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Subtropical-temperate forested wetlands of coastal southeastern Australia – an analysis of vegetation data to support ecosystem risk assessment at regional, national and global scales

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ABSTRACT

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Context. Forested wetlands occurring on fluvial sediments are among the most threatened ecosystems in south-east Australia. The first quantitative diagnosis of forested wetland types in NSW was completed in 2005. Since then, there has been a three-fold increase in survey data on coastal floodplains, vegetation classification systems have been developed in New South Wales, Queensland and Victoria, and methods for the assessment of ecosystem conservation risks have been adopted by the International Union for the Conservation of Nature (IUCN). Aims. To ensure an evidence base that can support conservation decisions and national conservation assessments, there is a need to review and update the classification of forested wetlands and integrate classification schemes across jurisdictions. Methods. We evaluated the efficacy of a multi-stage clustering strategy, applied to data from different sources with largely unknown methodological idiosyncrasies, to retrieve ecologically meaningful clusters. We assessed the veracity and robustness of the 2005 classification of forest wetlands as a framework for national risk assessments over an expanded range. Key results. We derived a quantitative, crossjurisdictional classification of forested wetlands based on a synthesis of 5173 plot samples drawn from three states and identified the status of our units in relation to IUCN's Global Ecosystem Typology. Conclusions. Our analyses support the retention of the five legacy types which are the basis for threatened ecosystem listings under the NSW Biodiversity Conservation Act 2016 and Commonwealth Environment Protection and Biodiversity Conservation Act 1999. Implications. Our results will support revised assessments of current listings and facilitate their integration at state, national and global scales.

Keywords: chameleon, clustering, CLUTO, conservation planning, Global Ecosystem Typology, IUCN Red List of Ecosystems, ecosystem classification, threatened ecosystems.

Introduction

Sustainable ecosystem management is of fundamental importance to the conservation of biodiversity. Ecosystems encompass assemblages of species, the environment in which they occur and the myriad of processes and interactions that sustain all species (Tansley 1935). The ecosystem concept is flexible, accommodating a wide range of natural systems and thematic scales and since it focuses on habitats and systems, it addresses conservation of habitats for threatened species, those which may become threatened in the future, those that are presently unknown, and those that are abundant and critical to ecosystem processes and function (Noss 1996; Keith *et al.* 2015).

Many legislatures now afford legal or public policy protection to threatened ecosystems (Keith 2009; Alaniz *et al.* 2019). In Australia, threatened ecosystems are recognised under both state and Commonwealth legislation. The IUCN Red List of Ecosystems protocol is a generic risk assessment framework designed to support consistent conservation assessments over a wide range ecosystem types (terrestrial, freshwater, marine, subterranean) and thematic scales (local–global) (Bland *et al.* 2019). It has been

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formally adopted for conservation assessments in New South Wales (NSW) and the Australian Capital Territory and is under consideration in other jurisdictions after adoption in-principle. The protocol addresses risks to ecosystems arising from processes affecting the spatial distribution of ecosystems, their biotic and abiotic components and attendant interactions (Keith et al. 2013). While it has the flexibility to accommodate variable data availability, a clear definition and description of ecosystem types is essential for its application (Bland et al. 2019). In Australia, this is problematic because classifications of terrestrial ecosystems have developed independently among the jurisdictions, and relationships between both classification units and the conservation assessments and ecosystem listings they support are unclear (Nicholson et al. 2015). There is a need to identify relationships between different classification systems and elucidate hierarchical relationships among their units so that future listings can be framed at thematic scales that realise efficient and effective conservation (Keith 2009). Furthermore, it is desirable to incorporate functional elements into ecosystem classifications to support generalisations in relation to their response to threats.

The IUCN Global Ecosystem Typology (GET) is a framework for integrating conservation risk assessments across local to global scales (Keith et al. 2020). The typology is hierarchical, representing functional features of ecosystems in three upper levels (1 - Realms; 2 - Biomes; 3 - Ecosystem Functional Groups) and compositional features in three lower levels (4 - Biogeographical Ecotypes; 5 – Global Ecosystem Types; 6 – Sub-global Ecosystem Types). The upper levels of the typology are primarily deductive, grouping ecosystems that share similar functions, processes and dynamics on the basis they are likely to respond in similar ways to environmental changes and threats. The lower levels are descriptive, identifying bioregional expressions of each functional ecosystem group, as well as global ecosystem types (assemblages of species in particular environments) and nested sub-global types (regional variants represented by units of established classifications). One of the advantages of the typology is its potential to leverage data describing well-studied ecosystems in order to draw inferences on the nature of threats to functionally similar ecosystems for which fewer data are available. The hierarchical structure also facilitates the integration of assessments made at regional scales with national and global assessments.

Here, we address the classification of Subtropical-Temperate Forested Wetlands (GET Level 3 – Ecosystem Functional Group) (Mac Nally *et al.* 2020) in coastal catchments of south-east Australia. Subtropical-Temperate Forested Wetlands occupy lowland flats, floodplains and riparian corridors within subtropical or temperate climate zones (Mac Nally *et al.* 2020). These ecosystems are net accumulators of resources (water, nutrients) and hence are more productive than surrounding lands from which some of those resources derive (Keith *et al.* 2020). One of their key characteristics is variability in water regime, regulated primarily by intermittent inundation by floodwater originating in upper catchment areas. Flood events are characterised by large sediment loads and marked depositional patterns, with coarse sediments disproportionately distributed on the upper floodplain and adjacent to channels, and silts and clays deposited on the lower reaches of the floodplain and its margins (Troedson *et al.* 2008). As a result, Subtropical-Temperate Forested Wetlands in coastal south-east Australia display strong zonation of vegetation. Extensive mosaics comprise tall forests in areas with deep fertile soils subject to infrequent inundation, and smaller areas subject to frequent inundation or permanent standing water, usually on the lower floodplain or its margins and often sustained by local rainfall (Keith 2004).

The first synthesis of coastal floodplain ecosystems in south-east Australia (GET Level 4 – Biogeographic Ecotype) identified five major types of forested wetland occurring primarily on fluvial sediments and distributed along gradients in soil moisture, fertility and salinity (GET Level 5 - Global Ecosystem Types). Although Keith and Scott's (2005) classification was based on data drawn only from NSW, their model of ecological relationships between different floodplain ecosystems is likely to be applicable to adjacent areas of adjoining states because NSW contains the largest area of floodplains and occupies the central portion of their distribution. However, the classification was also limited by relatively sparse data with clear geographic and thematic biases (Keith and Scott 2005) and warrants review and update, given substantial increases in the number of quantitative samples available, as well as increased demands for reliable inventory data generated by regulatory provisions for protection. In addition, there is a need to identify hierarchical relationships between these relatively broad units and those of finer classification systems adopted by respective state jurisdictions for applications in other regulatory processes (Fig. 1). A review of these fine-scale classifications with a substantially improved coverage of plot-based observations should enable the reliable identification of regional variants that were not formally or quantitatively described by Keith and Scott (2005).

Diagnosing hierarchical relationships among the units of different classification systems is not straight forward. First, data from different sources may be afflicted by methodological idiosyncrasies, which complicate the process of identifying types. Clustering solutions are highly sensitive to these, as well as both the clustering method and dataset structure (Wiser and De Cáceres 2013; Tichý *et al.* 2014). Hence, there is a degree of uncertainty in relation to whether clusters reflect ecological patterns or methodological artefacts. Second, traditional approaches (e.g. Kent 2011) employ agglomerative or divisive clustering algorithms that are not highly scalable and cannot easily accommodate large datasets. Furthermore, they suffer from the problem that successive merge/split operations are performed on clusters generated

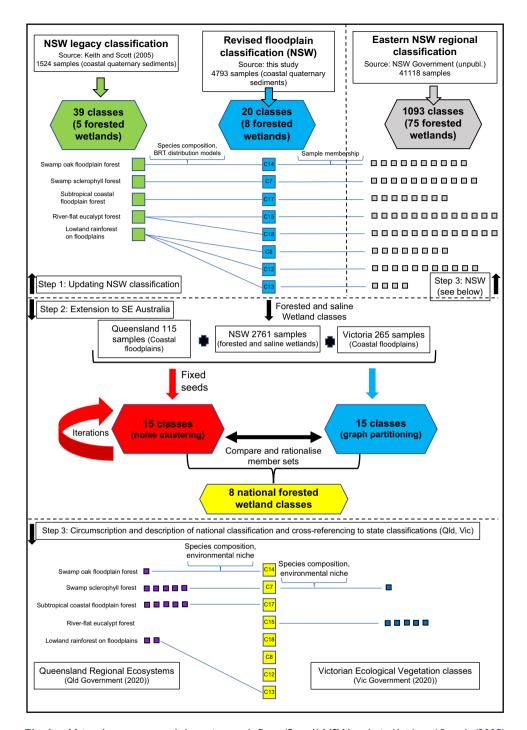


Fig. 1. Major data sources and clustering work-flow. (Step 1) NSW analysis: Keith and Scott's (2005) classification pertained only to NSW and was updated in the current project to reflect the increase in plot samples (1524 vs 4793). We used boosted regression tree models to locate our classes on critical gradients identified by Keith and Scott (2005). (Step 2) National Analysis: noise clustering (red) and graph partitioning followed by agglomeration (Chameleon, blue) were performed independently on the national data set and the respective solutions compared (see methods). Successive iterations of noise clustering were performed, progressively increasing the distance to noise class and reducing the fuzziness co-efficient to coerce samples from the noise and transitional classes. (Step 3): New South Wales Plant Community Types, Queensland Regional Ecosystems and Victorian Ecological Vegetation Classes were matched to the national classes based on species composition, environmental niches and shared plot membership (NSW only).

in preceding steps and, since there is no object-swapping among clusters, suboptimal decisions cannot be reversed if they lead to poor quality solutions (Han *et al.* 2012). Finally, while partitioning algorithms such as k-means (and its many variants) can produce clustering solutions at different levels of thematic scale (e.g. Wiser and De Cáceres 2013), hierarchical relationships between these are difficult to diagnose (Zhao and Karypis 2005).

In this paper, we describe a method that addresses these problems by incorporating multi-stage clustering applied sequentially to different combinations of the data. Our primary aim was to assess the veracity and robustness of the legacy classification as a framework for conservation risk assessment and listing over an expanded geographic domain. In compiling a revised classification of forested wetlands, we also aimed to determine the efficacy of our approach in: (1) updating a broad legacy classification of species assemblages (forested wetland types previously classified by Keith and Scott (2005)); and (2) identifying novel types in datasets that combine samples from different sources beyond the geographic extent of the legacy classification.

We first addressed the problem of identifying upperhierarchical groups by employing graph-partitioning in combination with agglomerative clustering, a method that requires no assumptions about the shape or structure of the clusters (Karypis et al. 1999). This method minimises errors in the agglomeration phase because it operates on interconnected sets of samples and combines sets on the basis of proximity and interconnectedness rather than central tendency. Second, we used a noise-clustering algorithm (Wiser and De Cáceres 2013) to identify potential methodological artefacts that may stem from synthesis of data from different sources. We used the relevant elements from the revised classification of NSW forested wetlands (generated in the graph partitioning step) as fixed seeds to analyse the clustering tendency of Victorian and Queensland samples among fixed, novel and noise classes under different parameterisations of the algorithm. We developed revised circumscriptions for forested wetland types across coastal south-east Australia, and described the key elements (characteristic native biota, abiotic environment, processes, interactions and spatial distribution) required to support national-scale assessment of conservation risk. Finally, we identified relationships between our units and those of regional typologies in NSW and Queensland at Level 6 (Sub-global Ecosystem types) within IUCN's Global Ecosystem Typology.

Materials and methods

Study area

The study area encompassed coastal lowlands south of the Tropic of Capricorn between Gladstone in Queensland (Qld)

(23.8°S) and Melbourne in southern Victoria (Vic) (37.8°S). Although the forested wetland ecosystems of interest in this region occur primarily on depositional sediments of Quaternary origin, they may extend to flat, occasionally inundated terrain that has not accumulated depositional sediments.

Quaternary deposits include sediments of both fluvial and marine origin occurring in three main depositional systems (alluvial, estuarine and coastal barrier), generally at elevations less than 100 m above sea level, although alluvial deposits may occur in limited areas in upper catchments up to approximately 450 m above sea level (Troedson et al. 2008). The study area encompassed significant climatic gradients, with rainfall in near coastal areas ranging from (approximately) 2150 mm near Cape Byron to 1850 mm at Maryborough (south-east Queensland) and Wollongong (NSW south coast), down to 850 mm at Cape Howe on the NSW far south coast, and as low as 600 mm in the coastal rain-shadow valleys in the coastal hinterlands. Average annual temperature maxima decrease from north to south from 27°C at Maryborough to 20°C near Melbourne. The corresponding annual average minima range from 16°C to 9°C (BOM 2020).

Compilation and analysis of floristic data

Plot sample data from NSW were sourced from the BioNet database compiled and administered by the Department of Planning, Industry and Environment (NSW DPIE 2020). We extracted all samples located on coastal Quaternary sediments mapped on the north and south coasts by Troedson et al. (2008) and on the central coast by Bannerman et al. (2010), Chapman et al. (2009), Hazelton and Tille (1990), Matthei (1995), McInnes (1997) and Murphy and Tille (1993). Samples were only included if the sample location was recorded with an accuracy of $\leq \sim 100$ m, the sample area was exactly 0.04 ha and all vascular plant species were recorded in the survey along with cover/abundance estimates. Individual species records were reviewed and modified to resolve inconsistencies in taxonomy (see methods in Tozer et al. 2010). Taxa identified only at the generic level were excluded from analysis, as were naturalised species. Cover/ abundance scores were transformed to an ordinal scale with six classes (1 = uncommon and cover <5%; 2 = common and cover <5%; 3 = 5% < cover <20%; 4 = 20% < cover <50%; 5 = 50% < cover < 75%; 6 = 75% < cover < 100%). This transformation was chosen to maximise the information content while ensuring compatibility among survey data recorded using different cover/abundance scales.

We sourced plot data from Qld and Vic from the Terrestrial Ecosystem Research Network (AEKOS 2021). Fewer data were available than for NSW and there was insufficient documentation to determine the compatibility of Qld and Vic data with those of NSW. For these reasons, we adopted more relaxed criteria for the inclusion of plots in our analysis (minimum sample area 0.02) and converted abundance data to presence/absence in order to avoid problems associated with differences in methods used to estimate abundance. We reviewed the taxonomic status, distribution and origin (native/introduced) of the taxa listed in the respective datasets and made alterations necessary to ensure each taxon was represented consistently across the three datasets at the level of species (or lower taxonomic levels) without duplication or overlap. Introduced species and genus-only records were removed.

Cluster analysis

Summary of approach

We undertook the analysis in three steps. The first step focused on NSW, which has the largest, most recent, environmentally and geographically representative set of floristic observations and the most diverse and extensive floodplain ecosystems in the subtropical-temperate zone (Fig. 1). We avoided pooling data from other states in this first stage of analysis due to uncertainties about compatibility of the data from these different sources. We identified clusters with a graph partitioning algorithm (details below) and reconciled them with the legacy classification (Keith and Scott 2005).

In the second step, we applied two types of analyses combining samples representing those classes with samples located on alluvium in Vic and Qld (Fig. 1). We first applied noise clustering (Wiser and De Cáceres 2013), allowing for up to five novel clusters and adjusting the fuzziness and distance to noise parameters to coerce different allocations of samples to NSW seeds. The second analysis applied the Chameleon algorithm (Karypis *et al.* 1999) to identify clusters unconstrained by a spheroidal model of cluster shape. We sought convergence in the respective clustering solutions as evidence for the existence of novel forested wetland types endemic to either Qld or Vic.

In the third step, we compiled a circumscription and description of the national classification, inferred the environmental relationships of the units based on locations of the samples in each cluster, and undertook crossreferencing of the classes to those of state classifications.

Step 1: clustering NSW samples

We diagnosed broad vegetation groups in the NSW data by clustering the floristic plot samples using the Chameleon algorithm (Karypis *et al.* 1999), a multi-phase clustering algorithm which does not assume clusters conform to a spheroidal model and can adapt automatically to the internal structure of the data by combining partitioning and agglomerative phases (Han *et al.* 2012). Analyses were performed using the CLUTO software version 2.1.2 (Karypis *et al.* 1999) applying the scluster function operating on pairwise similarity matrices calculated using the Bray– Curtis measure (Clarke 1993). We investigated solutions in the range of 20-26 clusters corresponding to range in number of broad groups we considered likely to resolve different types of forested wetlands based on a review of the broad groups retrieved in Keith and Scott's (2005) analysis. The algorithm was implemented using graphpartitioning in the partitioning phase, setting the neighbour range at 450 samples that corresponded to the limit imposed by the number of non-zero edge-weights. We varied both the link function (single or complete) and the number of sub-partitions in the agglomerative phase, increasing the latter from 50 to 500 in increments of 50 and comparing solutions in terms of the evenness of the distribution of samples among clusters, average internal cluster similarity and rates of misclassification as measured by the proportion of samples located in clusters other than those of their nearest neighbour.

We chose a 20-cluster solution because its clusters had high internal similarity, low rates of misclassification and sufficient thematic detail to represent vegetation types described in reference classifications. We characterised species composition by identifying species with a higher frequency of occurrence within the cluster than across the dataset as a whole as diagnostic (cumulative hypergeometric probability >0.999) (Tozer 2003). Resemblance among clusters was quantified by computing cluster centroids and calculating neighbour distances based on Bray-Curtis dissimilarity. We assessed the efficacy of solutions of different thematic resolution based on compositional and distributional resemblance to two reference classifications of different thematic scales (the floodplain classification of Keith and Scott (2005) and Keith's (2004) upper-hierarchical classification of vegetation classes) using a mixture of quantitative and qualitive methods to determine relationships between clusters derived in our analysis and reference classes. In particular, we focused on the subset of clusters with compositional features corresponding to Keith's (2004) Coastal Floodplain Wetlands because this class broadly encompasses forested wetlands. First, we matched our classification units to the classes of Keith (2004) by calculating the proportion of species diagnostic of our clusters that were designated characteristic of Keith's (2004) classes. Second, we compared plot memberships between our new units and those of Keith and Scott (2005). Finally, we reviewed descriptions of forested wetlands contained in Keith and Scott (2005) to determine their relationship to Keith's (2004) classes and to identify subsets of our clusters with similar diagnostics. We corroborated these relationships using statistical distribution models for each of the forest wetland classes.

Differences in the distribution of floodplain vegetation types in relation to environmental factors were explored using boosted regression tree (BRT) models. We chose this method over gradient analysis because it yields more direct insights into the environments in which different vegetation types occur and because we anticipated

gradients underlying such wide range of vegetation types would be complex and difficult to elucidate in a small number of dimensions. We built individual models for units of the classification corresponding to forested wetland types, referring to the conceptual models of Keith and Scott (2005) to select appropriate predictor variables. Model predictors included five variables representing physical features [elevation, distance to streams and distance to depositional features (alluvium, estuarine sediments, barrier sands) at 1 arcsecond resolution] and seven representing soil properties averaged over depths 0-100 cm [effective cation exchange capacity, total phosphorus (P) and nitrogen (N) and percent sand (S), organic (O), clay (C) and silt (S) at 3 arcsecond resolution CSIRO 2021]. We estimated the values of predictors by intersecting sample locations with relevant spatial data layers using a GIS. Models were fitted in R (version 4.1.0 2021-05-18, R Core Team 2021) using gbm package version 2.1.8 (Greenwell et al. 2020) and the BRT functions of Elith et al. (2008). Models were built with tree complexity set at three, holding out 25% of samples for cross-validation. For each model the learning rate was varied between 0.005 and 0.001 to ensure at least 1000 trees were fitted (Elith et al. 2008).

Step 2: Clustering Qld and Vic vegetation samples

We investigated the affinity of plot samples obtained from Qld and Vic to the units of our classification using both Chameleon and noise clustering (Wiser and De Cáceres 2013). We used Chameleon to retrieve a 15-class solution from the joint dataset and compared membership with the classes of our NSW classification. We used the parameterisation of the algorithm upon which the NSW solution was based. Noise clustering was performed in R using the vegclust package (De Cáceres 2008). We first transformed the NSW data to presence/absence and masked the data retaining only the 2761 samples representing forested wetlands. We then conformed the three data sets such that the complete inventory of species was represented in each data matrix. We used the NSW classification to calculate cluster centroids in the conformed space using the chord distance then joined the three state matrices. We performed noise clustering on the joint matrix specifying the cluster centroids as fixed centres and between one and six mobile centres to allow for assemblages not represented in the NSW classification. We then examined the composition of the clusters to determine representation of NSW units in Old and Vic, as well as additional units in Qld and Vic that were not represented in NSW.

Step 3: identifying hierarchical relationships between regional vegetation types

We compared plot membership of our newly derived forested wetland units with those of the NSW Plant

Community Type (PCT) classification and identified PCTs with a high proportion of member samples overlapping with clusters we identified as forested wetlands. We reviewed the descriptions of the PCTs to confirm they were faithful to Keith and Scott's (2005) original concepts and were likely to be equivalent in terms of conservation risk. Attributions of Queensland and Victorian plots to regional types (Regional Ecosystems (Queensland Government 2020), Ecological Vegetation Classes (Victorian Government 2020)) were not available, so we identified types potentially included in our forested wetland classes by intersecting the plot samples with the corresponding vegetation maps for those states. We then reviewed the descriptions of any map units intersecting samples we attributed to one of our forested wetland classes and made a qualitative appraisal of their fidelity to the original forested wetland concepts.

Results

Diagnosis of major vegetation groups on NSW floodplains

A total of 4793 plot samples retrieved from the NSW database met the criteria for inclusion in our analyses. Cluster solutions of 20 classes provided sufficient thematic detail to represent vegetation patterns at a scale comparable to Keith and Scott's (2005) forested wetland classification. We based our new circumscription on a solution agglomerated from 150 subpartitions because the resulting clusters had the highest cluster-weighted average internal similarity and lowest rate of misclassification (26%). Three groups of inter-related clusters were identified corresponding to the three depositional systems (alluvial, estuarine and coastal barrier; Fig. 2). Diagnostic species for each cluster are listed in Appendix S4.

Relationships between the units of the cluster solution and vegetation types identified by Keith (2004) and Keith and Scott (2005) are summarised in Table 1. A summary of changes in circumscription of vegetation communities occurring on Quaternary sediments is contained in Appendix S1. A summary of the main features of the revised forested wetland communities and their major variants is in Table 2 with full descriptions in Appendix S2. The distributions of samples representing each of the types (and their major variants are depicted in Fig. 3. We identified eight floristic clusters (8, 12, 13, 14, 15, 17 and 18) that occur primarily on alluvium and are characterised by species typical of either Keith's (2004) Coastal Floodplain Wetlands (which includes forested wetlands) or Rainforest (Table 1). Collectively, these represent Keith and Scott's (2005) original five units. Our additional clusters describe vegetation types that broadly fit the conceptual definitions of Coastal River-flat Eucalypt Forest (15 and 18) and Lowland Rainforest (8, 12 and 13), reflecting a greater

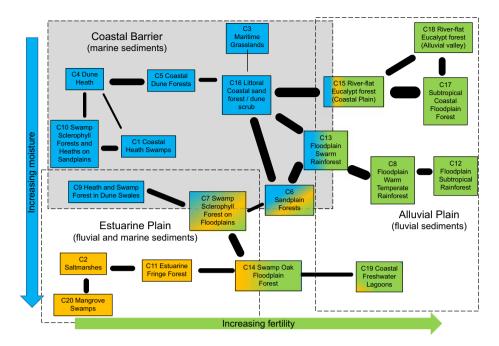


Fig. 2. Compositional relationships between global vegetation types defined in this paper and indicative environmental niches in relation to moisture and fertility gradients. Solid bars indicate relationships between clusters with the thickness of the bar proportional to compositional similarity between the respective cluster centroids. Shading reflects proportional representation on different substrates. Blue shading indicates distribution primarily on marine deposits, green indicates fluvial deposits and orange estuarine deposits (refer to Table 4 for proportions of forested wetland samples recorded on each medium).

range in composition in these types of forested wetland than other communities occurring on Quaternary alluvium (Tables 1, 2). This result is consistent with their distribution over a greater climatic and edaphic range than the other forested wetlands, from the coastal plains to the alluvial valleys of the hinterland. The omission of these units from Keith and Scott's (2005) classification is mostly likely due to gaps in the coverage of samples available at that time. As such, they arguably represent new units of equal status. However, since they share similar compositional and structural properties, we describe these variants informally as sub-classes, thus retaining five forest wetland classes as originally described by Keith and Scott (2005) (see Appendix S1 for further discussion).

A further three clusters represent forested wetlands occurring on a wider range of Quaternary sediments. Cluster 14 is characterised by species associated with slightly saline groundwater and corresponding to those occurring in Swamp Oak Forest (Keith and Scott 2005). The other two correspond to Keith and Scott's Swamp Sclerophyll Forests (Keith and Scott 2005), associated predominantly with either fluvial (7) or marine (6) sediments.

Forested wetlands in Qld and Vic

A total of 115 Qld and 265 Vic plot samples met our relaxed analysis criteria and were analysed for affinities

with NSW forested wetlands types. Of the 15 classes retrieved by the Chameleon algorithm (Table 4), nine were essentially facsimiles of the classes from the NSW analysis (1, 3, 5, 6, 7, 9, 11, 12, 13), four represented alternative partitions of compositional gradients between Saltmarsh and Estuarine fringe forest (2) or River-flat Eucalypt Forest and Subtropical Coastal Floodplain Forest (4, 8, 10) and one contained only 12 samples distributed across three states and three NSW classes (14). Only a single class contained a significant majority of samples located outside NSW (15), potentially defining a novel forested wetland class primarily distributed in Vic. In the noise clustering, a fuzziness coefficient of 1.1 and distance to noise class of 0.9 resulted in the majority of Qld and Vic samples categorised as unassigned (noise class) while relatively few were assigned to fixed centroids or new (mobile) clusters (Table 3). Decreasing the fuzziness coefficient and increasing the distance to the noise class reduced the proportion of unassigned plots. The majority of Old samples showed affinities to clusters derived using NSW data including Swamp Sclerophyll Forest (C7 - 22%), Lowland Rainforests (C8, C12 - 3%), Swamp Oak Floodplain Forest (C14 - 10%) and Subtropical Coastal Floodplain Forest (C17 - 27%), leaving 20% in the noise class, 9% seeding a new cluster and 9% were allied with communities other than forested wetlands (Table 3).

	Formation (Keith 2004)		Saline vetlan	-	Fres	hwater wetla	nds			Forested	wetland	ls		Rainforests			Dry Sclerophyll Forests and Heaths				
	Cluster	C20	C2	СП	CI9	C10	С9	C14	C7	C6	C15	C17	C 18	C 12	C 8	C 13	C16	C5	C4	СІ	C3
	Keith and Scott (2005) Unit	27	28	17	18, 32, 35, 36	9, 10, 11, 33, 34	29,30, 31, 32	2	I	(10)	7 (6)	8 (6)	7	3	3	3	4	22, 23, 24	20, 39	37, 38	25
Class (Keith 2004)	Mangrove Swamps (Q.S.)	0.63	I	0.38	0	0	0	0.38	0	0	0	0	0	0	0	0	0	0	0	0	0
	Saltmarshes (Q.S.)	0.45	0.68	0.82	0	0	0	0.5	0.14	0	0.05	0	0	0	0	0	0.09	0	0	0	0.09
	Coastal Freshwater Lagoons (Q.S.)	0	0.05	0.12	0.5	0.17	0.24	0.36	0.43	0	0.1	0.02	0.1	0	0.02	0	0	0	0	0.05	0
	Coastal Heath Swamps (Q.S.)	0	0	0	0	0.82	0.16	0	0.11	0	0.04	0.05	0	0	0	0	0.02	0.02	0.18	0.62	0
	Coastal Swamp Forests (Q.S.)	0	0.04	0	0.04	0.61	0.26	0.13	0.35	0.13	0.26	0.17	0	0	0.13	0.17	0	0	0.13	0.35	0
	Coastal Floodplain Wetlands (Q.S.)	0	0.08	0.15	0.13	0.08	0.03	0.45	0.28	0.15	0.58	0.25	0.38	0	0.23	0.2	0.13	0.05	0	0	0.03
	Sub-tropical RF (Q.S and L.S.)	0	0	0	0	0	0	0	0	0.05	0.02	0.02	0	0.88	0.6	0.18	0	0	0	0	0
	Littoral RF (L.S. and Q.S.)	0	0	0.05	0	0	0	0.05	0	0.21	0.26	0.11	0.05	0.26	0.79	0.58	0.32	0	0	0	0
	North. Warm Temp. RF (L.S. and Q.S.)	0	0	0	0	0	0	0	0.03	0.26	0.23	0	0.06	0.52	0.77	0.35	0.13	0	0	0	0
	Coastal Dune DSF (Q.S.)	0	0	0	0	0.12	0	0	0	0.24	0.2	0.16	0.04	0	0	0.04	0.2	0.92	0.52	0.2	0
	South Coast Sands DSF (Q.S)	0	0	0.04	0	0.39	0	0	0	0	0.06	0.08	0.02	0	0	0	0.04	0.51	0.47	0.06	0
	Wallum Sand Heaths (Q.S)	0	0	0	0	0.26	0	0	0	0	0	0.07	0.04	0	0	0	0	0.67	0.93	0.37	0
	Maritime Grasslands (L.S and Q.S.)	0.05	0.1	0.2	0	0.05	0	0.15	0	0.05	0.1	0.1	0.1	0	0	0.05	0.25	0.15	0.1	0	0.45

Table 1. Proportion of species diagnostic of our revised vegetation communities occurring on quaternary sediments (columns, maximum highlighted grey) that are listed as characteristic of sub-formational classes described by Keith (2004) (rows).

The first and third rows summarise qualitative relationships between the new communities and, respectively, the formations of Keith, and the units of Keith and Scott (2005). Units of the revised classification attributable to forested wetlands on alluvium by Keith and Scott (2005) are shaded grey in row two. Cells with solid borders indicate vegetation communities aggregated by Keith (2004) under the Coastal Floodplain Wetlands class. (Q.S) indicates the primary distribution of the class is on Quaternary sediments and (L.S.) indicates the class also occurs on lithic substrates.

Table 2. Summary of the main features of the revised forested wetland communities and their major variants compiled from Appendix S4 (frequency of occurrence and median cover/abundance score for diagnositic species across the range) in combination with descriptions of subglobal types from NSW, Qld and Vic. See Appendix S2 for full descriptions and Table 1 for a graphic representation of relationships between units.

Community (cluster)	Structure	Trees	Understorey	Distribution
Swamp sclerophyll forest on floodplains (C7)	Trees 10 to >25 m tall, foliage cover sparse to very dense, small trees and shrubs low to medium densities, non-woody ground layer frequently dense up to 3 m tall	Eucalyptus robusta, Melaleuca quinquenervia	Pteridium esculentum, Telmatoblechnum indicum, Hypolepis muelleri, Entolasia marginata, Baloskion tetraphyllum, Dianella caerulea, Viola hederacea (sens lat.), Imperata cylindrica, Parsonsia straminea, Gynochthodes jasminoides, Stephania japonica var. discolour	Very low-lying areas on lower floodplains and reworked barrier deposits on soils of clayey sandy silt texture with fine sand particles, almost always below 20 m elevation, primarily on floodplains between Gladstone to Sydney with outliers south to Moruya
Swamp Oak Floodplain Forest (C14)	Trees 8–28 m tall, foliage cover sparse to dense, small trees and shrubs occasional, up to 12 m tall, groundcover ranges from sparse to very dense	Casuarina glauca dominant with Melaleuca quinquenervia north from Illawarra region, Melaleuca ericifolia more common in south	Phragmites australis, Juncus krausii, Baumea juncea, Ottochloa gracillima, Eriochloa procera, Fimbristylis ferruginea, Viola hederacea (sens lat.), Pseudoraphis spinescens, Gahnia clarkei, Selliera radicans, Azolla pinnata, Utricularia aurea, Eleocharis equisetina, Parsonsia straminea	Very low-lying areas on alluvial and estuarine depositional environments, typically with brackish groundwater, almost always below 30 m elevation, Bundaberg to Merimbula
Lowland Rainforest on Floodplains (C12)	Tall to very tall closed mesic forest with trees typically 30 to 45 m tall, occasionally to 60 m, characterised by a dense and diverse mid-stratum and abundant vines	(C12 – Floodplain Subtropical RF) – Aphananthe philippinensis, Cryptocarya obovata, Archontophoenix cunninghamiana, Ficus coronata, Mallotus discolor, Neolitsea dealbata and Streblus brunonianus and Tabernaemontana pandacaqui	Calamus muelleri, Cissus antarctica, Gynochthodes jasminoides, Maclura cochinchinensis, Pothos longipes, and ground cover species Lomandra hystrix and Diplazium australe	Primarily found on fertile alluvial soils on floodplains receiving sediments derived from mafic substrates of the Tweed Caldera, Dorrigo Plateau, Mount Royal Range and the Illawarra lowlands
Lowland Rainforest on Floodplains (C8)		(C8 – Floodplain Warm Temperate RF) – Syzygium smithii, Archontophoenix cunninghamiana, Cryptocarya microneura, Eupomatia laurina, Ficus coronata, Glochidion ferdinandii, Guioa semiglauca, Livistona australis, Pittosporum, revolutum, Synoum glandulosum and Wilkiea huegeliana,	Cissus antarctica, C. hypoglauca, Eustrephus latifolius, Geitonoplesium cymosum, Gynochthodes jasminoides, Pandorea pandorana, Stephania japonica, Parsonsia straminea and Smilax australis. Common herbaceous species include Blechnum cartilagineum, Gymnostachys anceps and Oplismenus imbecillis	Widespread on floodplains on less fertile soils between Tathra on the NSW south coast and Maryborough in south-east Queensland
Lowland Rainforest on Floodplains (C13)		(C13 – Floodplain Swamp RF) – Syzygium smithii, Archontophoenix cunninghamiana, Cupaniopsis anacardioides, Glochidion ferdinandii, Livistona australis, Melaleuca quinquenervia and Melicope elleryana	Hibbertia scandens, Cissus antarctica, C. hypoglauca, Eustrephus latifolius, Geitonoplesium cymosum, Gynochthodes jasminoides, Pandorea pandorana, Stephania japonica, Parsonsia straminea, Smilax australis, Commelina cyanea, Lomandra longifolia and Hypolepis muelleri	Very warm and humid areas where annual rainfall exceeds 1600 mm, very low-lying parts of the floodplains close to the coast. Primarily distributed north from South-West Rocks although scattered outliers have been recorded in areas of lower rainfall south to Jervis Bay
Subtropical Coastal Floodplain Forest (C17)	Very tall, open forest with trees exceeding 40 m in height with a mid-stratum of shorter trees, a sparse to very sparse shrub stratum and a dense herbaceous ground cover with a strong representation of grasses	Eucalyptus tereticornis, Corymbia intermedia, E. siderophloia, E. bancroftii, E. moluccana, E. seeana, E. pilularis, E. resinifera, E. crebra, E. microcorys, E. fibrosa, E. propinqua, E. carnea, Lophostemon suaveolens, Glochidion ferdinandii, Acacia aulacocarpa, A. concurrens, A. disparrima, Melaleuca alternifolia, M. quinquenervia, M. nodosa, Allocasuarina littoralis and Alphitonia excelsa	Breynia oblongifolia, Imperata cylindrica, Lomandra longifolia, Dianella caerulea, Entolasia Themeda triandra, Vernonia cinerea and Dichondra repens, Ottochloa gracillima, Lobelia purpurascens, Lepidosperma laterale, Microlaena stipoides, Paspalidium distans, Polymeria calycina, Centella asiatica, Entolasia marginata, Oplismenus aemulus, Parsonsia straminea, Geitonoplesium cymosum and Gynochthodes jasminoides	Moderately low elevations, almost exclusively on fertile fluvial sediments including silts, sands clays and gravels. Predominantly on the upper floodplain on alluvial valley fill or Pleistocene terraces in the north, alluvial fans and backwater swamps in the south. Distributed mainly from Gosford to Hervey Bay with isolated outliers on the NSW south coast and north to Gladstone

Table 2. (Continued).

Community (cluster)	Structure	Trees	Understorey	Distribution
River-flat Eucalypt Forest on Coastal Floodplains (C15)	Very tall open forest with trees exceeding 40 m with either a dense tree substratum with abundant vines or an open grassy understory with few shrubs. Sites with impeded drainage may have a dense, even sub-canopy dominated by Melaleuca spp.	(C15 – Coastal Plains) – Eucalyptus robusta, Angophora costata, A. floribunda, E. resinifera, E. globoideaand, South from Sydney, Eucalyptus botryoides and E. elata	Acacia longifolia, Breynia oblongifolia, Callistemon salignus, Dianella caerulea, Entolasia stricta, Eustrephus latifolius, Gahnia clarkei, Geitonoplesium cymosum, Glochidion ferdinandii, Gynochthodes jasminoides, Hibbertia scandens, Imperata cylindrica, Melaleuca linariifolia, Parsonsia straminea and Pteridium esculentum	Restricted to low-lying areas below 120 m ASL on a wide range of soil textures incorporating varying proportions of silt, clay, fluvial sands and gravels, predominantly on fluvial sediments as well as backbarrier flats where marine or estuarine deposits have been reworked with fluvial silts and clays. Distributed from the Victorian border to Grafton with outliers as far north as the Tweed Valley
River-flat Eucalypt Forest on Coastal Floodplains (C18)		(C18 – Alluvial Valleys) – Eucalyptus tereticornis, Angophora floribunda and, South from Sydney, E. elata, E. viminalis and E. cypellocarpa	Bursaria spinosa, Cheilanthes sieberi subsp. sieberi, Clematis glycinoides, Commelina cyanea, Glycine tabacina. Species which occur frequently in both forms include Dichondra repens, Entolasia marginata, Glycine clandestina, Lobelia purpurascens, Lomandra longifolia and Microlaena stipoides	Occurs almost exclusively on fluvial sediments above 120 m on the central and upper floodplains, occupying elevated terraces and valley fill on a wide range of soils incorporating varying proportions of silt, clay, fluvial sands and gravels. East Gippsland to Grafton with possible outliers in south east Qld

The 10 samples that seeded a new cluster lacked clear unifying compositional features, apparently representing variants of (or intergrades between) either Swamp Sclerophyll Forest, Swamp Oak Forest or Subtropical Floodplain Forest and, as such, we conclude there is insufficient evidence to recognise a novel vegetation type based on these data. The Vic samples remained in the noise class under almost all parameterisations of the noise-clustering, only forming a single new cluster when the parameters approximated k-means. Thus, while Chameleon clustering suggests the possibility of a distinctively different assemblage of species occurring in Vic we conclude there exist substantial incompatibilities between samples for Vic and those of the larger data set. However, a few Vic samples showed affinities with River-flat Eucalypt Forest (C18 – 1%), which is consistent with descriptions of Eucalyptus dominated Ecological Vegetation Classes (EVCs) occurring on alluvium on the Gippsland Plains and East Gippsland Lowlands.

We identified a total of 71 NSW PCTs, 15 Qld Regional Ecosystems and five Vic EVCs that exhibit the structural, compositional, environmental and functional characteristics of forested wetland types identified in our cluster analysis (Appendix S3). Fifteen of these represent regional variants of Swamp Sclerophyll Forest on Floodplains, 22 are variants of Lowland Rainforest on Floodplains, 33 are variants of Coastal Floodplain Eucalypt Forest, 13 are variants of Subtropical Coastal Floodplain Forest and 12 are variants of Swamp Oak Floodplain Forest on Floodplains. Forested wetland types occurring in south-east Qld are Swamp Sclerophyll Forest (5 Regional Ecosystems (REs)), Subtropical Coastal Floodplain Forest (7 REs), Swamp Oak Floodplain Forest (1 RE) and Lowland Rainforest on Floodplain (2 REs) (Appendix S3.2). There is evidence that examples of the fifth type (River-Flat Eucalypt Forest on Coastal Floodplains may have a marginal presence in Qld (Table 3); however, we were unable to identify any REs compositionally compatible with the original type and conclude that the Qld border approximates the northern limit of the distribution of this ecosystem. Coastal River-flat Eucalypt Forest is the only forested wetland type likely to occur in Vic (4 EVCs) although marginal examples of one EVC occurring in the far northeast corner of the state may fall within either Swamp Oak Floodplain Forest or Swamp Sclerophyll Forest as circumscribed here (Appendix S3.3).

Diagnosis of environmental relationships between floodplain communities

BRT models explained between 34 and 76 percent of deviance in the distribution of forested wetland communities on NSW floodplains, with elevation, cation exchange capacity, organic content and silt content consistently among the most informative predictors (Table 5, Fig. 4). The models were least informative about the distribution of low-lying communities located on lower floodplains [Swamp Oak Floodplain Forest, Swamp Sclerophyll Forest, Coastal River-flat Eucalypt Forest (lower floodplain variant)], presumably because fine-scale local gradients in drainage and salinity are

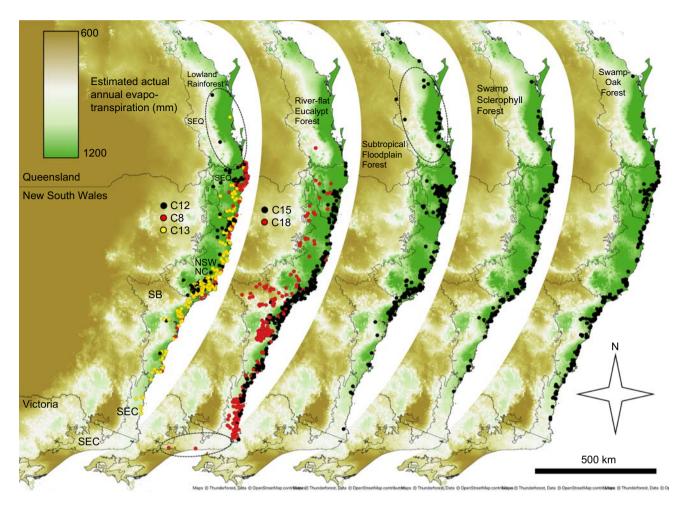


Fig. 3. Distributions of samples representing each of five forested wetland types in southern-eastern Australia in relation to water supply and Bioregional boundaries (SEQ, south-east Qld; NSW NC, NSW North Coast; SB, Sydney Basin; SEC, south-east corner). Three subclasses of Lowland Rainforest of Floodplains and two subclasses of River-flat Eucalypt Forest on Coastal Floodplains were recognised in the cluster analysis. Dashed ovals represent areas in which the ecosystem may be more widely distributed than indicated by the number of samples.

poorly reflected in spatial data layers. Predictive performance generally improved with increasing elevation, reflecting the predominance of Coastal River-flat Eucalypt Forest and Subtropical Floodplain Forest (north coast) on elevated terraces and mid-upper floodplain environments. Samples of Subtropical Rainforest (C12) were particularly strongly associated with soils with high phosphorus, organic and silt contents at intermediate elevations (Table 5).

Discussion

Our study reinforces the necessity of modification and extension of vegetation classifications as new data become available, in a way that addresses the sensitivity of clustering solutions to the choices of algorithms, resemblance measures, transformations and data structure (Wiser and De Cáceres 2013; Tichý *et al.* 2014). The relatively strong

correspondence between our revised classes and those of Keith and Scott's (2005) legacy classification is both surprising and re-assuring, given the biases and gaps they identified in the available data. Despite incorporating approximately three times the number of samples and a much larger geographic and climatic range than the original data set, Chameleon retrieved clusters that were clearly related to the units of both qualitative and quantitative reference classifications. Allowing for differences attributable to the geographic expansion of the original sample data set, we demonstrated that our new clusters represent a similar partitioning of the major environmental gradients underlying the definition of the original units, albeit with slightly different boundaries and levels of thematic detail.

Conservation implications

Our revised classification of coastal floodplain forested wetlands strengthens the capacity for effective conservation

Cluster		Qld			Vic	
Fuzziness coefficient	f = 1.1	f = 1.05	f = 1.0	f = 1.1	f = 1.05	f = 1.0
Distance to noise class	n = 0.9	n = 0.95	<i>n</i> = 1.0	n = 0.9	n = 0.95	<i>n</i> = 1.0
Noise	86 (75)	59 (51)	23 (20)	265 (100)	251 (95)	38 (14)
Mobile (most populous)	3 (3)	5 (4)	10 (9)		6 (2)	207 (78)
Other Mobile clusters		9 (8)			l (<l)< td=""><td></td></l)<>	
C2 Saltmarsh	3 (3)	2 (2)	6 (5)			
C7 Swamp Sclerophyll Forest	13 (11)	23 (20)	25 (22)			
C8 Lower Floodplain Rainforest			1(1)			
CII Estuarine Fringe Forest					4 (2)	6 (2)
C12 Subtropical Rainforest		1(1)	2 (2)			
C14 Swamp Oak Floodplain Forest	5 (4)	4 (3)	11 (10)			
C17 Subtropical Coastal Floodplain Forest	5 (4)	12 (10)	31 (27)			
C18 River-flat Eucalypt Forest			1(1)		l (<l)< td=""><td>3 (1)</td></l)<>	3 (1)
C19 Freshwater Wetlands			5 (4)		2 (<1)	9 (3)

Table 3. Attribution of Qld and Vic plots to NSW clusters by noise clustering.

Clusters with labels commencing with C refer to our preferred cluster solution (Fig. 1). Grey shading indicates the five forested wetland types. Mobile clusters potentially comprise new types identified by noise clustering. Three parameter settings were employed (columns) in which the fuzziness coefficient was progressively reduced and the distance to noise increased to force samples out of the noise class. Qld data were apparently somewhat incompatible with NSW data, but samples primarily attached to pre-defined clusters when forced. Vic data were even less compatible with NSW data and primarily formed a new cluster when forced, although a small number of samples attached to pre-defined clusters. Given the apparent incompatibilities between data sets, the results suggest there is only weak evidence for the existence of types other than those identified by the clustering of NSW data.

Table 4. Attribution of plots in a joint analysis using the Chameleon algorithm.

Class	Ι	2	3	4	5	6	7	8	9	10	П	12	13	14	15
C2 Saltmarsh	35	64												Ι	
C7 Swamp Sclerophyll Forest on Floodplains						3	93				3			I	
C8 Floodplain Warm Temperate Rainforest					3				85	12					
CII Estuarine Fringe Forest	2	67									12				19
C12 Floodplain Subtropical Rainforest					63				25				I		11
C14 Swamp Oak Floodplain Forest	3	6				T	5				75	2		I.	7
CI5 River-flat Eucalypt Forest (Coastal Plain)			T	28		23	3	18	T	22	I		3		
C17 Subtropical Coastal Floodplain Forest			38	14		2		28		15		2	Ι		
C18 River-flat Eucalypt Forest (Coastal Plain)			I.	I.				I	2			64	23		8
C19 Coastal Freshwater Lagoons								I		5	10	10	3	49	32
Queensland	8	3	П		I		21		I	3	П	10	13	6	12
Victoria		4											4	3	89

Rows 2–11 represent the distribution of NSW samples from each class (column 1) among Chameleon clusters (columns 2–16) (% of samples in each class). Rows 12 and 13 represent the distribution of Qld and Vic samples among clusters (% of all samples).

by promoting confidence in existing legislative instruments and providing a stronger evidence base for decisions and prioritisation. Our results demonstrate that units defined with relatively few data remain a robust basis for listings in NSW made 15 years ago. We identify only relatively minor adjustments required to recognise important compositional variation within the units that can easily be accommodated within the existing classification framework. This is significant because it avoids major changes to the concept of the communities as currently applied through the natural resource management infrastructure.

Our results demonstrate that methods capable of resolving complex patterns from semi-consistent data sets are critical to support evidence-based conservation decisions because erroneous or artefactual analyses may have conservation costs. For example, uncertainty around Keith and Scott's (2005)

Table 5.	Model statistics for	individual BRT mo	dels for floodplain f	forested wetlands and c	losely-related ecosystems.

	CI9	C7	C6	C8	C14	C15	C18	C17	C12	C13
Deviance total (residual)	0.277 (0.121)	0.338 (0.159)	0.200 (0.099)	0.412 (0.133)	0.471 (0.307)	0.545 (0.359)	0.454 (0.126)	0.376 (0.179)	0.200 (0.048)	0.159 (0.053)
Deviance explained (%)	56	53	50	68	35	34	72	52	76	67
Deviance cross-val. (±s.e.)	0.182 (0.004)	0.281 (0.008)	0.164 (0.006)	0.284 (0.008)	0.379 (0.009)	0.463 (0.006)	0.206 (0.016)	0.263 (0.008)	0.129 (0.006)	0.109 (0.005)
Correlation training data	0.742	0.755	0.670	0.854	0.567	0.586	0.842	0.704	0.863	0.802
Correlation cross-val. (±s.e.)	0.522 (0.026)	0.285 (0.024)	0.261 (0.041)	0.469 (0.02)	0.387 (0.018)	0.320 (0.015)	706 (0.027)	0.471 (0.025)	0.405 (0.034)	0.371 (0.033)
ROC training	0.961	0.980	0.974	0.99	903	0.915	0.988	0.964	0.997	0.987
ROC cross-val. (±s.e.)	0.893 (0.011)	0.822 (± .018)	0.839 (± .020)	0.892 (0.009)	0.812 (± .015)	0.790 (0.010)	0.959 (0.009)	0.877 (0.012)	0.955 (0.006)	0.922 (0.02)
Elevation med. (%)	3 (18.6)	6 (11.8)	7 (10.5)	21 (11.6)	3 (23.1)	11 (15.4)	60 (17.5)	30 (18.3)	30 (17.5)	7 (4.9)
Elevation range (m)	-3-330	-3-24	I-42	0–385	-2-35	-1-120	0-440	0-440	0-420	-1 - 39
Distance to stream med. (%)	90 (3.6)	230 (10)	180 (4.1)	29 (6.9)	100 (5.6)	80 (3.9)	30 (5.8)	70 (10.7)	30 (6.6)	108 (2.0)
Distance to stream range (m)	0-2180	0-2120	0–3820	0–2625	0–2490	0–2000	0-1260	0–1730	0–290	I-2670
Distance to alluvium med. (%)	0 (1.6)	490 (7.5)	300 (12.5)	0 ()	0 (6.3)	0 (11.7)	0 (16.6)	0 (7.9)	0 (0.7)	0 (12.6)
Distance to alluvium range (m)	0–8970	0–6530	04990	0-6413	0–9750	0–5580	0–1780	0-2310	0-1300	0–3253
Distance to barrier med. (%)	0 (4.1)	140 (10.3)	100 (4.8)	3920 (3.4)	1270 (21.3)	630 (12.6)	0 (0.7)	0 (2.8)	4290 (8.0)	126 (3.0)
Distance to barrier range (m)	0–9570	0–9680	0-9610	50–9990	0–9900	0-10,000	0–9600	0–9620	50-9910	0–9355
Distance to estuarine med. (%)	0 (3.3)	450 (6.0)	250 (7.1)	2300 (2.6)	100 (8.2)	920 (6.9)	0 (0.4)	0 (5.4)	4160 (7.0)	610 (5.6)
Distance to estuarine range (m)	0-9510	0–9700	0–5690	50–9970	0–9830	0-9410	0–9980	0–9980	70–9810	0–7760
Cation exch. cap. med. (%)	11.0 (19.6)	8.2 (8.5)	7.2 (12.1)	(3.3)	9.4 (2.8)	9.6 (8.9)	12.2 (7.5)	10.2 (9.9)	9.7 (4.4)	8.1 (1.8)
Cation exch. cap. range	6.2–23.4	3.7–12.5	3.7-11.4		3.6-14.2	4.2–14.7	7.5–19.6	5.2–18	6.0–16.1	4.2–11.4
Total phosphorus med. (%)	0.028 (4.9)	0.024 (7.6)	0.022 (7.6)	0.026 (2.3)	0.026 (3.6)	0.025 (8.1)	0.025 (2.1)	0.027 (6.0)	0.030 (12.0)	0.023 (5.9)
Total phosphorus range	0.017– 0.054	0.015-0.047	0.016-0.034	0.015– 0.047	0.015-0.044	0.016 0.045	0.015- 0.052	0.015– 0.054	0.018– 0.066	0.015– 0.042
Total nitrogen med. (%)	0.075 (2.3)	0.072 (5.4)	0.069 (9.8)	0.078 (4.1)	0.079 (2.1)	0.077 (5.3)	0.075 (2.9)	0.073 (3.8)	0.080 (0.9)	0.075 (1.7)
Total nitrogen range	0.050– 0.100	0.052-0.105	0.053-0.116	0.048– 0.134	0.054-0.115	0.057– 0.125	0.050– 0.112	0.051– 0.121	0.064– 0.109	0.043- 0.115
Sand content med. (%)	50 (2.4)	59 (10.7)	56 (6.9)	46 (4.5)	56 (6.0)	50 (7.6)	49 (1.5)	48 (7.0)	42 (4.5)	50 (5.6)
Sand content range	34–79	31–91	30–89	30–85	33–90	34–90	42–82	35–83	26–71	27–83
Organic content med. (%)	1.2 (7.3)	1.4 (9.4)	1.5 (10.4)	1.3 (3.3)	1.5 (10.3)	1.3 (5.7)	1.0 (32.7)	1.2 (6.6)	1.5 (15.0)	1.5 (4.7)
Organic content range	0.8–2.0	1.0–1.9	0.9–1.9	0.8–2.0	1.0–2.2	1.0–1.8	0.7–1.5	0.8–1.9	1.0–2.1	0.9–1.9
Clay content med. (%)	29 (6.0)	23 (6.3)	22 (3.8)	25 (3.9)	23 (3.6)	24 (7.3)	26 (3.8)	27 (7.6)	27 (2.6)	26 (4.1)

(Continued on next page)

Table 5. (Continued).

	CI9	C7	C6	C8	C14	C15	C18	C17	C12	C13
Clay content range	13-46	9–43	_4	15-43	10-47	9–46	16-40	18-40	18–36	8–42
Silt content med. (%)	15 (26.2)	13 (6.6)	15 (11.7)	18 (8.7)	13 (7.1)	14 (6.7)	15 (8.7)	17 (14.1)	21 (21.0)	16 (3.7)
Silt content range	4–33	4–37	5–30	6–34	3–31	4–28	7–24	5–26	8–3 I	5–27
Alluvial Plain	74	30	23	64	55	70	96	91	91	50
Estuarine Plain	18	25	27	5	33	7	I	3	I	19
Coastal Barriers	3	32	44	29	7	20	I	4	8	26
Undifferentiated	5	13	6	2	6	3	I	2	0	6

Column headings indicate samples comprising positive response (presence) values representing types described in Fig. 1 (samples in all other clusters were coded absent). Statistics for each predictor are contained in two rows and comprise the median value and percentage variance explained (1st row) and inter decile range (2nd row). Cells shaded grey collectively accounted for at least 50% of variation explained. The last four rows are the percentage of samples located on the major depositional systems described by Troedson *et al.* (2008).

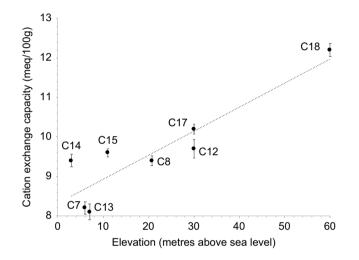


Fig. 4. Cation exchange capacity averaged $(\pm s.e.m.)$ over samples for each forested wetland cluster plotted against average sample elevation.

classification that arose from limited and geographically biased data or limited descriptions appears to have resulted in some misidentification of threatened ecological communities in the field, with implications for conservation decisions (e.g. NSWLEC 2005). Uncertainty in field identification may mean that resources are misdirected or offsets erroneously attributed. More broadly, failure to identify cross-jurisdictional relationships may mean that important examples of the remaining forested wetlands do not receive the full protection offered by conservation legislation. Our analytical approach produced strong evidence for the inclusion of ecosystems in Qld and Vic within the circumscription of Keith and Scott's (2005) legacy classes, thus providing a robust basis for national listing assessments, which are progressing with appropriate cross-jurisdictional extensions to distribution of NSW classes. Furthermore, hierarchical integration of the units of state-based vegetation classifications within our national classes (Appendix S3) opens opportunities to leverage the various resources (maps, descriptions, identification

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protocols) built to service state applications, because these will also have application to future state and national listings based on our forested wetland classes.

The thematic level of classification in our analysis [similar to Keith and Scott's (2005) earlier circumscription] facilitates efficient assessment, listing and protection of south-east Australian forest wetlands by aggregating a large number of functionally and compositionally related (and similarly threatened) state-based types (92 GET level 6 units, Appendix S3) in significantly fewer broad and ecologically robust units (5 GET level 5 units).

The environmental relationships identified in the analysis affirm prior conceptual models and provide a strong basis for spatial models that provide essential basis for conservation action. Key applications of such models include: (1) supporting regulatory assessments where proposed development may impact threatened remnant floodplain ecosystems; (2) identification of sites suitable for floodplain ecosystem restoration; (3) supporting projections of floodplain ecosystem distribution under future climates and planning climate adaptation strategies; and (4) calculating appropriate offset rules and ratios.

Performance of clustering algorithms

We attribute the performance of Chameleon in large part to its novel approach to modelling inter-sample relationships. Methods traditionally applied to clustering vegetation data typically employ either agglomerative or divisive methods that incorporate merge or split decisions based on the aggregate properties of intermediate clusters. Such methods require either unrealistic assumptions concerning the structure of the data and/or sequential merge/split decisions that cannot be reversed, and are necessarily sensitive to the composition of the dataset (Karypis *et al.* 1999; Han *et al.* 2012). In contrast, Chameleon operates on inter-connected neighbourhood sets structured, in our case, on the same similarity metric used in Keith and Scott's (2005) analysis. This approach confers at least two key advantages. First, given a sufficiently large neighbourhood (i.e. specifying a large number of nearest neighbours relative to the size of the expected cluster) the algorithm minimises the impact of incremental additions of new data because new connections can be built while retaining those between samples from the original set. Second, because the partitioning phase operates by dissolving connections between relatively weakly-connected samples, the resulting clusters comprise sets of samples unified by inter-connectivity rather than central-tendency. The significance of this is that the pairwise relationships between samples that underpinned Keith and Scott's (2005) agglomerative clusters were preserved (and reflected more faithfully) in our Chameleon clusters provided they were not displaced by a sufficiently large number of more strongly inter-connected samples.

Chameleon's relatively novel multi-stage clustering model also confers a sensitivity to the internal characteristics of individual clusters and the ability to adapt automatically to the structure of the dataset rather than being dependent on a static model (Karypis *et al.* 1999). These features underpin its capacity to detect clusters of irregular shape and density, although potentially at the cost of a greater risk of retrieving clusters, which represent noise or artefacts in the data. We concluded this was likely the case in analysis of the joint state data, where Chameleon retrieved a relatively large and heterogenous cluster of samples located predominantly in Vic.

We established independently, via noise clustering, that Vic data samples had very low affinity to clusters representing NSW forested wetland types, suggesting the data were either incompatible or sampled a novel vegetation type. Four lines of circumstantial evidence support the first interpretation. First, a very low fuzziness coefficient and high distance to noise class was required to force samples from the noise class and even then, the samples predominantly coalesced in a single mobile centroid. This suggests that the Vic data were characterised by a much higher degree of noise than NSW or Qld data which could explain why few samples had even moderate affinity to the fixed centroids. Second, Vic samples were characterised by very high percentages of exotic species and very variable diversity of native species suggesting a relatively high proportion of plots sampled vegetation in degraded states. Third, descriptions of Vic forested wetland types resemble Keith and Scott's description of River-flat Eucalypt Forest on Coastal Floodplains, at least qualitatively, in terms of composition and dominant species, suggesting that it is unlikely that forested wetlands of Victoria comprise an ecosystem so novel as to cause the behaviour of the data under semisupervised clustering described above. Finally, samples coerced from the noise class predominantly coalesced in a single mobile cluster (Table 3) characterised by a wide range of species, which although frequently recorded, rarely occur together. In summary, both the quantitative and qualitative evidence for the existence of subtropical-temperate forested wetland types other than those identified by Keith and Scott (2005) is weak, although this does not preclude the possibility of other types emerging following future sampling. We conclude that using Chameleon in combination with noise clustering enhanced our capacity to identify ecologically questionable clusters.

Overall, we placed less confidence in our attribution of Qld data to NSW types by noise clustering because it depended on a progressive tightening of the analysis parameters to coerce the samples from the noise class. In comparison, Chameleon was able to attribute the samples directly to NSW classes because they comprised (as determined by inter-sample similarity) parts of the interconnected sets. Noise clustering identified a small number of samples (10), which seeded an independent cluster potentially indicating the existence of a different forested wetland ecosystem occurring in Qld. While this is worthy of future investigation, we conclude there is insufficient evidence to warrant recognition of a novel ecosystem at this time because the number of samples is small, all of the REs identified as occurring on floodplains in Qld can be attributed with confidence to one of the five recognised NSW types and the samples, which made up independent cluster lacked any cohesive compositional features.

Environmental gradients

Our results corroborate Keith and Scott's (2005) model of the distribution of floodplain forested wetland communities in relation to gradients in soil fertility, salinity and moisture regime, further reaffirming the robustness of both the legacy and revised classifications (Table 4). Elevation was the most consistently informative predictor in modelling the distributions of different vegetation types in alluvial depositional systems, in combination with soil properties including cation exchange capacity and organic content (Table 4). We interpreted trends in elevation as an indirect measure of catchment position and soil moisture availability and/or degree of waterlogging because our spatial models indicated that soil organic matter content is higher in lowlying areas, consistent with the accumulation of peat layers in swamp communities (Units C6, C7). Although we were unable to quantitatively assess gradients in salinity, elevation is also a potential proxy for salinity through the influence of marine-influenced groundwater.

Aggregate patterns in different soil properties are consistent with a fertility gradient, with measures such as phosphorus and nitrogen content tending to rise in parallel with cation exchange capacity, even if those measures were not always informative of the distribution of individual communities (Table 4). Fertility was inversely correlated with the degree of waterlogging, tending to rise with increasing elevation (Fig. 4). Samples representing swamp sclerophyll forests (C7) and sandplain forests (C6) at lower elevations tended to be located further from streams than *Eucalyptus* forests at higher elevations (Table 4). This is consistent with depositional patterns on the floodplain, which are characterised by large quantities of coarse material deposited adjacent to channels with sediment quantities and particle sizes declining with distance from the channels over the floodplain (Troedson *et al.* 2008). High levels of organic matter were estimated to be present in samples representing cluster C12 (Subtropical Rainforest), which may reflect high levels of productivity in this vegetation type. Our results support the conclusion that the communities occurring on coastal alluvial floodplains occupy different parts of gradients in moisture and nutrient availability and our results offer a more nuanced interpretation than was possible with the original model (Fig. 2).

results indicate that Subtropical-Temperate Our Forested Wetlands of south-east Australia are strongly, but not exclusively associated on alluvial floodplains and may occur on other low-lying areas receiving minimal fluvial inputs or no supply of clastic sediments. Such sites may be influenced by near-surface groundwater or may accumulate surface water temporarily after heavy rain. In general, the distribution of forested wetlands on non-floodplain landforms is restricted to the landward portions of coastal barrier systems on back-barrier flats and swamps, as well as other parts of coastal barrier systems in areas where marine sediments have been reworked and silts, clays and organic matter have been incorporated. Such instances are most reliably diagnosed by the presence of characteristic species (Appendices S2, S4) and are generally restricted to the same climatic and geographic regions as documented floodplains.

Subtropical-Temperate Forested Wetlands may also occur on estuarine or marine depositional systems where these intergrade with fluvial deposits on the lower floodplains; however, it is unlikely that such examples ever made up more than a small proportion of the pre-European distribution. In those systems, Subtropical-Temperate Forested Wetlands are most frequently recorded on estuarine swamps in areas lacking saline groundwater, inter-barrier creek deposits within or along the margins of barrier systems where reworking of marine barrier sands has incorporated organic matter from local vegetation and fluvial sediments derived from upstream fluxes (Myerscough and Carolin 1986).

Application to global conservation assessments

Our quantitative synthesis of forested wetlands in south-east Australia constitutes one of the first applications of the GET, a framework for scaling up local typologies and integrating conservation risk assessments across local to global scales (Keith *et al.* 2020). Leveraging lower levels of the global ecosystem typology depends on comprehensive, internally consistent local classification systems, built from the bottom up using ground observations, as well as an understanding of hierarchical relationships among different systems. Forested wetlands are a form of Palustrine Wetlands (GET Level 2 -Biome) - azonal, vegetated ecosystems occurring at the interface between terrestrial and freshwater realms and regulated by water regimes ranging from permanent shallow water under which peat may accumulate in anoxic conditions, to intermittent or even highly infrequent inundation events (Keith et al. 2020). Subtropical-Temperate Forested Wetlands (GET Level 3 - Ecosystem Functional Group) occupy a niche found on lowland flats, floodplains and riparian corridors within subtropical or temperate climate zones (Mac Nally et al. 2020). These ecosystems are net accumulators of resources (water, nutrients) and hence more productive than surrounding lands from which some of those resources derive (Keith et al. 2020). Globally, Subtropical-Temperate Forested Wetlands are among the most threatened of ecosystems and there is anecdotal evidence to suggest the degradation of theses wetlands in south-east Australia may be more advanced than in other countries (Good et al. 2017).

Good et al. (2017) recognised eight compositionally and geographically distinct floodplain and riparian zones on the Australian continent. The distribution of Subtropical-Temperate Forested Wetlands covers all or part of four of these, namely the South West Coast, South East Coast, North East Coast and Tasmania. The forested wetlands of south-east Australia differ strongly in composition from those occurring in Western Australia and Tasmania, having no dominant species in common with the former, and only minor instances of overlap in dominant species with the latter (Good et al. 2017). As such, we define Subtropical-Temperate Forested Wetlands of coastal south-east Australia as a Biogeographic Ecotype (GET Level 4) below which our classification of forested wetlands is nested. Regional typologies (PCTs, REs and EVCs represent Level 6 units (sub-global ecosystem types) within IUCN's GET.

Eastern Australia contains the only substantial representation of Subtropical-Temperate Forested Wetlands in the Pacific region although they occur to a more limited extent in New Zealand (Mac Nally et al. 2020) where floodplains are smaller and predominantly occupied by sedgelands and scrubs. Despite its smaller geographic footprint, New Zealand hosts a similar range of temperature zones to south-east Australia. Singers and Rogers (2014) identified 22 wetland ecosystems distributed across zones ranging from warm humid to cold-subalpine. These encompass a diverse range of rushlands, tussocklands, sedgelands, cushionfield, reedlands, mossfield herbfield and flaxlands of which five occur in coastal lowland areas and only one is a forested wetland. These numbers are broadly comparable to the those of Keith and Scott (2005) (five forested and one non-forested wetland units) suggesting the two classifications are broadly similar in hierarchical status. Floodplains are of negligible size on the smaller islands of the South Pacific and thus unlikely to exhibit sufficient diversity of assemblages to assess their classification status.

Conclusion

Vegetation classification systems are typically dynamic and require modification to accommodate new classes and revised circumscriptions as new data become available (Wiser and De Cáceres 2013). Unlike species taxonomy, there are no formal conventions which support the development of vegetation classification systems. This is problematic when the units of those classifications are afforded legal status under conservation regulatory systems, because interpretations of circumscription other than those specifically referenced in the legal determination may have no legal standing (Smith 2009; NSWLEC 2010). Our approach illustrates three key requirements to address this problem: (1) an objective basis for a revised classification incorporating systematic field observations sampling the range of variation and appropriate numerical clustering techniques; (2) establishing explicit, quantitative links to the units of the original classification upon which current listings were based; and (3) the integration of classification systems from local to global scales (De Cáceres et al. 2015). Our analyses support the retention of the existing five types as a basis for a national classification and provide new insights into the distribution and composition of these ecosystems in relation to the major environmental gradients structuring floodplain ecosystems. Our approach facilitates the revision of existing listings to reflect new data on the composition and distribution of forested wetlands, while minimising the confusion and disruption which often results from a revised classification, and enables users to utilise information and tools pertaining to classifications of finer thematic scale in field applications.

Supplementary material

Supplementary material is available online.

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Data availability. Queensland vegetation plot sample data used in the analyses reported herein are available at http://www.portal.aekos.org.au/ AEKOS (2021). NSW plot data are available at https://www.environment.nsw.gov.au/research/Vegetationinformationsystem.htm (NSW DPIE 2020). Victorian plot data are available on request from the Victorian Department of Environment, Land, Water and Planning https://www.delwp.vic.gov.au.

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