

RESEARCH ARTICLE

Scoping the suitability of water-tolerant species of trees for swamp restorations across Australia and its Great Barrier Reef catchment

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Wetlands are vital for humanity and include some of the most productive, diverse, and service-rich ecosystems in the world. Services provided include food production (e.g., fish, birds, and vegetables), protection from flooding and storm surge inundation, provision of clean water and climate stability, and timber resources for construction. Despite these benefits, vast areas of wetlands have been drained across the globe, including in Australia. With growing awareness of the value of wetlands, there is increasing push to restore wetlands and the values they support, such as carbon sequestration. A major challenge for restoration practitioners is to identify what land parcels could be restored and what species they could support. This study scoped the environmental suitability of 125 water-tolerant species of trees across Australia, using random forest modeling to relate records observed within the Atlas of Living Australia database with spatial datasets of soil and climatic characteristics and water observations from space. Of the 125 species of trees examined, 105 species were modeled with excellent performance. Models were then used to predict tree suitability for existing wetlands nationally, as well as across potentially suitable restoration sites within the Great Barrier Reef catchment, given the strong push for wetland restoration to improve water quality. Within the Great Barrier Reef catchment, over 2200 land parcels covering over 20,000 ha were identified as being potentially suitable for restoration with diverse tree swamps. This study allows restoration practitioners to identify where swamp restoration could occur and potentially suitable trees for planting at those locations.

Key words: diverse planting, ecosystem services, *Melaleuca*, regeneration, tree species distribution, wetlands

Implications for Practice

- Most wetlands across Australia were considered suitable for multiple species of water-tolerant trees, with the southeastern coastal regions supporting the highest diversity of up to 45 species.
- Restoration practitioners should use the predictions made here, spanning 105 water-tolerant species of trees, to inform species selection in the restoration of floodplains and wetlands, as diverse and locally appropriate species enhance restoration success, resilience, and ecosystem service provision.
- Within Australia's Great Barrier Reef catchment, over 2200 potential wetland restoration locations were identified on marginal agricultural land, with almost all being suitable for supporting multiple water-tolerant tree species, providing practitioners with large suite of potential restoration sites and guidance on suitable species of trees for each site.

and climate stability, and timber resources for construction (Millennium Ecosystem Assessment 2005; Mitsch et al. 2015). Despite their benefit, wetlands have faced substantial drainage because of urban and agricultural development, with an estimated 87% decline in natural wetland extent since preindustrial times (Davidson 2014; Antonio Ballut-Dajud et al. 2022). Of those that remain, approximately 89% of wetlands globally are unprotected and often continue to be impacted by water abstraction, eutrophication, grazing, and climate change (Reis et al. 2017; Ostrowski et al. 2021). Wetlands in Australia also follow the global pattern of decline, with swamps being those most extensively drained (Davis & Friend 1999; Finlayson &

Author contributions: ADC conceptualized the idea, carried out all analyses, wrote and edited the entire manuscript.

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Introduction

Wetlands are vital for humanity and include some of the most productive, diverse, and service-rich ecosystems in the world (Gardner & Finlayson 2018), providing benefits such as food production (e.g., fish, birds, and vegetables), protection from flooding and storm surge inundation, provision of clean water

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doi: 10.1111/rec.14375
Supporting information at:
<http://onlinelibrary.wiley.com/doi/10.1111/rec.14375/supinfo>

Rea 1999). This extends to Australia's Great Barrier Reef (GBR) catchment where coastal wetlands provide critical habitat to migratory reef fish species and treat catchment run-off to the reef (Adame et al. 2019; Canning & Waltham 2021). Halting and reversing this decline will be necessary if we are to progress in achieving the United Nations Sustainable Development Goals, particularly the provision of clean water, sustainable food and resource security, climate security, and biodiversity conservation (Gardner & Finlayson 2018; United Nations 2020).

Payment for ecosystem service (PES) schemes provide an avenue for fund wetlands restoration as they make payments to those carrying out ecosystem restorations that provide desired benefits, such as water quality improvements, carbon sequestration, flood regulation, water security, or habitat for wild resources (Table 1; Farley & Costanza 2010; Salzman et al. 2018; Canning et al. 2021). Of national interest, the Australian Government recently released a statutory method for assessing and awarding carbon trading credits, under the Emissions Reduction Fund, for "blue carbon" projects focused on restoring coastal wetlands, such as mangrove forests and coastal tree swamps (Lovelock et al. 2023). Within Australia's GBR catchment, the Reef Credit Scheme is emerging, which aims to make payments for actions, such as wetland restorations, that deliver water quality benefits to the downstream GBR (Eco-Markets Australia 2020). In the GBR's Tully-Murray catchment, a PES scheme also financially supported wetland restorations for their hydrological benefits (Canning et al. 2023). More recently, the Australian Federal government is also developing the Nature Repair Market, set to be a world-first legislated, national, voluntary biodiversity market Nature Repair Act 2023 (Australian Government 2023). While payments from single PES schemes may not always render a wetland restoration financially viable, increasing interest in bundling payments from multiple schemes to reward the provision of multiple services may improve financial viability (Table 1; Canning et al. 2021; Robertson et al. 2014; Costanza et al. 2021).

Realizing the delivery of desired ecosystem services will be dependent on the success of restorations (Table 1), which can be bolstered by ensuring plantations are composed of diverse, locally suitable taxa, rather than monocultures (King et al. 2023; Veryard et al. 2023). Compared to forest monocultures, diverse forest plantations exhibit lower susceptibility to drought, fire, specialist pests and pathogens (Ennos 2015; Roberts et al. 2020), and storms, have greater provisioning of biomass, carbon sequestration (Hulvey et al. 2013; Chen et al. 2020), biodiversity conservation, soil protection, cultural services, and water security (Lamb 2018; Messier et al. 2022). Yet, restoration practitioners frequently overlook the importance of choosing suitable planting materials, with many communities limited by the availability of practical resources and guidance (Alexander et al. 2011; Perring et al. 2015; Sabogal et al. 2015). Improving knowledge around the distributions and habitat suitability of plant species used in restoration can, therefore, allow better decision-making in restoration planning and maximize the success of restored plants thriving (Miller et al. 2017; Fremout et al. 2022).

To help fill the knowledge gaps around habitat suitability of plants used in Australian wetland and floodplain restorations, this study aimed to model and predict the habitat suitability of water-tolerant species of trees across the entire extent of Australia. As a case study, the models were then applied to identify taxa potentially suitable for palustrine wetland restoration across the GBR catchment, given strong policy direction for large-scale wetlands restoration under the Reef 2050 Long-Term Sustainability Plan (Australian Government 2021).

Methods

Species Data

A list of water-tolerant species of trees, subspecies, and hybrids, that are native to Australian tree swamps, was compiled from the AusTraits database (Falster et al. 2021), comprising any tree with a water-logging tolerance greater than 1 month. For all species identified ($N = 125$; Table S1), all observations (including location) from across Australia were extracted from the Atlas of Living Australia (ALA), yielding 431,618 records. ALA is a large database that collates sightings of species from a wide range of organizations and contributors (Belbin & Williams 2016). Given the likely differences in survey method and intensity among observers (Canning & Waltham 2021), which could reduce the reliability of abundance data, this analysis only examined the presence of a species, rather than the abundance. Furthermore, surveys could not be used to indicate species absence. Nonetheless, the ALA dataset represents the most comprehensive observation dataset over the entire spatial extent and is, therefore, the best data available for this analysis.

Environmental Variables

At all observation locations, statistics for 19 climate variables were extracted from the WorldClim 2 database (Fick & Hijmans 2017), one metric of water inundation frequency from the Water Observation from Space (WoFS) database (Mueller et al. 2016), and 12 soil variables from the Soil and Landscape Grid of Australia (SLGA; Table 1; Viscarra Rossel et al. 2015; Grundy et al. 2015).

WorldClim 2 provides 19 climate metrics for baseline conditions (Table 2), using long-term average between 1970 and 2000, from between 9000 and 60,000 weather stations, that were then interpolated to provide global coverage at 1-km² resolutions (Fick & Hijmans 2017). Globally, the cross-validated correlations on baseline data were 0.86 for precipitation, 0.76 for wind speed, and ≥ 0.99 for temperature and humidity, though there is regional variation between models and parameters (Fick & Hijmans 2017). By using WorldClim, not only is it possible to model against recent climatic conditions but it is also possible to use the same models to predict suitability under future climate scenarios.

The WoFS database provides estimates of water coverage frequency using multi-decadal Landsat satellite imagery (1987–2014) at ~ 25 m resolution across Australia. For each image that could be clearly seen (i.e., not affected by clouds or shadows),

Table 1. The ecosystem services often provided by palustrine wetlands and examples of their benefits within Australia (Millennium Ecosystem Assessment 2005; Mitsch et al. 2015).

Ecosystem Service	Examples Within Australia
Fisheries support	Meynecke et al. (2008) found that the presence and connectivity of coastal wetlands was well correlated to the catch-per-unit-effort of Barramundi (<i>Lates calcarifer</i>) along the Queensland coastline. Hart et al. (2018) observed increased productivity of School Prawn (<i>Metapenaeus macleaya</i>) in the recovering Hexham wetland within the New South Wales Hunter River catchment.
Peat production for fuel and horticulture	Wild Sphagnum moss is harvested by hand as a soil amendment and growing media in horticulture, given its high-water retention, nutrient availability, and benefits to soil structure (Whinam et al. 2003).
Furbearer and other animal harvesting	In northern Australia, indigenous people have harvested crocodiles and their eggs for the use and commercial trade of leather (Corey et al. 2018).
Timber production	Two examples of harvesting trees for timber include river red gums (<i>Eucalyptus camaldulensis</i>) in New South Wales and various mangroves in the Torres Strait Islands (Weir et al. 2013; Duke et al. 2015).
Direct food production	Indigenous people across the Northern Territory frequently harvest bees, crocodiles, magpie geese, swamp buffalo, crabs, snakes, and turtles from wetlands (Gorman et al. 2010). Waterfowl, such as ducks, are recreationally harvested via hunting in several states and territories where it is permitted (Moloney et al. 2022).
Water quality improvement	Wetlands have been developed across Australia to improve water quality from stormwaters (Greenway 2017), wastewaters (Alatriza Gongora et al. 2021), and agricultural run-off (Adame et al. 2019; Wallace & Waltham 2021).
River flooding mitigation	In the Tully catchment (Australia's wettest catchment), constructed wetlands have acted as sumps to regulate downstream flows and reduce crop loss to flooding (Karim et al. 2012, 2014). Early work has begun investigation how wetlands can be incorporated into urban areas as a flood mitigation strategy, with Geelong as a case study (Li et al. 2020).
Protection of coastlines from tsunamis, cyclones, and other coastal storm surges	Coastal wetlands have been shown to significantly reduce storm damage, with a study in 2020 estimating that AU\$29.6 billion of damage has been averted from 54 cyclones across Australia between 1967 and 2016. This equates to an average damage saving of approximately \$4203/ha/year of wetland (Mulder et al. 2020).
Carbon sequestration	Estimates carbon storage (above and below ground) in swamps across Australia include 375 t C/ha for Coastal Swamp Oak Forests (Kelleway et al. 2021), 805–811 t C/ha in the New South Wales Temperate Highland Peat Swamps on Sandstone (Cowley & Fryirs 2020), and between 210 and 381 t C/ha in Melaleuca forests across Australia (Tran & Dargusch 2016; Adame et al. 2020).
Habitat for rare and endangered species	Across Queensland's Great Barrier Reef catchment, 500–600 vertebrate taxa have been recorded in coastal tree swamps (Canning & Waltham 2021). Examples of rare and endangered species in Australian swamps include the Blue Mountains water skink in montane southeastern Australia (Gorissen et al. 2017), the Western swamp tortoise near Perth, Western Australia, and the Leadbeater's possum in Victoria (Eyre et al. 2022).
Landscape aesthetics	A 2009 assessment of property values near wetlands in north Perth, Western Australia, estimated that a randomly selected 20 ha wetland with uniform density housing around it, yielded a cumulative premium of AU\$140 million (2009) across surrounding properties (Tapsuwan et al. 2009).
Sites for human relaxation	Users of the Swan Canning Riverpark in Perth, Western Australia, have referred to it as providing a "sense of freedom," space for both passive and active recreation and for generally relaxing (Carter 2015).
Ecology education	Wetland education centers exist across Australia, with almost half receiving more than 30,000 visitors per year, largely from local individuals and school groups (Finlayson 2018).
Sustenance of human cultures	Aboriginal management of the Kakadu National Park, Northern Territory, allows for cultural knowledge and practices to be passed on to future generations (McGregor et al. 2010).
Ecotourism, bird-watching	The conservation of The Mareeba Wetlands, Queensland, has been successfully funded through eco-tourism and bird-watching activities (Nevard & Nevard 2015).
Wetland functions such as hydric soil development, primary productivity, serving as chemical sources, sinks, and transformers, and water storage	The Temperate Highland Peat Swamps on Sandstone, New South Wales, act as water storage reservoirs for headwater catchments and reduce contaminants for downstream catchments (Cowley et al. 2018).

Table 2. Description of the climate variables sourced from Fick and Hijmans (2017), water permanency estimate from Mueller et al. (2016), and the soil variables sourced from Grundy et al. (2015) across Australia.

Variable Group	Variable	Description
Climate variables	PrecColdQ (mm)	Precipitation of coldest quarter
	PrecWarmQ (mm)	Precipitation of warmest quarter
	PrecDryQ (mm)	Precipitation of driest quarter
	PrecWetQ (mm)	Precipitation of wettest quarter
	PrecCOV	Precipitation seasonality (coefficient of variation)
	PrecDryMonth (mm)	Precipitation of driest month
	PrecWetMonth (mm)	Precipitation of wettest month
	AnnPrec (mm)	Annual precipitation
	MTempColdQ (°C)	Mean temperature of coldest quarter
	MTempWarmQ (°C)	Mean temperature of warmest quarter
	MTempDryQ (°C)	Mean temperature of driest quarter
	MTempWetQ (°C)	Mean temperature of wettest quarter
	TempRange (°C)	Temperature annual range (MaxTWarmMonth – MinTColdMonth)
	MinTColdMonth (°C)	Min temperature of coldest month
	MaxTWarmMonth (°C)	Max temperature of warmest month
	TempSD	Temperature seasonality (standard deviation × 100)
	Isothermality	Isothermality (MeanDiurnTRange/TempRange) (× 100)
MeanDiurnTRange	Mean diurnal range (mean of monthly [max temp – min temp])	
AnnMeanTemp (°C)	Annual mean temperature	
Water variable	WOFS	The frequency of water observation from space between 1987 and 2014
Soil variables	BD (g/cm ³)	Bulk density of the whole soil (including coarse fragments) in mass per unit volume by a method equivalent to the core method
	OC (%)	Mass fraction of carbon by weight in the <2 mm soil material as determined by dry combustion at 900°C
	Clay (%)	<2 µm mass fraction of the <2 mm soil material determined using the pipette method
	Silt (%)	2–20 µm mass fraction of the <2 mm soil material determined using the pipette method
	Sand (%)	20 µm to 2 mm mass fraction of the <2 mm soil material determined using the pipette method
	pH (CaCl ₂)	pH of 1:5 soil/0.01 M calcium chloride extract
	AWC (%)	Available water capacity computed for each of the specified depth increments
	TN (%)	Mass fraction of total nitrogen in the soil by weight
	TP (%)	Mass fraction of total phosphorus in the soil by weight
	ECEC (meq/100 g)	Cations extracted using barium chloride (BaCl ₂) plus exchangeable H + Al
DoR (m)	Depth to hard rock. Depth is inclusive of all regolith.	

the presence of water was detected using a decision tree classifier algorithm with an overall classification accuracy assessment of 97% and described in Mueller et al. (2016). For this study, water inundation frequency was used as environmental variable, calculated as the proportion of images at a given location where water was detected over the entire database period.

The SLGA provides Australia-wide coverage of 11 continuous soil attributes at 0.008 km² (90 × 90 m) resolutions (Table 2), across regolith depths between 0 and 2 m (Grundy et al. 2015; Viscarra Rossel et al. 2015), with predictions conforming to the GlobalSoilMap specifications (Arrouays et al. 2014). For this study, only those for regolith depths between 30 and 60 cm were extracted. The SLGA three-dimensional soil maps were derived from spatial models informed by 281,202 soil profiles in national soil visible-near infrared database (NSVNIRD) and 1315 sites from the NSVNIRD (Viscarra Rossel et al. 2015). Across all attributes mapped, models between 30% and 70% of their total variation, with near-surface estimates typically having greater accuracy with more training data (Viscarra Rossel et al. 2015).

Random Forest Models

Random forests are a machine learning method that uses a collection of regression trees, whereby each tree is fitted to a bootstrapped sample (with replacement) and then validated on the out-of-bag sample (Breiman 2001). Random forest predictions are the average of the predictions of each tree. Regression trees, and consequently random forests, work by partitioning observations at splits of predictors that minimize the sum of squares error. They have a high level of flexibility, can handle nonlinear relationships and complex interactions, and do not require cross-validation or a separate testing dataset as each tree is constructed using a different bootstrap sample (Cutler et al. 2007; Hastie et al. 2009; Ellis et al. 2012).

Random Forests were used to model the probability of occurrence for all taxa compiled based on the climatic, water, and soil characteristics (Table 2), relative to a random background, using the “randomForest” function (trees = 500) from the randomForest package in R (Liaw & Wiener 2002; R Core Team 2016). As the occurrence data used was presence-only, and could not indicate absence, an equal number of random background

locations were used instead of absences, to achieve a balanced presence-background predictive model. Only taxa with at least 30 observation records were modeled. Model performance was assessed by calculating the area under the receiver operating curve (AUC-ROC), calculated using the “auc” function from the pROC package (Robin et al. 2011). According to Šimundić (2009), AUC-ROC between 0.7 and 0.8 indicates good diagnostic accuracy, while 0.8–0.9 indicates very good, and 0.9–1.0 indicates excellent accuracy.

The “importance” function, from the randomForest package (Liaw & Wiener 2002), was then used to identify the globally important variables, which measure the decrease in Gini index from splitting on each variable, averaged over all trees. The importance of each variable in a random forest model reflects how much the model's accuracy improves when the data is split based on that variable. Specifically, the “importance” function measures the decrease in the Gini index, which is a metric of node impurity, resulting from splits on each variable. A larger decrease in the Gini index indicates a higher importance, suggesting that the variable plays a significant role in making accurate predictions. This measure is averaged over all the trees in the forest to provide a global assessment of each variable's importance. Consequently, variables with higher importance scores contribute more substantially to the model's predictive power.

Predicting Tree Suitability National and Within the GBR Catchment

Bolstering Diversity Within Australia's Extant Wetlands. To support conservation and restoration efforts within Australia's existing wetlands, for each mapped swamp, the well-performing random forest models (AUC-ROC > 0.7) were used to predict water-tolerant trees that are potentially suitable for establishment. Swamp locations and extents were sourced from the Australian Hydrological Geospatial Fabric (AHGF), which provides a nationally comprehensive geospatial database of surface waterbodies across Australia (Australian Government Bureau of Meteorology 2015). To conceptualize national patterns of water-tolerant tree diversity, the number of potentially suitable species of trees within each of Australia's 89 bioregions was determined by averaging the predicted diversity across all wetlands within each bioregion. Bioregions were sourced from the Interim Biogeographic Regionalisation for Australia (IBRA; Thackway & Cresswell 1995; Cummings & Hardy 2000). The IBRA (version 7.0) classifies Australia's landscape into 89 bioregions and 419 subregions, based on climate, geology, landform, and native species presence (Thackway & Cresswell 1995; Cummings & Hardy 2000), and is endorsed by all levels of government for use under Strategy for Australia's National Reserve System 2009–2030 (Australian Government 2009).

Scoping Trees for Restoring Swamps Across the GBR Catchment. Across the GBR catchment, mapping sourced from the Queensland Government wetland mapping was used

to identify locations where palustrine wetlands once occurred but are no longer present, indicating potential for palustrine wetland restoration. The mapping used represents the most comprehensive and definitive guide to current and pre-drainage wetland location and extent wetland and is used widely in the management of the GBR catchment (Environmental Protection Agency 2005; Department of Environment and Science 2019).

Not all drained wetlands are readily suitable or desirable for restoration, such as those with urban development or with highly versatile agriculture soils or very small parcels. In scoping potential restoration areas, land parcels constituting drained wetlands were reduced to only parcels that were classified as Class B, C, or D by the Queensland agricultural land audit to avoid urban and versatile agricultural areas (Queensland Government Department of Science 2015). The Queensland agricultural land audit classifies agricultural land into a four-tier hierarchy ranging from class A through to class D. Class A land is suitable for a wide range of current and potential crops with nil to moderate limitations to production. Class B land has limited cropping suitability due to severe limitations but is suitable for pastures. Class C is unsuitable for cropping and may tolerate low intensity grazing or short grazing periods. While Class D is nonagricultural land and land unsuitable to agricultural uses due to extreme limitations (Queensland Government Department of Science 2015). It is recognized that not all non-A land identified is suitable for restoration, and restoration practitioners will need to consider each location on a case-by-case basis.

Land parcels potentially suitable for restoration were further reduced based on size. Very small projects are likely undesirable as they would not allow for efficiencies from economies of scale and would not be eligible for earning carbon credits. A minimum land parcel size of 0.2 ha was adopted as this is the minimum area required for projects to earn Australian carbon credit units (ACCUs) under Australia's Emissions Reduction Fund (Carbon Credits [Carbon Farming Initiative—Tidal Restoration of Blue Carbon Ecosystems] Methodology Determination 2022 and Carbon Credits [Carbon Farming Initiative—Reforestation and Afforestation 2.0] Methodology Determination 2015). In practice, however, land parcels will likely need to be much larger than 0.2 ha to be financially viable, and projects using parcels this size may benefit from combining sites. Nonetheless, this study presents options that restoration managers can consider in their scoping of viable sites.

Using the well-performing random forest models (AUC-ROC > 0.7), the suitability of each species was predicted across the entire extent of each identified land parcel, and a list of all species likely suitable within each wetland was identified.

Results

Of the initial 125 candidate taxa identified, 105 had sufficient observations to be modeled and all had model excellent predictive accuracy with AUC-ROC values greater than 0.9 (Table S1; Šimundić 2009). The majority of taxa (species, subspecies, and varieties) included 17 taxa from the *Acacia* genus, 33 from the *Eucalyptus* genus, and 14 from the *Melaleuca* genus (Table S1).

Table 3. Summary statistics of the potential number of water-tolerant trees supported by mapped swamps within IBRA V7.0 bioregions (Cummings & Hardy 2000). Only regions with a mean potential tree richness greater than 30 are listed here, see Table S1 for all bioregions.

Region	Mean	SD	Max	Min
Sydney Basin	45.1	5.2	53	21
South East Corner	43.4	6.6	55	32
South East Coastal Plain	40.7	5.5	52	29
NSW North Coast	35.1	5.0	47	12
Ben Lomond	34.2	7.2	46	14
New England Tablelands	33.7	9.5	48	21
South Eastern Highlands	33.1	6.6	49	22
Furneaux	32.7	3.1	45	25
Victorian Midlands	32.0	6.0	50	20
Southern Volcanic Plain	31.3	3.1	42	21
Tasmanian Northern Slopes	31.1	5.9	42	17
Naracoorte Coastal Plain	30.1	3.0	36	13

Identifying Suitable Trees at Multiple Scales

Bolstering Diversity Within Australia's Extant Wetlands.

The AHGF contained 25,150 polygons mapped as swamp across the country. Swamps in the coastal bioregions of New South Wales, Victoria, and Tasmania were predicted to potentially support the highest diversity of water-tolerant species of trees, typically predicted to support more than

30 taxa (Table 3; Fig. 1). While most swamps elsewhere in the country are typically predicted to support fewer than five taxa (Table 3; Fig. 1). The taxa suitable at the greatest number of wetlands nationwide include *Eucalyptus camphora*, *Banksia marginate*, *Melaleuca squamea*, *Leptospermum lanigerum*, *Melaleuca armillaris*, and *Eucalyptus ovata* var. *ovata*.

Scoping Trees for Restoring Swamps Across the GBR Catchment.

Within the GBR catchment, 20,200 ha of land parcels ($N = 2230$) were identified as being potentially suitable for palustrine wetland restoration (drained historic wetland, larger than 0.2 ha, on low versatility agricultural land). The river basins with the largest area of restoration potential (>1000 ha) include the Fitzroy basin (5799 ha), Kolan basin (2272 ha), Mulgrave-Russell basin (1714 ha), Baffle basin (1617 ha), Burdekin basin (1593 ha), Mary basin (1492 ha), and the Haughton basin (1145 ha; Fig. 2).

Across all the land parcels identified ($N = 2230$) for potential palustrine restoration within the GBR, on average 9.4 (SE = 2.8) water-tolerant tree taxa are predicted suitable at these locations (Fig. 3). The most widely suitable taxa across all identified parcels include *Melaleuca trichostachya*, *Melaleuca bracteata*, *Leptospermum brachyandrum*, *Melaleuca viridiflora*, *Ventilago viminalis*, *Aegiceras corniculatum*, and *Avicennia marina*.

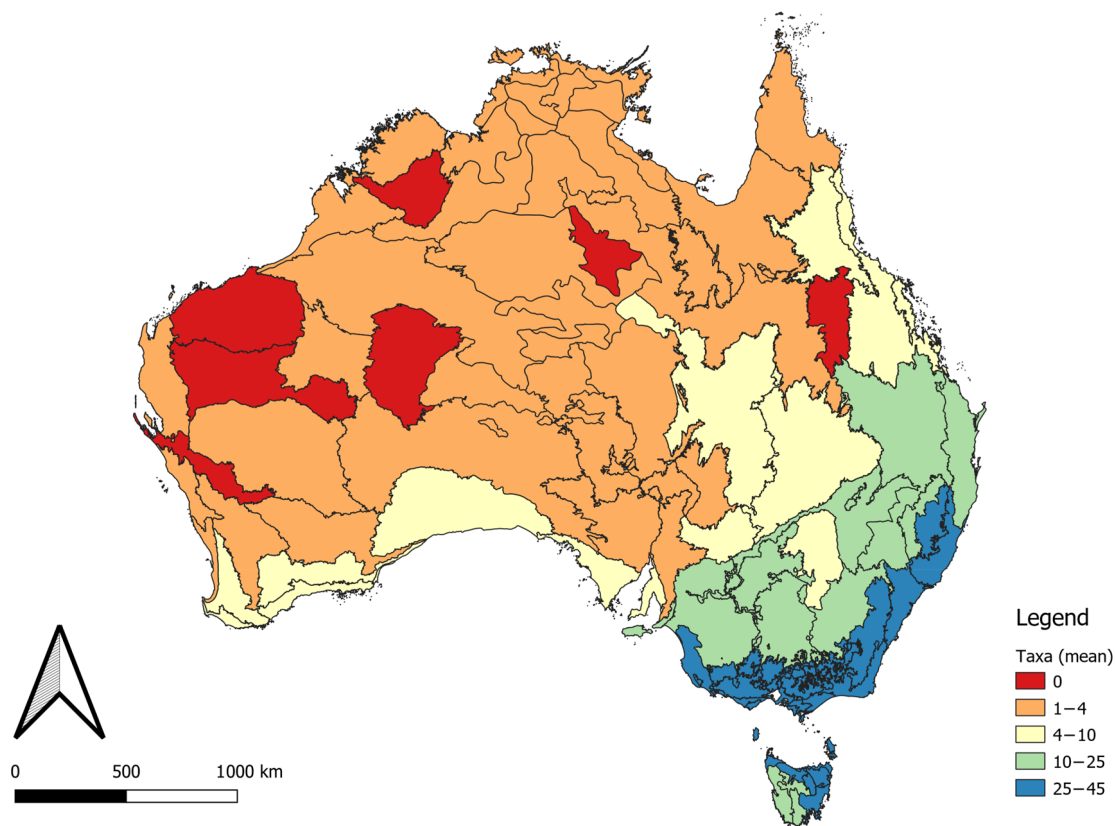


Figure 1. The average number of water-tolerant tree species potentially supported by wetlands within bioregions across Australia.

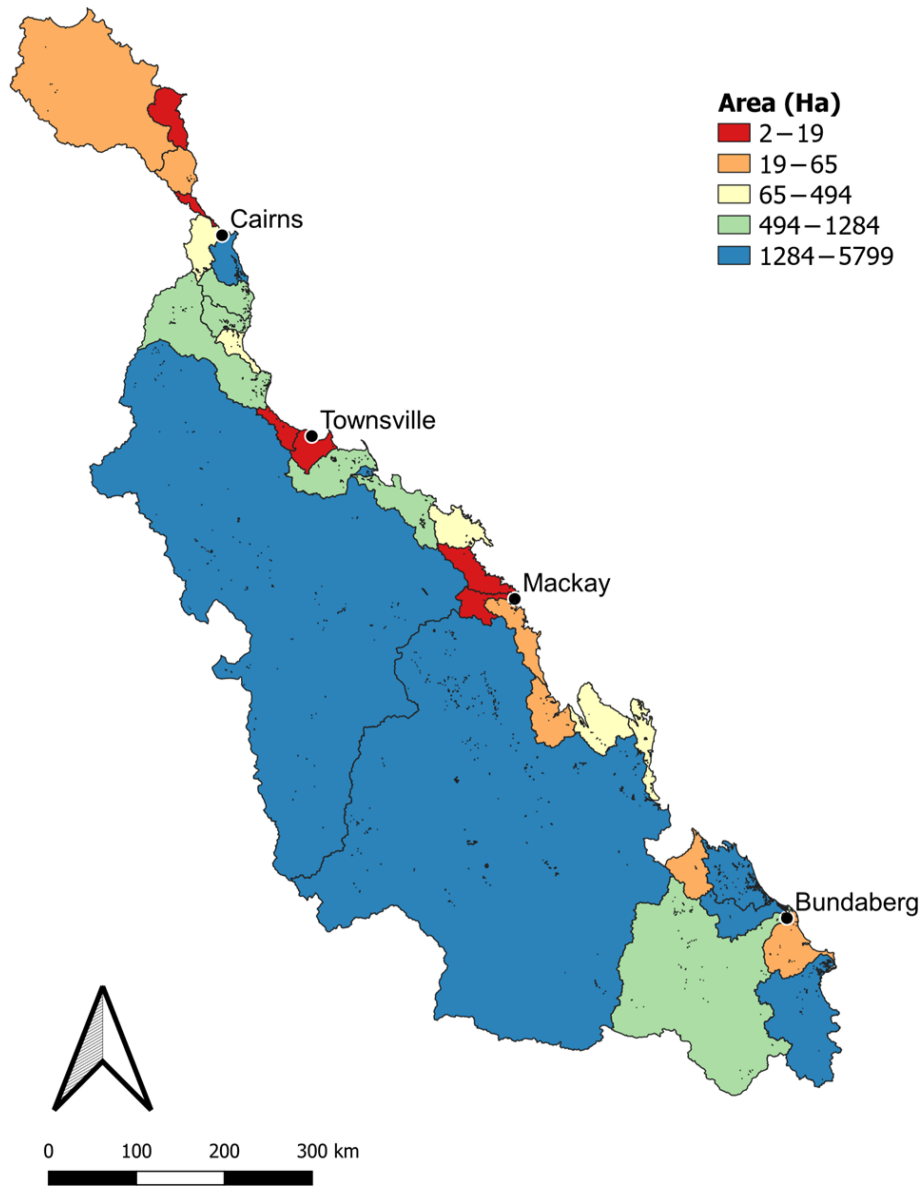


Figure 2. The area of land potentially suitable for wetland restoration across the river basins within the Great Barrier Reef catchment.

Discussion

To inform swamp and floodplain restoration decision-making, the present study modeled the habitat suitability of 105 water-tolerant species and varieties of trees across Australia, based on climate, soil, landscape, and water permanency. Despite high model performance for all taxa, several considerations are noteworthy, including the potential impact of climate change, the use of presence-only observations from a public database, and the accuracy of the predictor variables.

While this study identified potentially suitable habitats for a contemporary climate, the impacts of climate change may alter habitat suitability. Australia's climate is predicted to indicate fewer cool years, more frequent record-breaking temperatures, longer fire seasons in the south and east, increased dangerous

fire weather days, reduced cool season rainfall leading to prolonged droughts in the south and east, and more intense heavy rainfall events nationwide (Bureau of Meteorology & CSIRO 2022). The models produced in this study use the WorldClim (Fick & Hijmans 2017) hindcast climate estimates and can be readily applied to predict potential suitability under any of the future climate scenarios mapped by WorldClim (Fick & Hijmans 2017). If predicting to future climates, it is important to recognize that different modeling algorithms (random forest in this case) perform variably depending on the context, with some excelling in extrapolation under certain conditions and others not (Heikkinen et al. 2006; Norberg et al. 2019). As such, it is recommended that using predictions of future climates from the current models be compared against predictions from alternative models using species distribution and climate model

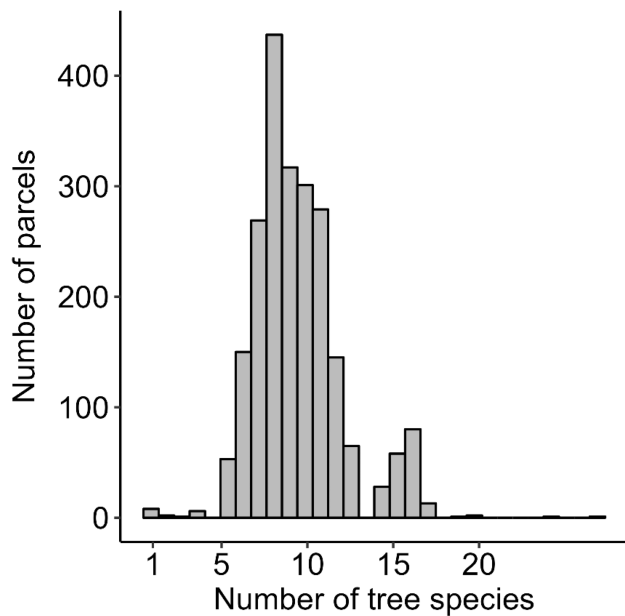


Figure 3. The number of water-tolerant tree species with a probability of occurrence greater than 0.5 (relative to random background conditions) at each of the 2,230 parcels considered suitable for wetland restoration across the Great Barrier Reef catchment.

algorithms to better understand the model-driven variability (Thuiller et al. 2019; Brun et al. 2020).

The accuracy of the environmental predictors can also affect the reliability of the species distribution predictions, particularly given that all variables were derived from other models. As with any model, prediction accuracy is heavily dependent on the data used to train the model, the validation procedures used, and the distance of extrapolated predictions from training data. The environmental variables used in the current study may also not be of sufficient resolution to adequately depict highly localized variation, which can also affect the accuracy of the derived species distribution predictions. However, models are useful in that they can demonstrate broader patterns while smoothing variation that could have also arisen from measurement uncertainty. Furthermore, all climate and soil predictors were trained and validated against large datasets (Grundy et al. 2015; Viscarra Rosset et al. 2015; Fick & Hijmans 2017). The estimates of water inundation frequency, included as a predictor, may benefit from temporal ground-truthing and calibration. Water inundation frequency was derived from long-term Landsat imagery (Mueller et al. 2016), and assumes that temporal distribution of the available images does not significantly bias the frequency estimates. While the study that derived the predictions showed high accuracy in spatial classification, it did not account for the extent to which image collection affects temporal accuracy. Landsat imagery is collected at approximately equal intervals (every 16 days for a given location), which reduces the probability of overinflation by temporal clustering; however, the removal of images with cloud cover can introduce a systematic bias. Given that clouds often accompany rainfall events, images where clouds obscure the ground may coincide with periods of

water inundation. This correlation could result in an underestimation of inundation frequency if cloud-covered images are excluded. Further work could compare the inundation frequency estimates (Mueller et al. 2016) with long-term water level monitoring of intermittent wetlands and derive calibration factors to correct the bias.

As the models were trained using a dataset with observations collated from many different studies with different aims and survey methodologies, it cannot be ascertained whether surveys were suitable to determine the absence of species or species abundance. As a result, models were trained by comparing detected presence against random background values where species may or may not be present, a common practice in species distribution modeling (Guillera-Aroita et al. 2015; Araújo et al. 2024). Consequently, predictions may underestimate the true extent of species, particularly in locations where species were removed from locations representing the extremes of the environmental envelope or remote locations that may not have been surveyed to the same intensity as areas close to urban centers. Users need to be cognizant that the probability of occurrence is relative to a random background, not absence, and that there are likely locations within background predicted areas that would also be suitable for any given species.

National-Scale Patterns

Coastal areas of southeast Australia were predicted to support the greatest diversity of water-tolerant species of trees. This pattern is consistent with more general biodiversity patterns detailed elsewhere, and it is correlative of potential driving forces, such as energetic and landscape characteristics (Venevsky & Veneskaia 2003), and evolutionary histories (Martin 2006; Cowling et al. 2015). Restorations that can support a diversity of trees will not only be able to support a wider range of consumer species but also likely benefit from greater resilience if the different species are similarly abundant influential on the food web (Canning & Death 2017; Miller et al. 2017; King et al. 2023). Furthermore, mixed species plantings are likely to have greater resilience to disturbances (Carvalho et al. 2013), such as floods and droughts. Restoring a resilient ecosystem is critical to the healthy functioning of an ecosystem and to ensure a high probability of long-term persistence of an ecosystem—the latter is necessary for those seeking funding through carbon trading markets (Farley & Costanza 2010; Canning et al. 2021).

The locations with greatest diversity potential are also the locations where agricultural land uses are most intensive—including the Murray-Darling basin and the GBR region. In many instances, wetlands were drained or heavily modified to allow intensive agriculture and are regions that would potentially benefit the most from restored ecosystems (Davis & Froend 1999; Finlayson & Rea 1999; Davidson 2014). Furthermore, intensive agriculture often results in considerable nutrient pollution to downstream aquatic ecosystems, and restoring wetlands may help with reducing nutrient run-off if appropriately positioned and designed (Allred & Baines 2016; Land et al. 2016; Martínez-Espinosa et al. 2021). Reducing nutrient run-off is of particular importance within the GBR region, where

a 60% reduction in dissolved inorganic nitrogen lost the reef is targeted for by 2025 under the Reef Plan 2050 (Queensland). In achieving this, the emerging “Reef Credits” scheme seeks to financially incentivize actions that show demonstrable reductions in run-off, including the restoration of wetlands and floodplains (Eco-Markets Australia 2020).

Restoration Opportunities Within the GBR Catchment

Within the GBR region, over 2000 land parcels, covering over 20,000 ha, were identified as potential opportunities for tree swamp restoration, satisfying the criteria of previously being a wetland that is now drained, having limited agricultural versatility and having sufficient area for participation in Australia's carbon market. Furthermore, almost all parcels were predicted to be suitable for supporting multiple water-tolerant tree taxa. It must be cautioned, however, that the Queensland Government mapping of drained wetlands only provides a coarse approximation of location and extent. Furthermore, extensive drainage structures and landscape reshaping can make restoring a wetlands hydrological function challenging. The land parcels delineated here should be used as a guide in desktop scoping studies that then further physically investigate a refined set of potential interest sites.

Realizing restoration across the potential 20,000 ha will, however, require substantial and reliable funding. Given an approximate cost of tree planting restoration in Queensland at \$40,000/ha (2023 AUD; Catterall & Kanowski 2010; Mappin et al. 2022), then restoring all areas via tree planting could require approximately \$800,000,000 (2023 AUD). While carbon markets are growing, at present potential carbon funding would be inadequate to break-even on planting costs. Assuming matured tree swamp restorations sequestered and stored approximately 360 t C/ha, which is a typical above- and belowground carbon storage in Queensland swamps (Adame et al. 2020; Kelleway et al. 2021), then 7.2 million tons of carbon could be stored. With an approximate spot carbon trading price in 2023 under the Australian Government Emissions Reduction Fund, of approximately \$30/t C (2023 AUD), then the total carbon storage value if all potential tree swamp restorations occurred and reached maturity, would be approximately \$216 m (2023 AUD), or approximately \$11,000/ha restored—leaving a considerable shortfall in funding.

As wetlands can provide multiple ecosystem services, a more viable and stable approach to funding could be to draw income from the provision of multiple ecosystem services. Tree swamps and restored floodplain ecosystems can also reduce nitrogen run-off to the GBR, and support biodiversity, both of these services could attract additional funding in the future through schemes such as Queensland's Reef Credit Scheme (Eco-Markets Australia 2020) and the Federal Nature Repair Market (Nature Repair Act 2023 [Aus]). Despite the potential for greater income, restoration for multiple services is complex, requiring multiple values to be balanced and multiple assessments to verify the delivery of each service (Farley & Costanza 2010; Salzman et al. 2018; Canning et al. 2021). Furthermore, managing

the administrative and monitoring logistics of multiple schemes would be challenging.

Canning et al. (2021) suggest that a Wetland Investment Fund (WIF), operating as a Common Asset Trust, similar to The Nature Conservancy Water Funds (Goldman-Benner et al. 2012; Kauffman 2014; Nelson et al. 2020), could provide a robust and efficient avenue to fund large-scale restoration efforts in future. This innovative financial model would gather investments from diverse sources to fund a variety of wetland restoration efforts, aiming to generate both monetary and non-monetary benefits. Like a traditional managed fund, the WIF would pay out dividends to investors, which can be direct or indirect based on the nature of the ecosystem services generated. These dividends might come from carbon credits, improved water quality, or other ecosystem services that wetlands provide. The fund would employ a reverse-auction mechanism to allocate funding efficiently to restoration projects that anticipate delivering large ecosystem services and aim to be a “one-stop-shop” for wetland restoration funding to reduce the administrative and monitoring burden, ensuring cost-effectiveness. Fund management would be collaborative, involving stakeholders from various sectors, and aims at increasing ecosystem service flows over time. This includes strategic planning, operation, information dissemination, and advocacy, supported by a local scientific/technical partner for guidance on restoration activities. Investors benefit from the dividends and the broader environmental and societal impacts, while project developers compete for funding through reverse auctions, proposing and implementing wetland restoration projects. This approach not only seeks financial viability but also aims to establish credibility and social acceptability, presenting a robust framework for large-scale wetland restoration (Canning et al. 2021; Costanza et al. 2021).

Going Forward

This desktop study provides initial guidance for planning what species of trees could be used where during the restoration of wetlands and flood-prone areas. If multiple PESs are to be a viable avenue for funding restoration efforts, then complementary work is required to identify locations where plantings could occur and yield high returns for multiple ecosystem services at minimal restoration cost. For example, a wetland restoration being funded for delivering the benefits of flood control, improved water quality, and mental well-being, would likely need to be sited somewhere downstream of intensive agriculture or wastewater discharges, be sufficiently large to dampen large water pulses and regulate outflow. Site consideration would also need to appraise the potential legislative barriers and costs associated with restoration works, for example, areas which have been highly modified may require extensive earthworks that may impact project viability.

With the emergence of schemes seeking to fund restorations for their biodiversity benefits, such as Australia's Nature Repair Market, developing tools to better support restorations for supporting biodiversity would be valuable. One tool could be the development of spatially explicit species-interaction databases that allow practitioners to identify and use species that support

a wide range of species or are beneficial to endangered species. Another potentially useful tool, would be the development of maps that guide restoration priority for the enhancement of landscape connectivity and resilience through the use of ecological corridors that connect fragmented habitats.

Acknowledgments

The author thanks Lynise Wearne and Greening Australia for providing funding to support this study. Open access publishing facilitated by James Cook University, as part of the Wiley - James Cook University agreement via the Council of Australian University Librarians. [Correction added on 15 January 2025, after first online publication: CAUL funding statement has been added.]

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Importance of each variable, used in Random Forest modeling.