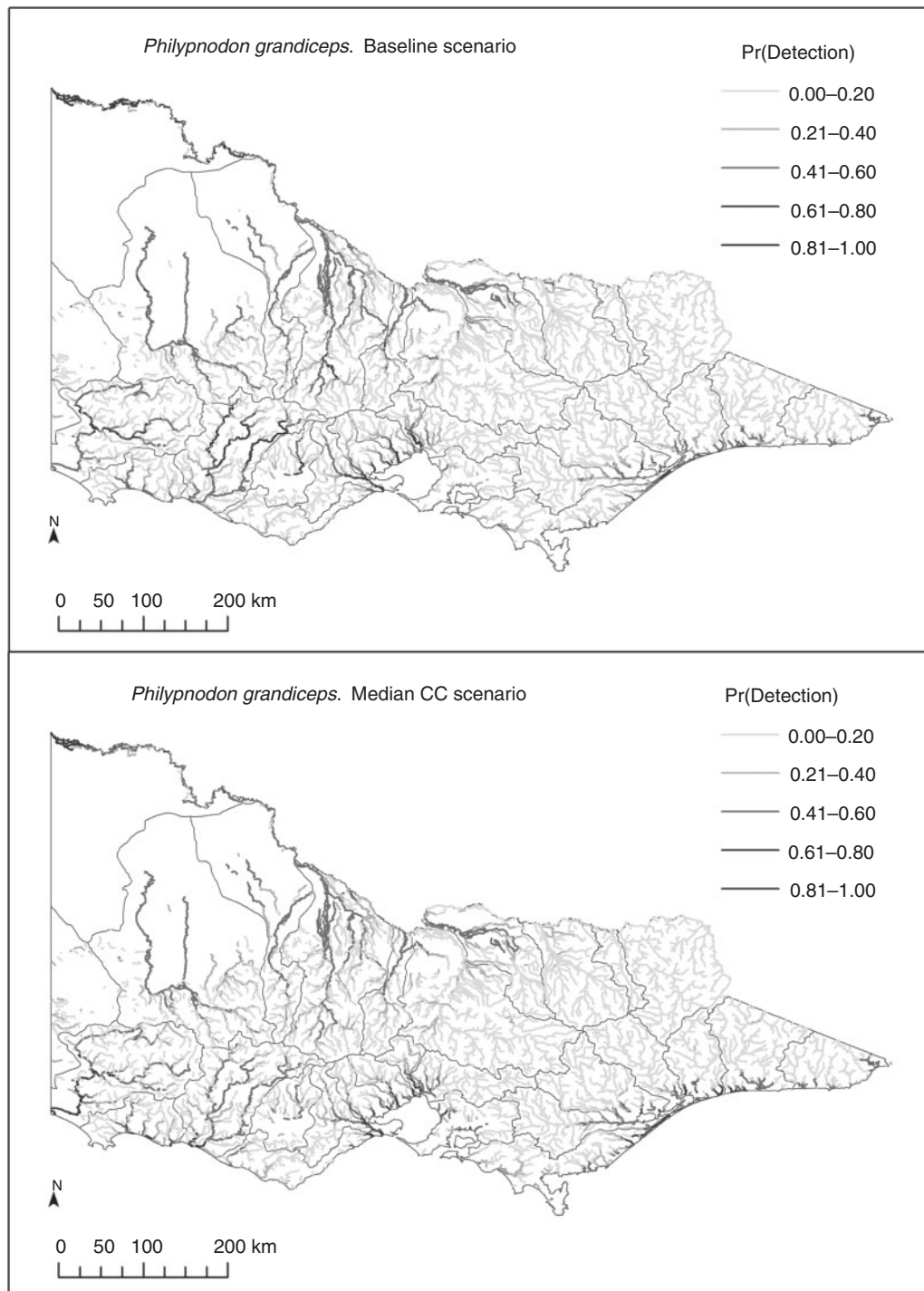
of the modelled climate scenarios. Additional uncertainty in global circulation models (GCMs) and future CO<sub>2</sub> concentrations (expressed here as different scenarios) also adds substantially to uncertainty in future predictions when expressed quantitatively alongside uncertainty in the species models



**Figs 3.** (Continued).

(Lyons *et al.* 2010). Differences between our scenarios support the fact that even if species distributions can be modelled well, there is still much uncertainty in how species ranges may change because of uncertainty about how the climate will change. There is also a host of other sources of uncertainty that we have not touched on, including the extent to which SDMs can be used to

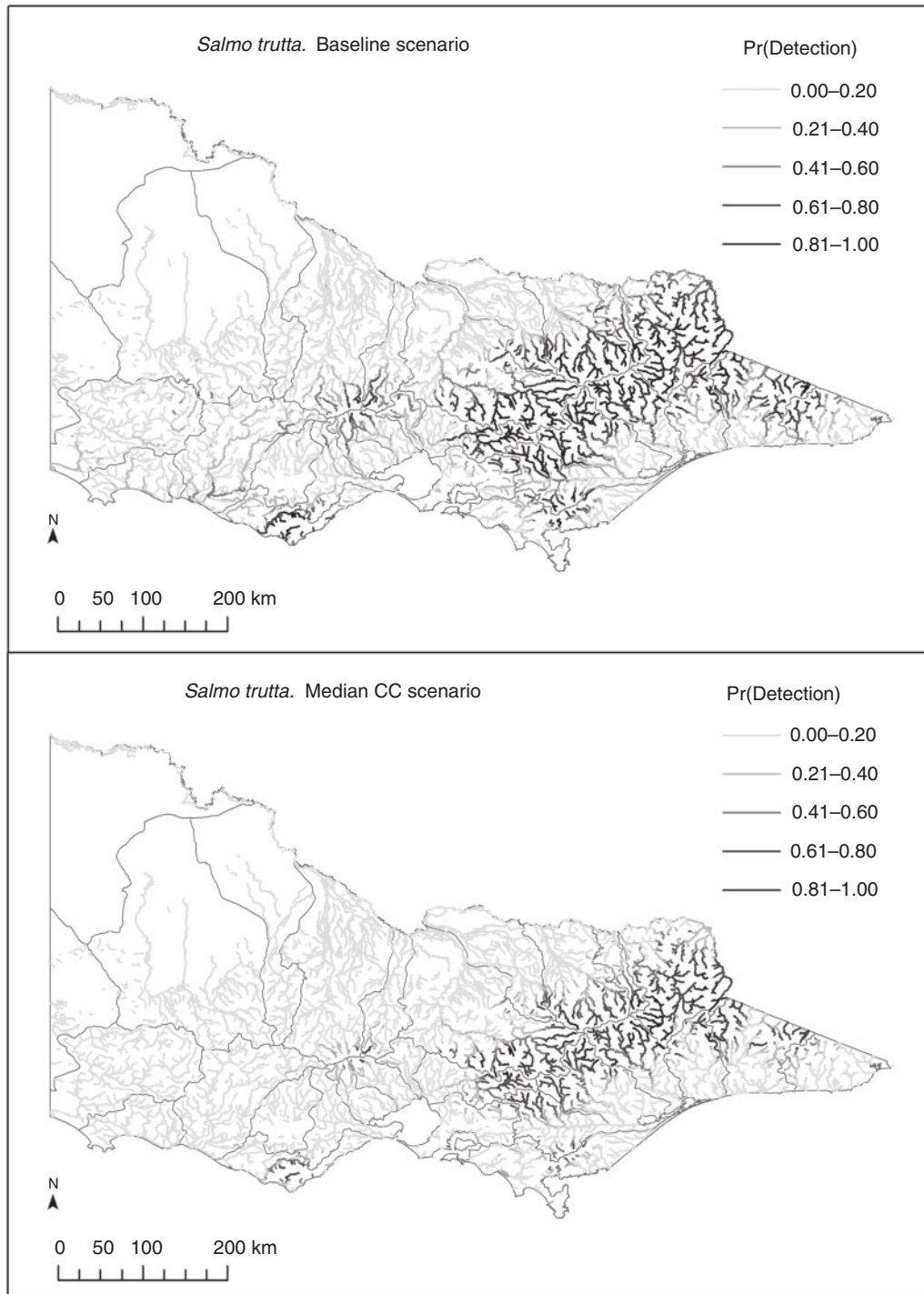
extrapolate to novel climates (e.g. see Williams and Jackson 2007; Elith *et al.* 2010), and the way that hydrologic characteristics may change as a result of altered ground–surface water interactions under a drier climate – again something that is not captured in our efforts to model hydrology. Thus, although incorporating uncertainty in predictions based on the capacity of



Figs 3. (Continued).

the models to predict historic distributions is important in demonstrating their validity, this aspect of uncertainty is just one of those that needs to be considered when extrapolating to the future (Elith and Leathwick 2009). SDMs can also be highly sensitive to species prevalence in the datasets used to derive the models, both in terms of their predictive performance (Olden

et al. 2002), and also in the extent to which existing distributions (the realised niche) may influence predictions of future range (Dormann 2007). In the present study, there were several now relatively rare, but historically more common and widespread taxa for which models of the realised niche based on contemporary data probably underestimate the historical realised niche.



**Figs 3.** (Continued).

Examples include *Bidyanus bidyanus*, *Galaxias fuscus*, *Maccullochella macquariensis*, *Macquaria australasica* and *Prototroctes maraena*. For the reasons discussed above, we would expect greater uncertainties in the predicted impacts of climate shifts on these rare species relative to those that are more common.

#### *Pros and cons of using SDMs to predict range shifts*

Much of the discussion of possible climate-change impacts on species distributions in Australia has been based on relatively simple qualitative assessments of existing observational and experimental data (e.g. Morrongiello *et al.* 2011; Booth *et al.* 2011). One strength of these approaches is the ability to



**Table 5. Summary of confidence intervals expressed as the 50th, 2.5th (lower) and 97.5th (upper) predictions based on boot-strap estimates for a subset of species**

Parameter	<i>Gadopsis marmoratus</i>			<i>Macquaria ambigua</i>			<i>Salmo trutta</i>			<i>Philypnodon grandiceps</i>		
	50th	2.5th	97.5th	50th	2.5th	97.5th	50th	2.5th	97.5th	50th	2.5th	97.5th
Baseline	7298	6954	8330	3895	3527	4693	11545	10786	11537	8244	8752	9993
Median climate change	4703	3701	4981	4952	5013	6276	6522	7673	8762	8179	9465	11495
Difference	-2595	-3740	-2275	1057	1486	2524	-3066	-4130	-2348	65	-10	3849

incorporate novel aspects of species biology that may be important in determining climate-change responses, but which may be difficult to infer from SDMs because of their specific data requirements and application at large scales. At the same time, generic statements of possible impacts are also much less well suited to producing spatially explicit predictions that can feed into decisions about how to prioritise restoration and conservation programs in the face of climate change. There has been much debate about the relative merits of SDMs in predicting climate change-induced range shifts. For example, numerous authors point to the potential pitfalls associated with the exclusion of species interactions, dispersal constraints and the potential role of evolution (adaptation capacity) in determining how species will respond to climate change (e.g. Davis *et al.* 1998; Sinclair *et al.* 2010). At the same time, there is a pressing need to begin developing quantitative predictions, not least to enable the strengths and weaknesses of different modelling approaches to be evaluated – either explicitly through field validation or by comparing the results derived from qualitatively different modelling approaches (e.g. Elith *et al.* 2010).

### Summary and conclusions

Overall, our models predicted the combined impacts of altered temperature and hydrologic regimes arising from climate change to cause marked shifts in the distribution of many freshwater fish species. Primary axes of response were shifts upward along altitudinal gradients and shifts southward (including both range expansions and contractions) in response to climate warming, and the loss of species from increasingly intermittent and ephemeral waterways, which overall were predicted to become more common. Similar climate-change impacts have been predicted in other parts of the world (e.g. Chu *et al.* 2005; Lyons *et al.* 2010). An obvious next step from a management perspective is to combine the model results for these and other species, and to apply conservation-planning approaches to identify river reaches that maximise species-occupancy patterns under both historical and potential future climate regimes. Results from such an analysis would support efforts to prioritise investment in restoration and protection strategies, and also guard against investing in reaches that may fail to support currently occurring species in the future.

Although the predictions from these models remain just that, we contend that, together with the additional information on species responses to environmental gradients, they represent an important step in gaining a more complete understanding of how climate-change impacts may play out in the long term, and an essential step in developing appropriate response strategies.

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