



# Reconciling approaches to biogeographical regionalization: a systematic and generic framework examined with a case study of the Australian continent

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## ABSTRACT

**Aim** To develop a systematic and generic framework for biogeographical regionalizations that can assist in reconciling different approaches and advance their application as a research tool.

**Location** The Australian continent is used as a case study.

**Methods** A review of approaches to biogeographical regionalization revealed two basic methodologies: the integrated survey method and the parametric approach. To help reconcile these different approaches, we propose a simple, four-step, flexible and generic framework. (1) Identification of the thematic foci from the three main themes (composition and evolutionary legacy; ecosystem drivers; ecosystem responses). (2) Proposal of a theory defining the purpose. (3) Application of a numeric agglomerative classification procedure that requires the user to make explicit assumptions about attributes, the number of classification groups, the spatial unit of analysis, and the metric for measuring the similarity of these units based on their attribute values. (4) Acquisition of spatial estimates of the required input attribute data. For this case study, an agglomerative classification strategy was applied using the functions within PATN 3.03, a software package facilitating large-scale, multivariate pattern analysis. The input data to the classifications were continental coverages of 11 environmental variables and three indices of gross primary productivity stored at a grid cell resolution of *c.* 250 m. The spatial units of analysis were surface hydrological units (SHU), which were derived from a continental digital elevation model based on the contributing areas to stream segments or the area draining into a local sink where there is no organized drainage. The Minkowski series (Euclidean distance) was selected as the association measure to allow weightings to be applied to the variables.

**Results** Two new biogeographical regionalizations of the Australian continent were generated. The first was an environmental domain classification, based on 11 climatic, terrain and soil attributes. This regionalization can be used to address hypotheses about the relationship between environmental distance and evolutionary processes. The classification produced 151 environmental groups. The second was a classification of primary productivity regimes based on estimates of the gross primary productivity of the vegetation cover calculated from moderate resolution imaging spectroradiometer (MODIS) normalized difference vegetation index (NDVI) data and estimates of radiation. This classification produced 50 groups, and can be used to examine hypotheses concerning productivity regimes and animal life-history strategies. The productivity classification does not capture all the properties related to biological carrying capacity, process rates and differences in the characteristic

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biodiversity of ecosystems. Some of these ecologically significant properties are captured by the environmental domain classification.

**Main conclusions** Our framework can be applied to all terrestrial regions, and the necessary data for the analyses presented here are now available at global scales. As the spatial predictions generated by the classifications can be tested by comparison with independent data, the approach facilitates exploratory analysis and further hypothesis generation. Integration of the three themes in our framework will contribute to a more comprehensive approach to biogeography.

### Keywords

Biogeographical regionalization, conservation biogeography, continental classification, environmental domains, evolutionary processes, gross primary productivity, habitat template.

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## INTRODUCTION

Biogeographical regions are used for various purposes, including systematic conservation planning (Olson & Dinerstein, 1998; Olson *et al.*, 2001; Whittaker *et al.*, 2005). For example, the Interim Biogeographical Regionalisation of Australia (IBRA; Environment Australia, 2000a) was used to evaluate the conservation status of species and ecosystems (Land and Water Australia, 2002), and a global biogeographical regionalization has been used to evaluate international conservation priorities (Olson *et al.*, 2001; Kier *et al.*, 2005). Biogeographical regions are also considered useful for identifying areas that can be subject to similar natural resource management prescriptions and for extrapolating the results of site-scale experiments (Hobbs & McIntyre, 2005).

The concept of biogeographical regions, however, remains vexed, and there is no agreed theoretical basis as to what class of phenomena they represent. As discussed below, biogeographical regions are generated to reflect a range of biological, physical and ecological phenomena. It is debatable whether biogeographical regions are in fact natural objects that can be revealed through research, or just artificial constructs. In addition, an accepted methodology and a standardized approach to their identification and mapping have yet to emerge. Consequently, a plethora of methods are applied by different schools of biogeography in terms of the chosen scale of analysis, the types of variable used to delineate areas, data sources (e.g. *in situ* vs. *ex situ* observations), and methods of classification (in particular, numeric vs. qualitative techniques).

In this paper we consider the problem of identifying and mapping biogeographical regions. We review current approaches in terms of their intended purposes, major differences and limitations. A new framework is proposed that may have potential to help reconcile the different approaches and facilitate the research value of biogeographical regionalizations. We then investigate the utility of this approach by examining geographical patterns in measures of environmental similarity and vegetation productivity, using the Australian continent as a case study.

## Current approaches

Various approaches have been developed for mapping the distribution of biological and ecological phenomena. The land surface can be geographically delineated biotopically on the basis of discontinuities in the abiotic environment, biocoenotically using discontinuities in the distribution of biota (Clifford & Stephenson, 1975), or by some combination or integration of the two. At smaller (in cartographic terms) geographical scales, the stated intention is usually to map geographical entities referred to as bioregions, biomes or, more recently, ecoregions. At larger cartographic scales, mapped units are referred to as regional ecosystems, land systems or landscape ecosystems.

Biogeographers have long been concerned with biocoenotic classification based on significant regional differences in the distribution of plant and animal species, with early biogeographical regions reflecting globally scaled delineations in taxonomic compositions, inferred evolutionary histories, and usually shared climatic domains (Sclater, 1858; Wallace, 1859; see Ebach & Goujet, 2006).

Global biomes are recognized based on quantifiable relations between climate, plant primary productivity, and correlated vegetation growth forms and structure (the height, density and layering of the vegetation; Holdridge, 1947; Budyko, 1974; Box, 1981; Prentice *et al.*, 1992). Biomes thus defined do not attempt to map the taxonomic characteristics of the vegetation cover. They have been developed in the field of Earth systems and global change science, and are commonly used to map continent-scale potential vegetation cover and as input to climate change models (Cramer, 2002).

Interest in Victorian-era bioregions has been rekindled through their use in global ecoregionalizations. Olson *et al.* (2001) defined ecoregions as relatively large units of land containing a distinct assemblage of natural communities and species, with boundaries that approximate the original extent of natural communities prior to major land-use change (Dasmann, 1973, 1974; Udvardy, 1975; Bailey, 1989). The global ecological regionalization of Olson and colleagues used both biotopic and biocoenotic classification approaches. At a

continental level, ecoregionalizations have been produced for the USA and Canada based on a four-level nested hierarchy of ecoregions (Bailey, 1995; Loveland & Merchant, 2004; Omer-nik, 2004). In these systems, higher hierarchy levels are determined biotopically (e.g. based on gradients in selected climatic variables), while lower levels are defined by a combination of biotopic (e.g. landform) and biocoenotic (e.g. vegetation formation) considerations. Ecoregionalizations have also been developed for the Netherlands (Klijn *et al.*, 1995), New Zealand (Warry & Hanau, 1993), Bolivia (López and Zambrana-Torrel, 2006), Germany (Haase, 1989) and the world (Bailey & Hogg, 1986). Bailey (2005) argued that ecoregions can be thought of as ‘macroecosystems’: ecosystems of a higher order.

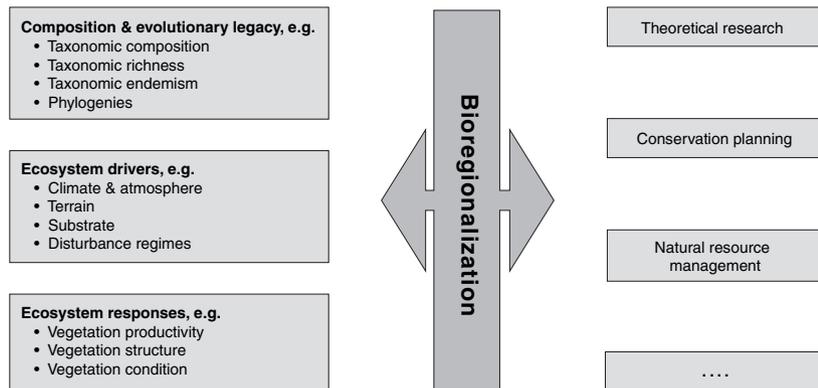
At a finer geographical resolution, land systems (or their equivalent) remain the cornerstone of many conventional mapping exercises. These were defined by Christian & Stewart (1968) as an area, or group of areas, throughout which a recurring pattern of topography, soils and vegetation can be recognized. Sub-continental regional land system studies have been undertaken for extensive areas (c. 500,000 ha) of Australia (Christian & Stewart, 1953) and Papua New Guinea (Scott *et al.*, 1985). Land systems are usually subdivided into land units largely on the basis of topographic sequences. Land-system mapping has also been undertaken in Lesotho (Bawden & Carroll, 1968), Nigeria (Bawden & Carroll, 1972), Zambia (Mansfield *et al.*, 1975–1976) and Ethiopia (King & Birchall, 1975). The subcontinental regional ecosystem mapping of Neldner *et al.* (2005) reflects the influence of both the hierarchically structured

ecoregions concept and land-system mapping. Landscape mapping has also been applied in Russia, with a comparable mix of ecoregion and land-system approaches (Wagner, 1997). The vegetation classification of Mucina & Rutherford (2006) for southern Africa covered three levels (biome, bioregion, vegetation type).

**Methodological issues**

Our brief review of biogeographical regionalizations suggests that there are three main thematic foci: (1) the composition and evolutionary legacy as represented by the taxonomy, phylogeny and genetic structure of plant and animal species, (2) the drivers of ecosystem processes (usually exogenous environmental variables such as climate, water availability, soil and air), and (3) measures of ecosystem responses, such as vegetation productivity (Fig. 1).

A biogeographical regionalization can reflect variables from any one or combination of these themes, depending on the purpose of the exercise. Distinguishing between the three is critical to understanding biogeographical patterns. For example: (1) the taxonomic composition of an area can reflect historical contingencies rather than prevailing environmental conditions; (2) system-level properties can be maintained despite changes in species composition; (3) a focus on ecosystem drivers can be necessary if the purpose of the biogeographical regionalization is to predict future patterns, such as responses to future climatic conditions; and (4) analyses based on ecosystem response variables enable exploration of extant conditions and impacts.



**Figure 1** The three main themes used as foci of study for biogeographical regionalization. Variables from any one theme, or any combination of variables from the three, can be used to define biogeographical regions with the choice of variables depending on the purpose of the mapping exercise. Here we assume the purpose is related to the conservation of biodiversity. First, variables can be used that account for the taxonomic composition and evolutionary genetic legacy that characterizes an area. These variables can include primary data on species distributions and secondary variables such as taxonomic richness and endemism, along with variables that can be inferred from molecular data related to phylogenies and genetic structures. From an ecosystem perspective, the other categories of variables can be considered as either ecosystem drivers or ecosystem responses. Ecosystem drivers are usually exogenous physical environmental variables. The primary environmental regimes can be approximated using climatic and atmospheric parameters, substrate attributes (soil/regolith), terrain attributes, and data that describe both natural disturbance regimes (most commonly fire regimes, but also flooding regimes in certain landscapes) and human land-use impacts. Ecosystem responses most commonly account for the productivity, structure and condition of the vegetation, where productivity refers to gross primary productivity; structure refers to the height, density and layering of vegetation cover; and condition refers to the extent to which the vegetation has been degraded by human impacts.

The issue of historical contingencies warrants further comment. Species evolve within areas from which they subsequently disperse. The taxonomic composition of a region will therefore reflect the extent to which it contains centres of origin, has been exposed to (or blocked from) dispersing organisms and propagules, or has been subject to large-scale destructive forces such as the Pleistocene glaciations. For example, Hopper & Gioia (2004) discussed the high level of localized endemism among the flora of south-western Australia resulting from that region's long period of isolation and environmental stability. The taxonomic composition of a region therefore can be the result of such historical processes and not the consequence of extant environmental ecosystem drivers. On the other hand, plant physiognomy and vegetation structure directly reflect the influence of insolation, water and nutrient availability on plant ecophysiology (Specht, 1981). In this way, similar vegetation structural formations are recognized in similar climatic conditions around the world (Box, 1981), although certain growth forms, with their associated levels of productivity, may not evolve or arrive by unassisted dispersal in all suitable areas. The widespread dispersal of plants and animals by humans, especially over the past few hundred years, is another contingency influencing a region's taxonomic composition. Freed from many ecological restraints, and given a helping hand by people to overcome natural barriers, invasive species can spread rapidly into new regions, especially if ecological equivalents are absent, extending into climatic conditions beyond those of their natural distribution. The invasion of Australia by the common prickly pear [*Opuntia stricta* (Haw.) Haw.] is a classical example (Johnson & Mayeux, 1992).

The question of the best method to identify and map biogeographical regions is strongly contested. Opinion is divided between an integrated survey approach (relying on qualitative, weight-of-evidence, expert interpretation) and a quantitative numeric parametric approach (Stewart, 1968; Loveland & Merchant, 2004; Hargrove & Hoffman, 2005). A fundamental limitation of the integrated survey approach is the assumption that biogeographical entities comprise spatially nested hierarchies (McMahon *et al.*, 2004), hence the use of a divisive classification procedure whereby a particular variable (or set of variables) is used to identify classes of biogeographical regions in each level of the nested hierarchy. However, geographical distance does not necessarily entrain biological, environmental or ecological distance (Mackey *et al.*, 1988); locations can be biologically similar yet geographically disjunct, and *vice versa*. Some natural phenomena are spatially nested, such as water catchments, but most ecological systems are not (Allen & Hoekstra, 1993).

Parametric approaches to land classification emerged following developments in GIS, environmental modelling and remote sensing (Austin & Cocks, 1978), leading to the development of a numeric approach to environmental classification and mapping (Mackey *et al.*, 1988; Belbin, 1989). Comparable approaches have been developed and applied to environmental classification and mapping in Canada (Mackey

*et al.*, 1996), the conterminous USA (Hargrove & Hoffman, 2005), South Africa (Fairbanks, 2000), New Zealand (Leathwick *et al.*, 2003), and tropical Australia (Mackey *et al.*, 1989, 2001). The parametric approach uses a bottom-up classification procedure, where geographical patterns are generated based on analysis of a relatively large number of spatial units such as grid cells or micro-catchments. The spatial units are agglomerated into classes based on a measure of their biological, environmental or ecological similarity. Thus classes of biogeographical regions can be spatially disjunct, adjacent or nested, depending on the measured similarity. Being an explicit procedure, the parametric approach has the advantage of forcing theoretical assumptions about how the land is classified to be made explicit. The use of an association metric allows the relative similarity of the resultant classes to be determined and also mapped.

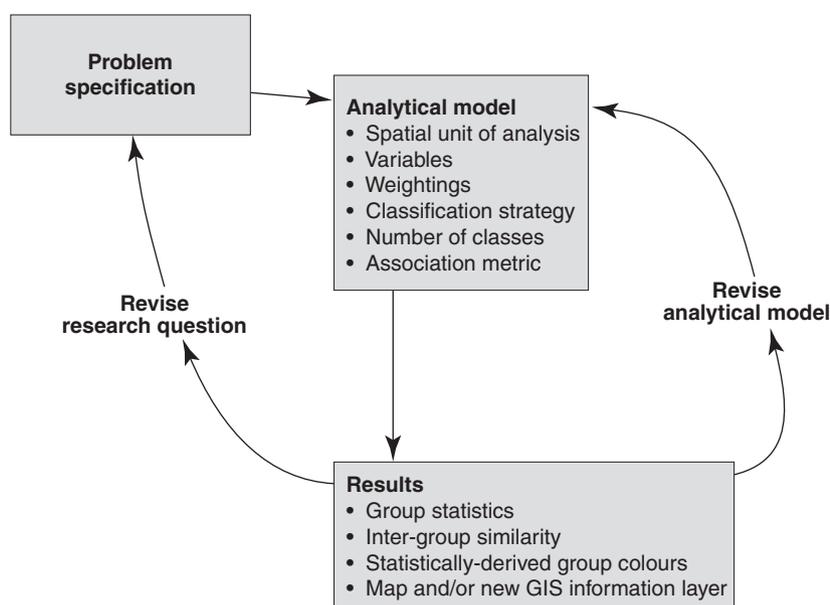
The various approaches to biogeographical regions can be reconciled by accepting that they are valid representations of different characteristics of the land and related biological, environmental and ecological processes. This is not to say that all biogeographical regionalizations are equally valid scientifically. Rather, we reject the notion that there is any single optimum regionalization, and argue that the adequacy of a classification must be tested using appropriate criteria for the intended purpose or application (Bailey, 1984). We argue that the parametric approach best facilitates such testing as it requires explicit statements of purpose and methods.

### Elements of a generic framework

The starting point for a biogeographical regionalization exercise should be a formal statement of the theoretical basis for the classification: what theory is invoked to explain the object of study? The resulting regionalization can then be viewed as an expression of the underlying theory, and interpreted as a working hypothesis on which testable predictions are based. The adequacy of a regionalization can be tested using independent data, acknowledging the difficulty of conducting robust tests of rejection in this field of study.

A generic analytical framework for biogeographical regionalization based on the parametric approach is described in Fig. 2.

The reference to 'ecosystems' also invites further explanation. Ecosystems are complex phenomena with properties that confound their identification, classification and mapping. Tansley's (1935) and other (e.g. Troll, 1950) views of ecosystems imply specific and natural geographical scales of expression. Alternatively, Allen & Hoekstra (1993) proposed that the ecosystem concept is scale-independent, being applicable at any scale, and serves only as a heuristic (albeit an important and useful one). Golley (1993) evaluated the concepts of ecosystems as natural objects vs. as an organizing scientific paradigm. Ecotopes (Tansley, 1935) are one expression of the former, and were defined by Troll (1950) as the smallest spatial unit that has homogeneous properties. However, logically, ecotopes can be recognized at various



**Figure 2** The parametric approach to biogeographical regionalization can be applied using a numeric geographical classification technique. The purpose of the regionalization mapping exercise must first be specified. An analytical model must be then proposed that details, *inter alia*, (1) the spatial unit of analysis; (2) the variables used to describe the spatial units; (3) the relative weightings of each variable; (4) the number of desired classes. An appropriate metric must be selected to measure the similarity (or dissimilarity) between spatial units based on the values of the input variables. It is assumed here that an agglomerative (cluster) numeric classification procedure is being applied. The results comprise a statistical summary of the resultant classification groups; measures of intergroup similarity; and the use of these statistics to map groups with colours indicating intergroup similarity. The results can be tested against hypothesized expectations, and the procedure revised and repeated as needed.

geographical scales depending on the scale of the defining properties.

We use the ecosystem concept here in both senses – as an organizing paradigm and as a natural object. However, we assume that ecosystems: (1) can be recognized at multiple space/time scales; (2) occur as non-nested hierarchies; and (3) are structured primarily by energy and material flows. We also note that many animals commonly utilize resources from many ecosystems (when defined in terms of the structure or floristic composition of the dominant autotrophs) and that, however defined, ecosystems are influenced by teleconnections (large-scale biophysical phenomena and processes that link geographically adjacent and disjunct ecosystems; Soulé *et al.*, 2004).

Figures 1 and 2 together outline the main elements of a generic framework for biogeographical regionalization. The other major element is the need to state the theoretical basis for the classification, as this provides the hypotheses and predictions that enable a regionalization's adequacy to be tested.

## Theory

The theoretical basis for a biogeographical regionalization will depend on the purpose of the exercise. Here we assume the purpose is to provide national-level information relevant to systematic planning (Margules & Pressey, 2000) for the conservation of biodiversity and related natural heritage values

(Mackey *et al.*, 2001). If a regionalization was sought for a different purpose, then other theories would need to be considered, for example, a regionalization to enable extrapolation of agricultural experiments might invoke Liebig's Law of the Minimum (van der Ploeg *et al.*, 1999). Here, our interest is in identifying theory that seeks to explain broad patterns in the three levels of biodiversity recognized internationally by the Convention on Biological Diversity: genetic, species and ecosystem (CBD, 1992). A major requirement is that it must be possible to generate spatial predictions based on the selected theories that can be tested with independent data. Here we consider two relevant theories that provide the basis for biogeographical regionalizations relevant to the 'ecosystem drivers' and 'ecosystem responses' themes of our framework.

### *Environmental domains and related speciation processes*

The modern evolutionary synthesis posits 'populations' as the unit of evolution (Mayr, 2001). Significant environmental differences between regions can function as the extrinsic isolating barriers that instigate allopatric speciation. Also, environmental gradients can provide the selective pressures that result in parapatric speciation. Furthermore, even if populations of a species are currently genetically identical, significant environmental differences in their locations may be harbingers of potential evolutionary change. Given this, we can hypothesize that a plausible indicator of actual or potential intraspecific genetic diversity, which may be leading to, or

indicative of, allopatric or parapatric speciation processes, as distinct from sympatric speciation (Bush, 1975), is a measure of the environmental distance (or dissimilarity) between the locations of populations of a species.

The extent of actual intraspecies variability (between the populations of a species) can be determined using appropriate molecular data. However, such data are currently available for only a limited number of species. In the absence of relevant molecular data for species, a biogeographical regionalization based on a classification of the environmental distance (dissimilarity) of landscapes would provide a generic, geographically based surrogate of intraspecies genetic variation and the extent to which populations of a species are potentially heading down the path of speciation. The geographical entities produced by such a classification can be called environmental domains.

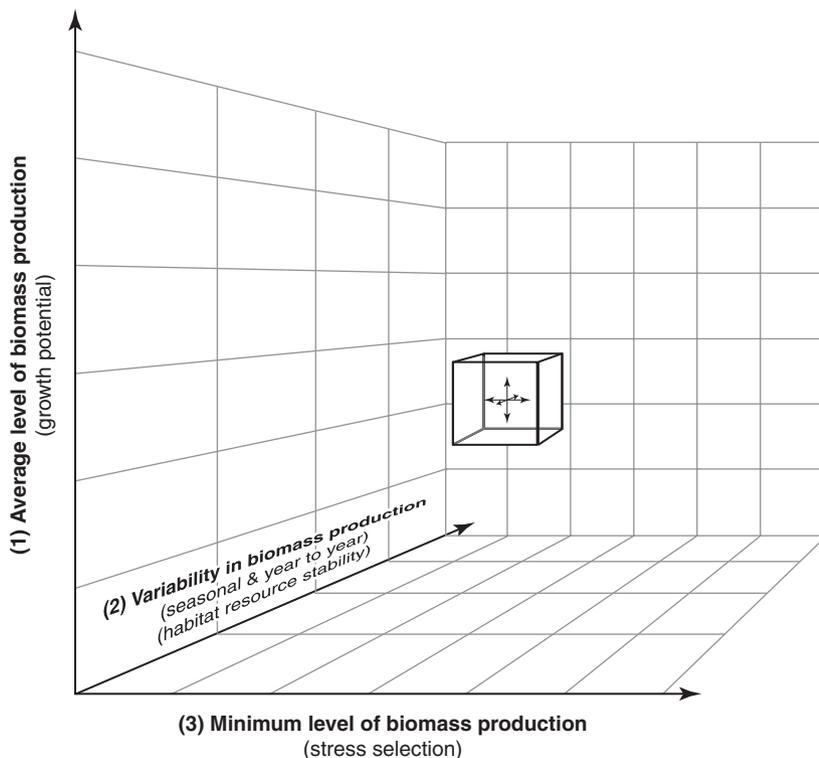
*The habitat templet and animal life histories*

In a series of papers, T.R.E. Southwood investigated how variability in the distribution and availability of habitat resources operates as a selective force on the evolution of animal life-history strategies and tactics (Southwood, 1962, 1977, 1988; Southwood *et al.*, 1983). The vegetation cover and structure can be considered as the habitat templet on which animal life-history strategies are forged (Townsend *et al.*, 1997), with natural selection promoting the persistence of species that can exploit the available habitat. In reviewing habitat templet models, Southwood (1988; see also Grime, 1977; Greenslade, 1983) identified a set of axes common to

various habitat templet schema: (1) habitat productivity as a measure of growth potential, (2) habitat resource stability, (3) adversity or stress. Theoretically, a given volume can be specified within the three-dimensional space defined by these axes that represents a 'productivity regime' (Fig. 3). Temporally, the set of conditions defining a given productivity regime can vary at the same location seasonally and from year to year. In the spatial dimension, there can be variability in the spatial extent and configuration of a given productivity regime.

Vegetation productivity can be defined in terms of the rate of plant photosynthesis: the rate of carbon assimilation or gross primary productivity (GPP). The biomass produced from the resulting photosynthate is the basis of terrestrial food webs (Berry *et al.*, 2007). A continental regionalization based on a classification of the spatial and temporal variability in the GPP of the vegetation cover would provide an approximation of productivity regimes as defined by Southwood's habitat templet theory, and enable testing of hypotheses based on this theory.

For example, we would expect that patterns in the large-scale movement of bird species reflect continental-scale productivity regimes. Gilmore *et al.* (2007) identified 342 Australian land and freshwater bird species known to move over large geographical distances. Different movement behaviour strategies are employed by bird species to obtain required habitat resources in a continent largely characterized by high levels of variability in both seasonal and year-to-year primary productivity. However, species can utilize the same productivity regime by possessing different movement behaviour strategies and utilizing resources at different spatial and



**Figure 3** Schematic representation of the three dimensions to the habitat templet defined as (1) average level of biomass production; (2) seasonal and year-to-year variability in biomass production; and (3) minimum levels of biomass production. Conceptually, a three-dimension productivity regime can be identified in this data space and the geographical distribution subsequently mapped so long as the necessary spatial and temporal data are available for a study area – in this case, the Australian continent. As used here, 'productivity' is defined as the gross primary productivity (GPP) of an area's vegetation cover.

temporal scales. Nonetheless, we could predict that species with particular patterns of movement behaviour are more likely to be found in a given productivity regime, so that, for example, broad-ranging nomads should be more prevalent in landscapes with low levels of highly variable primary productivity, while largely resident bird species should be better supported in reliable and highly productive locations.

## METHODS

We used the Australian continent as a case study to explore our claim that the framework is generic (in that it is relevant to all kinds of terrestrial landscapes), and that it facilitates a systematic approach to developing biogeographical regionalizations. The Australian continent is a suitable case-study system because it encompasses a wide variety of environments (Groves, 1999) and is biologically mega-diverse.

We generated two biogeographical regionalizations of the Australian continent to provide examples of the second and third of the three main thematic foci (composition and evolutionary legacy, ecosystem drivers, ecosystem responses) (Fig. 1). These biogeographical regionalizations were designed to address the two theories discussed above (the environmental domain and habitat templet theories). Ongoing research is addressing questions aimed at the first thematic focus (composition and evolutionary legacy) and will be reported elsewhere.

The analytical model described in Fig. 2 was applied here. The same spatial units of analysis, association metric and classification strategy were selected for both regionalizations. However, the variables, variable weightings and number of final classes (or classification groups) differed. A significant effort was invested in developing the necessary continental spatial data of the selected variables. While existing data based on standard methods were used where possible, a number of variables (specified below) needed to be generated using novel approaches, as they did not exist in a suitable form.

### Spatial units of analysis

The surface hydrological unit (SHU) was selected as the spatial unit of analysis for the regionalizations. SHUs delineate the subcatchments of the segments of a gridded stream network that represents the streamlines mapped on the 1 : 250,000 topographic map series of Australia, where a segment is the section of a stream between tributary junctions (Stein, 2005). Where there are no mapped streamlines, subcatchments were supplemented by the catchment areas of sink points such as local depressions or ephemeral lakes. The resulting data set, generated using a 9-s digital elevation model (DEM) (Hutchinson *et al.*, 2001), comprised approximately 1 million SHU for the Australia continent.

We selected SHUs as the spatial units of analysis, rather than a conventional grid of graticules defined by a usually arbitrary cell size, because they have the advantage of being natural features that relate to the local fluxes of water and nutrients,

vary in size according to terrain complexity, and generate classification boundaries that are ecologically relevant and transparent to interpretation (Mackey *et al.*, 2001).

### Environmental domains – variables and spatial data sets

We selected variables using the primary environmental regime (PER) schema proposed by Mackey *et al.* (1988). The PERs comprise processes that determine the distribution and availability of heat, light, water and mineral nutrients, the drivers of biotic response. At smaller cartographic scales, the PERs are dominated by physical processes, while at larger scales they are biologically regulated (Mackey & Lindenmayer, 2001). Based on previous research (Mackey *et al.*, 1988, 1989, 1996, 2002; Mackey, 1993), 11 environmental variables were selected to approximate the PERs at a continental scale: six climatic variables, four terrain variables and one substrate variable (Table 1).

We used variables from both the meso- and topographic scales that are known to affect the primary environmental regimes. The landforms distinguished by the terrain attributes capture important differences in hydrological, geomorphological and ecological processes. For example, the distinction between hill slopes and valley bottoms is recognized as identifying erosional and depositional environments, both of which have different geomorphological processes driving substrate development which, in turn, influences vegetation response (Gabler *et al.*, 1994). At the landscape scale, the flatness class variable data set (Figure S1i in Supplementary Material) provides an indication of the distribution of these biogeomorphic processes (Stallins, 2006) and the spatial relationships between them. Surface slope (Figure S1h) is correlated with the velocity of surface and shallow subsurface flow, influencing soil water content, erosion potential and soil formation (Gallant & Wilson, 2000) and associated biological responses such as GPP (Roxburgh *et al.*, 2006). Catchment contributing area (Figure S1g) is correlated with the volume of water flowing to a point and hence is a major determinant of the catchment water balance (Gallant & Wilson, 2000).

Spatial data sets were generated for the 11 variables by first generating values at a 9-s cell (World Geodetic System 84) resolution and then calculating aggregated values for each SHU. The methods used to generate the 9-s cell resolution data are described below.

### Climate

Gridded estimates of five interpolated climate surfaces were generated using the ANUCLIM program (Hutchinson, 2005) and a 9-s DEM (Hutchinson *et al.*, 2001). The interpolated surfaces are based on long-term monthly averages from the available weather-recording network. A sixth surface, annual availability of water in the environment (*W*) (mm), was generated using the formulation of Berry & Roderick (2002).

Variable	Spatial statistic calculated for each SHU (surface hydrological unit)
Annual mean temperature (°C)	Mean
Maximum temperature of warmest month (°C)	Mean
Minimum temperature of coldest month (°C)	Mean
Precipitation of coldest quarter (consecutive 3 months; mm)	Mean
Precipitation seasonality (coefficient of variation based on long-term monthly means)	Mean
<i>W</i> , annual availability of water (mm)	Mean
Catchment contributing area (km <sup>2</sup> )	Mean and maximum (log)
Surface slope (°)	Mean and maximum (log)
Flatness class (categorical data)	Mode
0 Erosional	
1 Indeterminate	
2 Valley bottom flats	
3 Ridge top flats	
Surface drainage class (categorical data)	Mode
1 Direct external	
2 Indirect external	
3 Coordinated interior	
4 Uncoordinated interior	
5 Riverless	
Substrate class (categorical data) (see legend in Figure S1)	Mode

**Table 1** The 11 variables used as attributes in the climatic and environmental domain classifications (Figs 4 and 5) (maps of these variables are given in Figure S1).

*W* requires as input variables gridded estimates of annual precipitation and annual mean radiation surfaces, also derived here from ANUCLIM. Where *W* has a negative value, potential evaporation exceeds rainfall.

### Terrain

Four terrain variables were used: terrain flatness, surface slope, catchment contributing area and surface drainage. The same 9-s DEM was used to generate the terrain variables. Terrain flatness was calculated using the method of Gallant & Dowling (2003). This variable describes the relative flatness and topographic position (lowness) of the land surface relative to the surrounding landscape. Flatness is measured as the inverse of slope, and lowness is measured by a ranking of elevation with respect to a circular surrounding area. The index identifies the spatial difference between valley bottom flats, upland flats and hill slopes. Surface slope was calculated using the SLOPEGRID program of Hutchinson & Gallant (2000), which measures the rate of change in elevation in the direction of steepest descent. Catchment contributing area is the upstream area (km<sup>2</sup>) flowing to any given pixel and was calculated using functions within ARCMAP ver. 9.0 (ESRI, 2004).

Surface drainage patterns of Australia were generated based on a classification system of Hills (1953). Each SHU was assigned a surface drainage class based on drainage lines mapped on the 1 : 250,000 topographic map series of Australia. The drainage classes describe the extent to which topographic basins are effectively occupied by their drainage

nets, not merely if they are endoreic or exoreic systems (Jennings & Mabbutt, 1978).

### Substrate

A single variable was selected to represent major classes of soil orders at the landscape level based on the Australian Soil Classification and associated GIS (Northcote *et al.*, 1960–1968; McKenzie *et al.*, 2004).

### Habitat templet – variables and spatial data sets

The three dimensions of the habitat templet used to approximate productivity regimes were based on estimates of the gross primary productivity (GPP) of the Australian continental land surface calculated by Berry *et al.* (2007). Briefly, GPP was calculated using the radiation-use efficiency (RUE) model of Roderick *et al.* (2001; also see Berry & Roderick, 2004). Input variables for the RUE model are: (1) fPAR (fraction of photosynthetically active radiation) calculated from remotely sensed greenness index (normalized difference vegetation index, NDVI) and (2) long-term mean monthly surface radiation generated by ANUCLIM. Monthly estimates of NDVI-fPAR were calculated from a continental time series of moderate resolution imaging spectroradiometer (MODIS) NDVI imagery with a spatial resolution of 9 s covering the period 1 July 2000 to 30 June 2005. For each grid cell, values were calculated for (1) mean GPP (GPP<sub>mn</sub>), (2) minimum GPP (GPP<sub>min</sub>), and (3) GPP standard deviation (GPP<sub>SD</sub>).

**Table 2** Parameter values required by the PATN program for numeric agglomerative classifications; subsequent ordination based on intergroup similarities to generate the colours used for mapping the classified spatial units of analysis (surface hydrological units, SHU).

Agglomerative (non-hierarchical) classification	
Association measure	Minkowski
Association constant	$P = 2.00$ (Euclidean distance)
3D ordination	
Association measure	Minkowski
Association constant	$P = 2.00$ (Euclidean distance)
Cut-off value	0.90
Number random starts	10
Random seed	1235
Max. number of iterations	50

### Classification strategy and outputs

An agglomerative classification strategy was used for both regionalizations using the functions within PATN 3.03, a software package facilitating large-scale, multivariate pattern analysis (Belbin, 1989). The PATN parameter values for the agglomerative classifications are provided in Table 2. PATN calculates a measure of the similarity (or dissimilarity depending on the association metric used) between a set of objects based on the values for the variables used to describe the objects. In our case, the objects were SHUs and the variables were various kinds of ecosystem measure. Details of the agglomerative classification methodology using PATN are documented elsewhere (Mackey *et al.*, 1988).

The Minkowski series (Euclidean distance) was selected as the association measure to allow weightings to be applied to the variables (Belbin, 1989). The 11 environmental variables used in the classifications were therefore assigned into three groups: (1) six climatic variables, (2) four terrain variables, and (3) one soil variable. All three groups of variables were assigned the same weighting. If the variables had been unweighted, for example, a single climatic variable would have the same weighting as the soil variable, producing a classification biased towards the climatic variables. However, we sought a classification reflecting a balance of climatic, terrain and soil variable influences.

The numeric classification procedure generated various outputs for each biogeographical regionalization, including a 9-s resolution grid recording the classification group to which each SHU was allocated; a table detailing the mean values of the selected environmental variables for each classification group, from which box plots are produced; a dendrogram showing the hierarchical relationship of the classification groups; and a three-dimensional plot indicating the relative position of the groups in ordination space. This is another representation of the intergroup relations, but is generated to produce the group colours for mapping purposes.

To illustrate the effect of combining additional types of variable, two environmental domain classifications were generated: (1) a climatic classification based on the six climate variables listed in Table 2, and (2) a classification based on the

six climate variables, four terrain variables and one soil variable listed in Table 2. (see Figure S1 for maps of the input environmental variables).

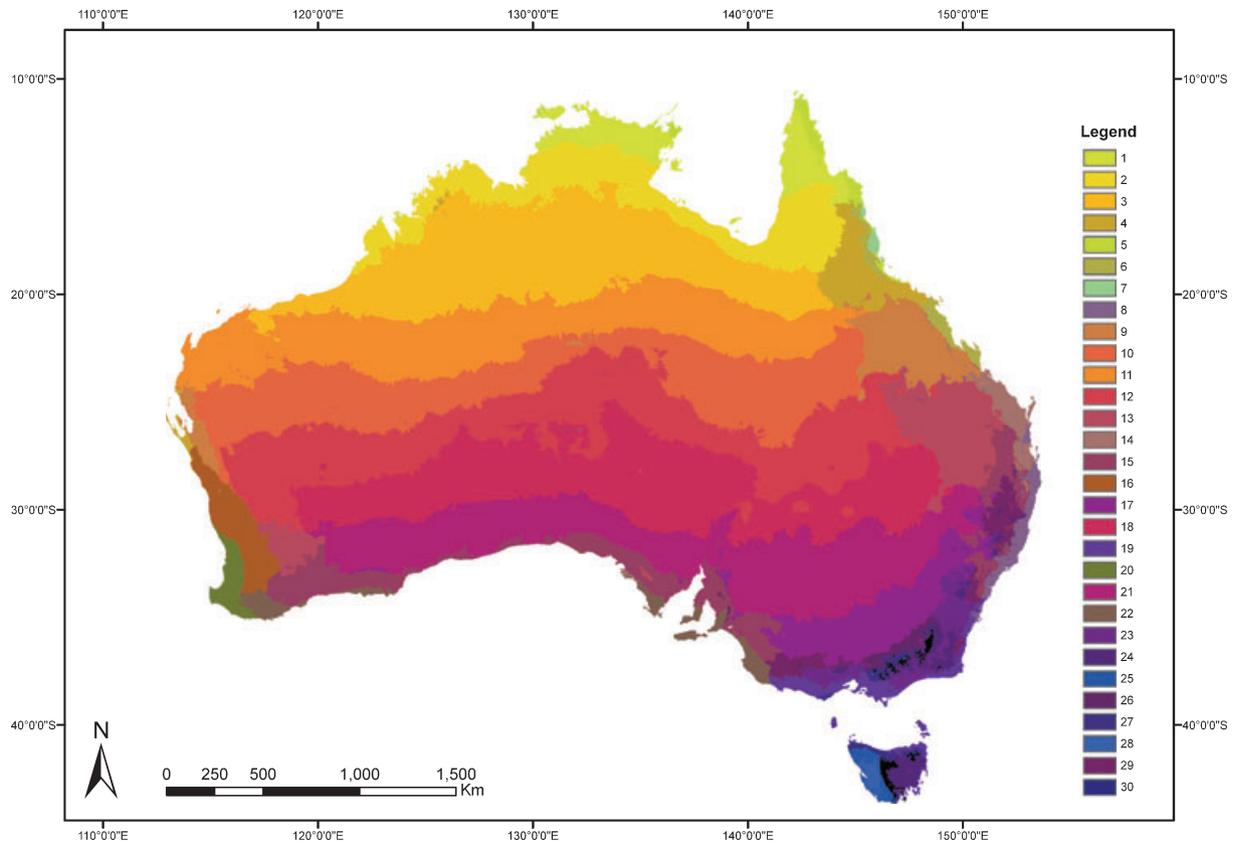
### RESULTS

The map of the 30-group climate classification is shown in Fig. 4, and the 151-group environmental domain (climate, terrain, soil) classification in Fig. 5. The broad bands of climate groups across the middle of the continent reflect higher temperatures with increasing latitude (e.g. groups 10, 11, 12). Thermal 'archipelagos' of eastern mountain peaks are evident as northern outliers of lower latitude climates (group 24). The more humid monsoonal climates of Northern Australia (wet summers, dry winters) are represented by groups 1 and 5. The south-west corner of the continent has 10 distinct climate groups (4, 9, 10, 12, 13, 15, 16, 18, 21, 22) reflecting a complex interzone of coastal southern mediterranean-type climates (hot dry summers, cool wet winters) merging into more arid inland areas, and subtropical conditions with increasing latitude. Group 7 equates with the so-called Wet Tropics, a region fed by both summer monsoonal rains and winter rains brought onshore by the easterly trade winds.

The 'imprint' of the climate classification can be seen on the environmental domain classification (Fig. 5; group 66 vs. 40; group 28). However, around five times more groups were generated in this classification, and the finer patterning reflects the terrain and soil attributes. The linear features represented by group 92 are flood plains associated with major drainage lines, including the Murray River and the inland 'channel country'. Geographically extensive groups generally have few topographic features, and are distinguished by surface hydrology and substrate. For example, the large southerly expanse of group 110 corresponds to the Nullarbor Plain, a treeless region underlain by limestone substrate and characterized by an absence of surface water.

The productivity regime classification is shown in Fig. 6. As one would expect, the general geographical pattern generated by the productivity regime classification strongly reflects continental patterns in precipitation and climatic water availability, with plant productivity generally decreasing inland. The blue-coloured tones (e.g. groups 14, 15, 16, 24) correspond to the distribution of Australia's remaining forests and woodlands, which are restricted to areas with a positive climatic water balance. Vegetation cover dominated by perennial herbaceous plants is identified by groups such as 38, 42 and 46.

For the climate classification (Fig. 4), Table S1 contains (1) box plots of the classification group statistics, (2) a visualization of the three-dimensional ordination of the classification groups, and (3) a dendrogram of the classification's intergroup relations. Table S2 shows the same information for the environmental domain classification (Fig. 5) plus the legend, which was too large to include in Fig. 5. The three-dimensional ordinations enable something of the hierarchy represented in the dendrogram to be mapped geographically. This is



**Figure 4** The continental climatic classification. The main output from the numeric classification where the  $c. 1 \times 10^6$  SHU (surface hydrological units, spatial unit of analysis) were classified into 30 groups based on a measure of their similarity for six climatic variables. Group colours used for mapping were based on a three-dimensional ordination of their intergroup similarity.

an important feature of the statistical analyses, as classification groups are not equally different, and mapping their relative similarity conveys useful information.

Table S3 contains, for the productivity regime classification, (1) box plots of the classification group statistics, (2) a visualization of the three-dimensional ordination of the classification groups, and (3) a dendrogram of the classification's intergroup relations. Again, mapping the relative similarity of the groups is useful in that vegetation structure at continental scales naturally changes across a gradient of canopy height and density.

The productivity regime classification (Fig. 6) used remotely sensed data of current land cover. Large areas of southern and eastern Australia have been cleared of native vegetation for intensive agriculture (Environment Australia, 2000b). Therefore the patterns in Fig. 6 reflect an integral of natural biogeographical patterns and those resulting from human forced land-cover change. In contrast, the environmental variables used to generate Fig. 5 reflect natural processes relating to potential rather than actual ecological patterns.

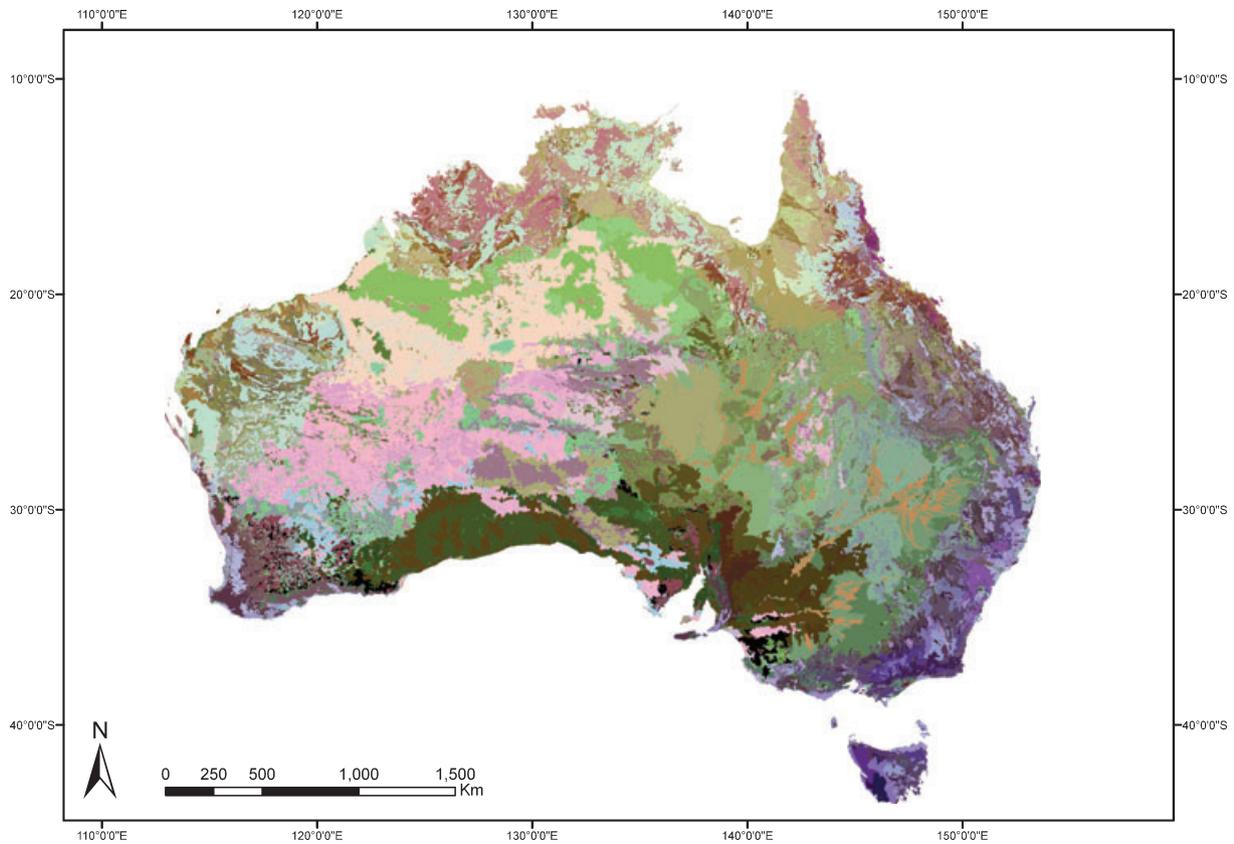
As an additional comparison, the IBRA boundaries were also overlaid on the environmental and productivity classifications (Figure S2). The IBRA biogeographical regions were produced by the Australian government, which requested each of the six state and two territorial governments to provide a

biogeographical regionalization of their respective jurisdictions. The method was not specified, thus IBRA comprises a mosaic of regions generated using seven different approaches. However, none of the methods used the parametric approach. Rather, each used a version of the integrated survey method and gave different emphasis to the three themes in Fig. 1.

## DISCUSSION

The three classifications (Figs 4–6) provide new insights into biogeographical patterns on the Australian continent. The main patterns revealed in the climate classification have been largely recognized previously (Gentilli, 1977; Hutchinson *et al.*, 2005). However, the results of the intergroup analysis (Appendices S2–S4) identified interesting similarities between geographically disjunct areas. This point illustrates a major feature of the numeric agglomerative approach, that the mapped classification is invariably characterized by groups with complex spatial patterns; a group can often have more than one geographical occurrence with many outliers from the main body. This differs from the integrated survey approach, where the tendency is to delineate large, homogeneous regional patterns with few outliers.

The environmental domain classification (Fig. 5) is of particular interest for the patterning it reveals in the interior



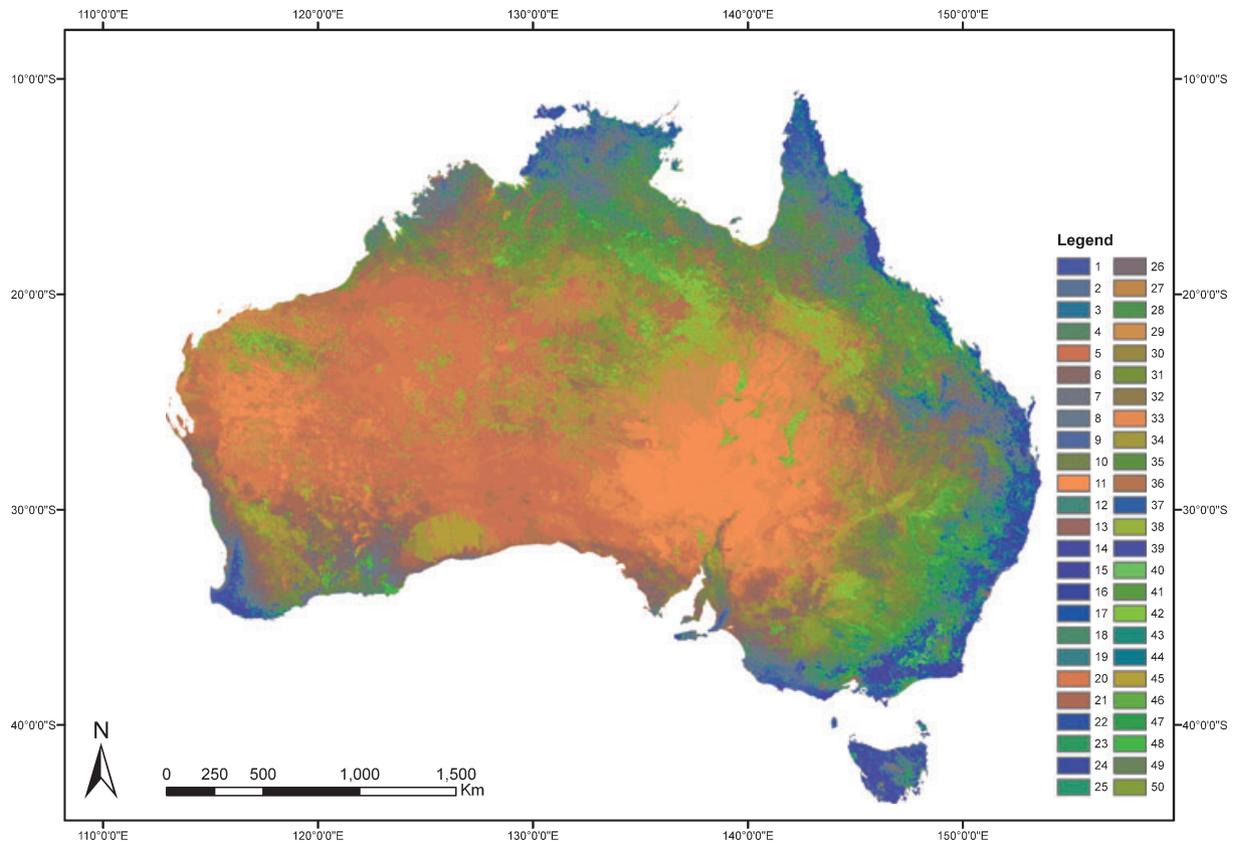
**Figure 5** The continental environmental domain classification. The main output from the numeric classification where the  $c. 1 \times 10^6$  SHU (surface hydrological units, spatial unit of analysis) were classified into 151 groups based on a measure of their similarity for 11 environmental variables. The group colours used for mapping were based on a three-dimensional ordination of their intergroup similarity.

of the continent, which others have noted is often poorly differentiated in biogeographical regionalizations (Hobbs & McIntyre, 2005). The influence of an energy (radiation, thermal) latitudinal gradient is apparent (Figure S1a–c), along with the decrease in climatic water balance from the coast to the centre (Figure S1f), and major classes of terrain and soil types (Figures S1g–i and S1k, respectively). The surface hydrology classes (Figure S1j) are biologically important in distinguishing interior landscapes that differ in the distribution and availability of surface water, which is critical for many animals (e.g. emus, Dawson *et al.*, 1984; red kangaroos, Munn & Dawson, 2001).

A visual comparison of Figs 5 and 6 reveals correspondence in the geographical patterns between the two classifications. This is to be expected, as the primary environmental regimes also represent key determinants of GPP, particularly with respect to environmental controls on water availability. But this is not to say the two classifications are therefore ecologically equivalent. The GPP analysis captures some, but not all, of the properties related to biological carrying capacity, process rates, and differences in the characteristic biodiversity of ecosystems. The environmental domain classification captures ecologically significant properties that are not correlated with GPP *per se*. For example, there is a generic sigmoidal (or

sometimes exponential growth) empirical relationship between GPP and biomass (Brack *et al.*, 2006; Roxburgh *et al.*, 2006). However, both the vertical structure and horizontal patterning of vegetation (which are critical elements of animal habitat) can reflect disturbance regimes (Mackey *et al.*, 2002). Also, there are many abiotic components of habitat (e.g. surface water, physical shelter) that cannot be predicted from GPP, but are better correlated with variables used in the environmental domain classification, such as surface drainage class. Furthermore, the GPP analysis did not distinguish explicitly between plant functional types, although the productivity regimes do reflect different plant phenologies. The proportion of GPP arising from different leaf types can be calculated explicitly from time-series analysis and then correlated with vegetation formations, providing additional habitat resource information (Berry & Roderick, 2002; Berry *et al.*, 2007).

Following from our framework, Figs 5 and 6 were based on explicit theories concerning the evolution of species and life-history strategies, respectively. The classifications can therefore be viewed as generating spatial predictions amenable to testing by comparison with independent data. Thus for Fig. 5, based on environment–speciation theory, the working hypothesis could be established that, for a given species, there is a greater genetic difference between populations that occur in different



**Figure 6** The continental productivity regime classification. The main output from the numeric classification where the  $c. 1 \times 10^6$  SHU (surface hydrological units, spatial unit of analysis) were classified into 50 groups based on a measure of their similarity for three gross primary productivity variables. The group colours used for mapping were based on a three-dimensional ordination of their intergroup similarity.

environmental domains compared with those occurring within the same domain. However, other responses are possible: secondary overlap can occur among allopatric species; species may differ in how their populations respond to the same environmental differences; or there may simply be no response. For Fig. 6, based on Southwood's habitat templet theory, the working hypothesis could be established that the kinds of and differences between vertebrate animal life-history strategies across productivity regimes are greater than those found within the same regime.

While it was beyond the scope of this paper to test such working hypotheses, the kinds of data needed to test them can be collected, time and resources permitting. However, further testing would still be needed to reveal underlying causal mechanisms. For example, if significant genetic differences were found between populations of the same species occurring in different environmental domains, then various mechanisms could be invoked to explain these differences, such as Allen *et al.*'s (2002) biochemical kinetics extension to the energetic-equivalence rule. The parametric approach facilitates exploratory analysis and further hypothesis generation, rather than providing *in toto* the results needed for confirmatory analysis.

As noted in the introduction, the IBRA is being widely used for conservation evaluation purposes, among other things. Its interim status reflects the need for further refinements in the light of new information. A visual comparison of the environmental domain and productivity regime classifications with the IBRA boundaries (Figure S2) suggests that many of the IBRA boundaries can be explained by patterns in either the environmental domains or the productivity regimes. IBRA was produced by a collaborative effort, whereby a national biogeographical regionalization was generated from a mosaic of maps produced by the governments of each Australian state. Each state's regionalization was produced using different methodologies, and the mappers gave varying emphases to the three themes identified in our framework (Fig. 1). An advantage of the parametric approach is that the variables and their weightings are made explicit. Existing biogeographical regionalizations such as IBRA can be retrospectively refined, boundary definitions clarified, and spatial units evaluated in terms of their taxonomic/genetic, environmental and vegetation response characteristics. In this way our approach can be used to help reconcile differences in biogeographical regionalizations of the same area (Jepson & Whittaker, 2002). However, note that the classifications shown in Figs 5 and 6

cannot be considered as replacements for IBRA as such, because IBRA also aims to map patterns in the taxonomic composition and evolutionary genetic legacy that characterize regions (the first theme in our framework).

As we have made reference to ecosystem theory in our framework, the question arises as to whether the classification units produced here constitute ecosystems. Ecosystem theory has its roots in thermodynamics, where systems have boundaries with which they exchange energy and matter with their surroundings (Tansley, 1935). Problems emerge when we try to map their geographical distributions, for a number of reasons. In most cases ecosystems lack a physically distinct 'membrane' – the notable exception being the Earth system (the oceanic domain may also qualify). Also, as ecosystems are recognized at progressively larger cartographic scales, their volume increases, along with the heterogeneity of their composition. Finally, it is simply not possible fully to represent a four-dimensional object in two dimensions – distortions in either space or time are inevitable.

Bioregionalization aims to reduce the Earth system into a number of smaller subsystems that are internally relatively more homogeneous with respect to the characteristics of interest. Other researchers have defined ecosystems using water catchments as spatial units and based on criteria related to the stocks and fluxes of energy, water and nutrients (Golley, 1993). Building on this work, our SHU-based classifications can be interpreted as representing one class of ecosystems, acknowledging that ecosystem processes and properties find expression from global to microbial scales, and that terrestrial ecosystems can be validly and usefully recognized based on other kinds of spatial units.

Despite their recognition in international law (CBD, 1992), ecosystems have received little conservation attention compared with the genetic and species levels of biodiversity. This is probably at least partly because of the lack of an accepted operational definition of ecosystems and a practical approach to their identification and mapping. Our approach could be used to produce a geographically based inventory of one type of terrestrial ecosystem to assist in conservation assessment and planning.

## CONCLUSIONS

Our framework is generic in that it can be applied to all terrestrial regions, and the necessary spatial data for the variables used in this study are now available at global scale (e.g. NASA, 2007a,b). However, spatial data base development is required in most countries to undertake classifications at finer geographical scales. Also, research is needed before a standardized method can be recommended. In particular, an objective function is needed that enables the optimal number of groups to be generated automatically based on properties of the variables and the data. Significant progress has been made in addressing this problem (Fairbanks, 2000; Jenerette *et al.*, 2002) and further developments can be expected.

We were unable to present here an analysis based on the first theme of our framework (Fig. 1): the composition and evolutionary legacy of a region as represented by the extant taxa and their genetic structures. This theme is central to the study of biogeographical regionalization, and for many is the prime focus of investigations. The increasing digitization of museum and herbarium species location data (and other observation data on species presence and abundance) is enabling systematic spatial analyses of species richness and endemism for many plant and animal taxa at global, continental and regional scales (Myers *et al.*, 2000; Crisp *et al.*, 2001; Procheş, 2005; Slatyer *et al.*, 2007). Furthermore, molecular data are providing new opportunities for mapping biogeographical patterns in the phylogeny and genetic structure of taxa and analysis of their environmental relations (Hawkins *et al.*, 2005; Kirchman & Franklin, 2007) and modes of speciation (Norman *et al.*, 2007). Integration of all three themes in our framework will contribute to a more comprehensive approach to biogeography (Wiens & Donoghue, 2004; Crisp, 2006).

When a field of study is new, the object of study is naturalistically defined as a phenomenon directly perceived by the primary senses, and particularly by the sense of sight. As a field of study matures, the object of study becomes more of an intellectually constructed object, taking on an abstract form with less direct physical equivalence perceptible by the human senses (see discussion by Ravetz, 1971). Integrated survey approaches to biogeographical regionalization have generally reflected a naturalistically defined object of study – objects conceptualized from land surface patterns perceived by the mapper through field survey or interpretation of remotely sensed images.

The object of study conceived and investigated by the parametric method is a more abstract, intellectually constructed object. The focus of our approach is such an object – the 'footprint' ecological and evolutionary processes leave on the land surface in three themes (composition and evolutionary legacy, ecosystem drivers, ecosystem responses). However, the more intellectually constructed the object of study, the more stringent the criteria for assessing the adequacy of the methods and the significance of the outcomes – suggesting an important direction for future research in this field.

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## SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online:

**Figure S1** Maps showing the continental distribution of the variables used as inputs to the numeric agglomerative climatic and environmental classifications. Each map is generated from a GIS data layer where the data values are geographically referenced against a 9-s (c. 250 m) resolution regular grid of cells. (a) Annual mean temperature (°C); (b) maximum temperature of the warmest month (°C); (c) minimum temperature of the coldest month (°C); (d) precipitation of the coldest quarter (consecutive 3 months; mm); (e) precipitation seasonality (coefficient of variation based on long-term monthly means); (f) *W*, annual availability of water (mm); (g) catchment contributing area (km<sup>2</sup>); (h) surface slope (°); (i) flatness class; (j) surface drainage class; (k) substrate class.

**Figure S2** (a) Boundaries of the Interim Biogeographical Regionalisation of Australia (IBRA) overlaid on the environmental domain classification; (b) IBRA boundaries overlaid on the productivity regime classification.

**Table S1** Diagnostic output for the 30-group climate classification: (a) box plots of group statistics (showing mean, SD, maximum and minimum values), and the intergroup relations visualized as (b) a 3D ordination; (c) a dendrogram.

**Table S2** Diagnostic output for the 151-group environmental domain classification: (a) box plots of group statistics (showing mean, SD, maximum and minimum values); the intergroup relations visualized as (b) a 3D ordination; (c) a dendrogram; and (d) the legend for the map of the classification.

**Table S3** Diagnostic output for the 50-group productivity regime classification: (a) box plots of group statistics (showing mean, SD, maximum and minimum values); and the intergroup relations visualized as (b) a 3D ordination; (c) a dendrogram.

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