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Incorporating ecological and evolutionary processes into continental-scale conservation planning

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Abstract. Systematic conservation planning research has focused on designing systems of conservation areas that efficiently protect a comprehensive and representative set of species and habitats. Recently, there has been an emphasis on improving the adequacy of conservation area design to promote the persistence and future generation of biodiversity. Few studies have explored incorporating ecological and evolutionary processes into conservation planning assessments. Biodiversity in Australia is maintained and generated by numerous ecological and evolutionary processes at various spatial and temporal scales. We accommodated ecological and evolutionary processes in four ways: (1) using sub-catchments as planning units to facilitate the protection of the integrity and function of ecosystem processes occurring on a sub-catchment scale; (2) targeting one type of ecological refugia, drought refugia, which are critical for the persistence of many species during widespread drought; (3) targeting one type of evolutionary refugia which are important for maintaining and generating unique biota during long-term climatic changes; and (4) preferentially grouping priority areas along vegetated waterways to account for the importance of connected waterways and associated riparian areas in maintaining processes. We identified drought refugia, areas of relatively high and regular herbage production in arid and semiarid Australia, from estimates of gross primary productivity derived from satellite data. In this paper, we combined the novel incorporation of these processes with a more traditional framework of efficiently representing a comprehensive sample of biodiversity to identify spatial priorities across Australia. We explored the trade-offs between economic costs, representation targets, and connectivity. Priority areas that considered ecological and evolutionary processes were more connected along vegetated waterways and were identified for a small increase in economic cost. Priority areas for conservation investment are more likely to have long-term benefits to biodiversity if ecological and evolutionary processes are considered in their identification.

Key words: adequacy; Australia; connectivity; ecological processes; evolutionary processes; gross primary productivity; refugia; river; spatial prioritization; sub-catchments; systematic conservation planning; waterway.

INTRODUCTION

Systematic conservation planning aims to identify priority areas that comprehensively, adequately, and efficiently protect representative samples of biodiversity (Possingham et al. 2006). Over the past 25 years, conservation planners have focused on designing systems of conservation areas that ensure that comprehensive and representative sets of species and habitats are protected efficiently. More recently, there has been an emphasis on designing these areas to be adequate for the persistence of biodiversity. Planners generally deal with adequacy by setting conservation goals in the form of a target percentage of original extent or a target population size for each species, with these targets, in some cases, based on the requirements of species for persistence (Williams and Araújo 2000, Nicholson et al. 2006). Others address adequacy by defining a minimum size for conservation areas (Siitonen et al. 2002) or implementing corridors between conservation areas to promote dispersal (Briers 2002). However, few studies have explored incorporating large-scale (i.e., geographically extensive) ecological and evolutionary processes within the framework of efficiently representing a comprehensive sample of biodiversity features (Cowling and Pressey 2001, Rouget et al. 2003, Possingham et al. 2006, Pressey et al. 2007).

Ecological and evolutionary processes maintain and generate biodiversity (Pressey et al. 2003). The utility and necessity of incorporating these processes into the design of protected areas has been discussed (Morton et

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al. 1995, Moritz 2002, Forest et al. 2007) and earmarked as a conservation research priority (Cowling and Pressey 2001, Mace et al. 2003, Possingham et al. 2005). Although some conservation planners have attempted to identify sensible approaches to incorporating ecological and evolutionary processes into conservation plans (Dinerstein et al. 2000, Groves et al. 2000, Margules and Pressey 2000, Pressey and Cowling 2001, Saunders et al. 2002), little progress has been made toward implementing these ideas (Cowling and Pressey 2001, Possingham et al. 2005). Studies that target both biodiversity patterns (i.e., species and habitats) and processes in a systematic conservation planning exercise are rare. Cowling et al. (1999, 2003) target the entire extent of spatial surrogates for ecological and evolutionary processes (edaphic interfaces, upland–lowland interfaces and gradients, sand movement corridors, interbasin riverine corridors, macroclimatic gradients), along with conservation features that represent the biodiversity pattern at a regional scale in South Africa. Rouget et al. (2006) incorporate large-scale processes into their plan by identifying conservation priorities along major environmental gradients. Neither study addressed cost efficiency in conservation plans. Substantial gains in efficiency are possible if economic information is considered when designing systems of protected areas (Faith et al. 2001, Stewart et al. 2003, Carwardine et al. 2008). In this paper, we identify spatial priorities that represent biodiversity and ecological and evolutionary processes, while minimizing the acquisition cost of the priority areas across an entire continent, Australia.

Biodiversity in Australia is maintained and generated by numerous processes at various spatial and temporal scales (Soulé et al. 2004, Gilmore et al. 2007, Mackey et al. 2007). Processes occurring at small scales (e.g., pollination) are often captured in a conservation plan without specific planning considerations, whereas very large-scale processes (e.g., plate tectonics) are beyond the influence of conservation planning (Pressey et al. 2003, Possingham et al. 2005, Rouget et al. 2006, Hannah et al. 2007). Conservation planning can influence the persistence of processes occurring on a mesoscale, e.g., connectivity between conservation areas to facilitate animal migrations (Pressey et al. 2007). However, the dynamic nature of ecological and evolutionary processes makes them difficult to quantify for conservation planning (Possingham et al. 2005). For example, many animals, particularly birds, are known to exhibit temporally and spatially variable movement patterns that are difficult to predict (Olsen 1995) and are a consequence of heterogeneity in resource availability in space and time. Data for use in conservation planning for such dynamic processes is often unavailable, especially at a continental scale. Even for processes that are better understood, it can be difficult to obtain consistent and credible spatially explicit data across an entire planning region (i.e., fire frequency in Australia) (Morton et al. 1995, Cowling and Pressey 2001, Gilmore et al. 2007). In this paper, we use four methods to represent a selection of ecological and evolutionary processes and use relevant data to identify spatial priorities for conservation investment across Australia.

First, we used sub-catchments as planning units (instead of regular polygons like squares or hexagons) to facilitate the protection of the integrity and function of ecosystem processes occurring on a sub-catchment scale (Everard and Powell 2002, Pressey et al. 2003, Nel et al. 2007, Mackey et al. 2008). Using sub-catchments as planning units is one way to integrate freshwater and terrestrial conservation planning, which are typically treated independently (Pringle 2001, Abell et al. 2002, Tetzlaff et al. 2007). Second, we targeted one type of ecological refugia, drought refugia, which are critical for the persistence of many species during harsh climatic conditions (James et al. 1995, Berry et al. 2007, Mackey et al. 2008). We identified drought refugia, areas of high and regular herbage production in arid and semiarid Australia, using estimates of gross primary productivity modeled from high-resolution satellite data and spatially interpolated climate data. Third, we targeted one type of evolutionary refugia, areas where certain organisms are able to persist during periods when most of the original geographic range becomes uninhabitable because of long-term climatic changes (Morton et al. 1995). Evolutionary refugia were identified by experts in Morton et al. (1995) as areas in Australia important for generating species. Finally, we developed a novel method to preferentially group priority areas along waterways to account for the importance of connected waterways and associated riparian areas in maintaining ecological and related evolutionary processes (Soderquist and MacNally 2000, Pringle 2001, Pringle 2003, Catterall et al. 2007). Connected waterways are known to facilitate processes such as the redistribution of nutrients (Cowling et al. 2003), plant species diversification (Bayer 1999), another evolutionary process, and the movement of wildlife. Protecting sub-catchments along waterways, and the associated ecological and evolutionary processes, will contribute toward the maintenance of whole-river integrity (Cowling and Pressey 2001, Pringle 2001, Bunn and Arthington 2002, Rouget et al. 2003, Nel et al. 2007).

Incorporating the importance of protecting sub-catchments along waterways is one way to bridge the common gap between freshwater and terrestrial conservation assessments, which are often done independently (Abell et al. 2002). There are few examples of approaches to spatial prioritization that integrate principles important for both freshwater and terrestrial conservation planning (Pringle 2001, Abell et al. 2002, Tetzlaff et al. 2007). Cowling et al. (2003) targeted entire riverine corridors along with conservation features that represent biodiversity pattern. This method fixed planning units into the solution and does not allow for trade-offs to be made between the economic costs of conservation and waterway connectivity. Given that the budget for conservation is limited, we developed a unique method for identifying priorities along waterways that allows for trade-offs to be made between connectivity and acquisition costs.

METHODS

Planning for biodiversity representation

Using the best national scale, publicly available biological data available for Australia (identified in Carwardine et al. 2008), we represented static elements of biodiversity using major vegetation types, environmental domains (Mackey et al. 2008), bird and threatened species distributions. We identified vegetation types by intersecting 62 native vegetation subgroups (National Vegetation Information System 2001) with the 85 bioregions (IBRA Version 6.1; Australian Government 2000–2004). Environmental domains were represented by a continental environmental classification calculated by Mackey et al. (2008) based on a set of key climatic, topographic, and substrate conditions that characterize the landscape. Bird species distributions were modeled from bird location data (Birds Australia 2005) using alpha hulls (Burgman and Fox 2003, Birds Australia 2005, Carwardine et al. 2008). We did not include distribution data for introduced, vagrant, wintering, or sea birds. We identified data for the flora and fauna (excluding birds) listed as threatened in the EPBC Act (Commonwealth of Australia 1999). In total we considered 1763 unique vegetation types (vegetation subgroup/bioregion combinations), 151 environmental domains, 563 bird species, and 1222 species of national significance, referred to herein as biodiversity features. We determined the current extent of each biodiversity feature in each sub-catchment and the extent prior to 1770, which was assumed to represent pre-clearing estimates.

Because our prioritization analyses concerned only areas of native vegetation, we did not consider biodiversity features that occurred in areas that have been cleared or contain extensively modified vegetation, thereby assuming that areas of nonnative vegetation do not contribute to our conservation targets. A more detailed description of the data and processing methods are described in Carwardine et al. (2008).

Planning with biodiversity processes

We considered four approaches to include ecological and evolutionary processes. We considered processes that occur across the entire continent or across the arid and semiarid region (about 70% of Australia). Although we considered the importance of waterway connectivity across Australia, a majority of the waterways occur in the non-arid region. The arid and semiarid region was defined by areas of Australia that have a negative long-term annual mean climate water balance (Berry and Roderick 2002, Mackey et al. 2008).

Process approach 1: sub-catchments as planning units.—We derived sub-catchments using an interim version of a new catchment reference system for the Australian continent (Stein 2005, 2006), and used these as the planning units for this study. The nine-level nested catchment framework was delineated by successively subdividing topographically defined drainage basins using a modified version of the Pfafstetter system, a global reference scheme for subdividing and coding drainage basins on the basis of the topology of the drainage network and the size of the drainage area (Verdin and Verdin 1999). At each level, the area of sub-catchments varied greatly depending on the size of the drainage basin and the level at which it was first subdivided. To provide units of a more consistent size for use in conservation planning, sub-catchments were extracted from the basin-specific level that produced units with an average area closest to 50 km^2 and 800 km^2 in the intensive and extensive land-use zones, respectively. These are the average sizes of current protected areas (IUCN I-IV) in these land-use zones and were chosen as they indicate implementation realities (Australian Government 2004). Very small main stem sub-catchment units (defined to have an area smaller than 5 km^2 and 150 km^2 in the intensive and extensive land-use zones, respectively) were combined with the upstream tributary catchment. Closed (internally draining) basins of combined area less than the desired area were iteratively aggregated with a lower neighboring catchment via the lowest point on the drainage divide. In total, we defined 62 630 sub-catchments, each of was a candidate priority area for conservation.

Process approach 2: ecological refugia.—One type of ecological refugia, drought refugia, in the arid and semiarid zones were identified on the basis of gross primary productivity (GPP in units of moles of CO_2 assimilated per square meter per year) (see Berry et al. 2007, Mackey et al. 2008), calculated from high-resolution time-series satellite data (Barrett et al. 2005) using a radiation use efficiency model (Roderick et al. 2001) and spatially interpolated mean monthly estimates of global solar irradiance (Hutchinson 2005). We considered drought refugia to be places with the highest productivity during the least productive years over the five-year period from July 2000 to June 2005 (Berry et al. 2007). During this period, Australia experienced its sixth wettest and ninth driest years since recording of rainfall commenced in 1902. To identify the locations of refugia, we first determined the minimum GPP from July 2000 to June 2005 for each 9 × 9 second pixel. Second, we selected areas that had a GPP value greater than 95% of the highest value in each bioregion. By analyzing refugia within bioregions, we identified areas that were productive relative to each bioregion in order to account for the contrasting environmental attributes and associated adaptations of biota in each bioregion. If we identified refugia across the entire arid/semiarid zone without reference to bioregionalism, a majority of the refugia areas would fall along the arid/non-arid transition zone. Because many biota are adapted to the arid and semiarid climatic zone, they are less likely to seek out the most productive regions in the arid/semiarid zone as their needs could be met in a less productive (yet productive relative to local conditions) area closer to their preferred habitat. We ensure that a portion of these areas is included in our reserve system.

Process approach 3: evolutionary refugia.—Twenty-eight areas of evolutionary refugia in the arid and semiarid zones have been previously identified by experts and were used in this study. The refugia include islands, mound springs, caves, gorges, and mountain ranges containing relictual species (Morton et al. 1995). These refugia contain large numbers of species considered endemic, relictual, threatened, or otherwise significant because they respond to range contractions by evolving differences from their original stock (Morton et al. 1995). We ensure that a portion of these areas is included in our reserve system.

Process approach 4: connected waterways.—We identified adjacent sub-catchments along waterways and preferentially prioritized groups of sub-catchments containing native vegetation along waterways. Watercourse data from 1:1 million scale continental topographic maps (Geoscience Australia 2001) were used to identify perennial and non-perennial waterways in Australia.

Identifying priorities

We aimed to include 30% of each biodiversity conservation and process feature while minimizing the acquisition cost of the system of selected areas. We used a sub-catchment cost measure that represents the cost of acquiring all areas of native vegetation within each sub-catchment, generated from average unimproved land values in each local government area (Carwardine et al. 2008). By using the acquisition cost of land, we assume that the conservation action under consideration is land acquisition (i.e., reservation). We set conservation targets for each feature at 30% of their pre-clearing (year 1770) extent to be consistent with international recommendations (IUCN 2003) and to ensure that biodiversity features are represented in proportion to their natural extent. Sub-catchments that are currently greater than 50% protected (IUCN status I–IV) were not available for selection, but the biodiversity contained within them contributed toward the biodiversity targets.

We identified spatial priorities across Australia using the MARXAN conservation planning software (Ball and Possingham 2000). MARXAN uses a simulated annealing algorithm to configure areas that minimize the sum of the planning unit costs while ensuring that biodiversity targets are met (Possingham et al. 2000). We chose MARXAN over other iterative and optimizing algorithms because of its unique ability to provide multiple solutions that meet the planning objectives, incorporate the cost of a conservation action, accommodate spatial design constraints (e.g., connectivity), use variable size/shape planning units, and handle a large number of planning units and features (Leslie et al. 2003).

To preferentially select vegetated sub-catchments along waterways, we incorporated a connectivity parameter, CP, into MARXAN. This parameter allowed us to trade off the importance of connectivity with minimizing the total acquisition cost of a solution. To do this, it was necessary to determine which sub-catchments contained spatial connections desirable for maintaining ecological processes. We defined desirable connections for maintaining ecological processes as those that occurred between vegetated sub-catchments along major waterways. Each pair of adjacent sub-catchments that were connected by a waterway were assigned a connectivity cost equal to the product of the percentage of native vegetation in each sub-catchment (A_i and A_j) and the length of their shared boundary (L_{ij}):

$$\text{Connectivity cost} = A_i \times A_j \times L_{ij}.$$

The connectivity cost is the expected fraction of the boundary between sub-catchments that are vegetated on both sides. A high relative connectivity cost between two sub-catchments means that it is more important to connect those sub-catchments in a solution, because they are likely to have a long vegetated boundary (Possingham et al. 2005). We used the percentage of native vegetation in a sub-catchment as a multiplier because sub-catchments that have limited or no native vegetation will not contribute toward biodiversity conservation (Catterall et al. 2007). The sum of connectivity costs of selected sub-catchments that are not connected was multiplied by the connectivity parameter, CP, and added to the sum of the relative sub-catchment acquisition costs:

$$\text{Total cost} = \sum \text{Sub-catchment cost} + \text{CP} \times \sum \text{Connectivity cost}.$$

Increasing CP from 0 puts greater emphasis on maximizing sub-catchment connections relative to sub-catchment acquisition costs. Using this information, MARXAN favored sub-catchments that minimize the total cost of the reserve system while ensuring that biodiversity targets were met (Possingham et al. 2000). We varied CP to explore the trade-off between achieving connectivity between vegetated sub-catchments along waterways and the overall cost of the reserve system. In addition, we explore the relationship between biodiversity targets and connectivity.

We implemented MARXAN for three different planning scenarios using sub-catchments as the planning unit for all scenarios. Each of the three scenarios separately incorporates the four process approaches.

1) *Scenario 1: Biodiversity representation and process approach 1.* We targeted 30% of each feature ($n = 3699$) representing biodiversity while minimizing the cost of acquiring all areas of native vegetation within each sub-catchment.

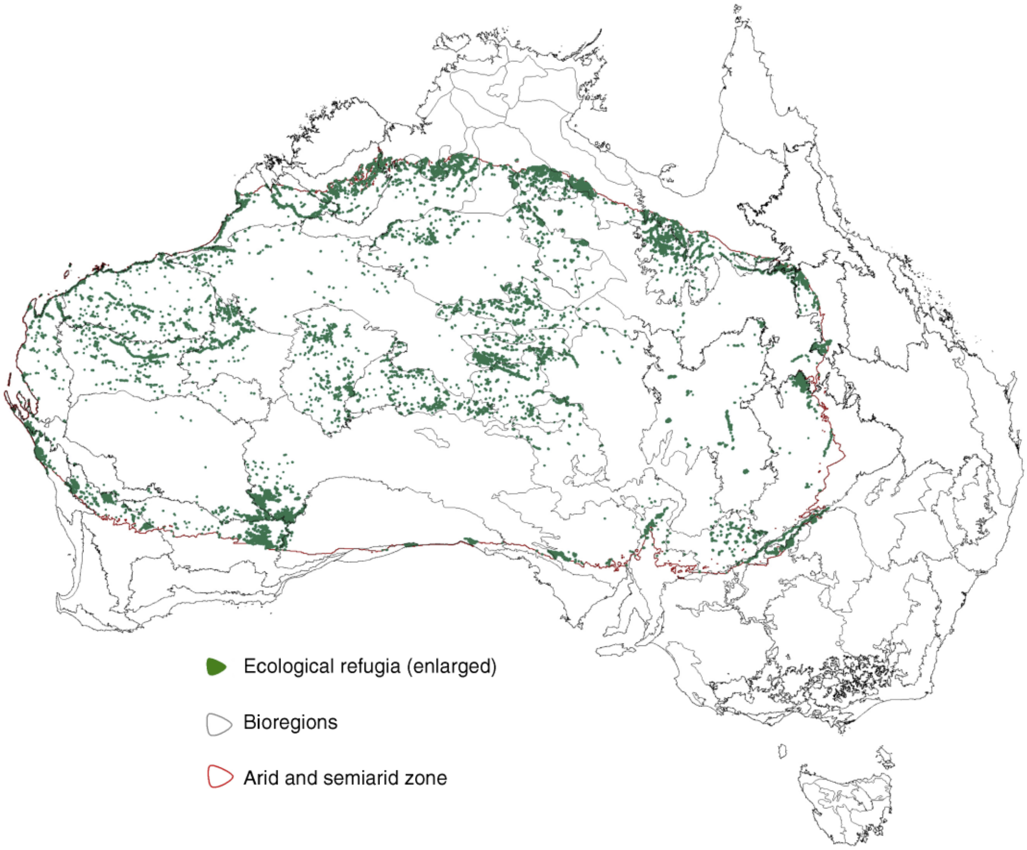

FIG. 1. Ecological refugia within each bioregion in the arid and semiarid region of Australia. Refugia are enlarged in this figure so that they can be seen at this scale. We define refugia here as places having the highest productivity during the least productive years.

2) *Scenario 2*: *Biodiversity representation and process approaches 1, 2, and 3*.We targeted 30% of each feature ($n = 3918$) representing biodiversity and ecological and evolutionary refugia, while minimizing the cost of acquiring all areas of native vegetation within each sub-catchment.

3) *Scenario 3*: *Biodiversity representation and process approaches 1, 2, 3, and 4*. We targeted 30% of each feature ($n = 3918$) representing biodiversity and ecological and evolutionary refugia, while minimizing the cost of acquiring all areas of native vegetation within each sub-catchment. In addition, we preferentially selected groups of adjacent sub-catchments containing native vegetation along waterways.

Using the simulated annealing and iterative improvement features of MARXAN, we generated 500 different solutions to the problem. Simulated annealing finds many good solutions with different spatial configurations. Given 500 solutions, we can determine the frequency at which each sub-catchment was selected, henceforth referred to as the selection frequency. Sub-catchments with a high selection frequency contain native vegetation that is a high conservation priority to satisfy the objectives of the scenario. We displayed the difference in selection frequencies between scenarios to show how the incorporation of each ecological and evolutionary process approach changes the selection frequencies. Using a single efficient solution, we examine the trade-offs between cost, representation targets, and connectivity.

RESULTS

Ecological refugia

Drought refugia for each of the 41 bioregions in the arid and semiarid zone were determined using high-resolution satellite data of gross primary productivity (Fig. 1). The area of refugia per bioregion ranged from 0.05% to 4.63%. This reflects how much of the bioregion remained relatively productive during the driest years from 2000 to 2005.

Priority areas for conservation investment

We compared spatial priorities in scenario 1 (biodiversity representation) with those from scenarios 2 and 3 (biodiversity representation and processes) by investigating differences in selection frequencies (Fig. 2). Approximately 90% of all sub-catchments had similar selection frequencies in scenarios 1 and 2. The addition

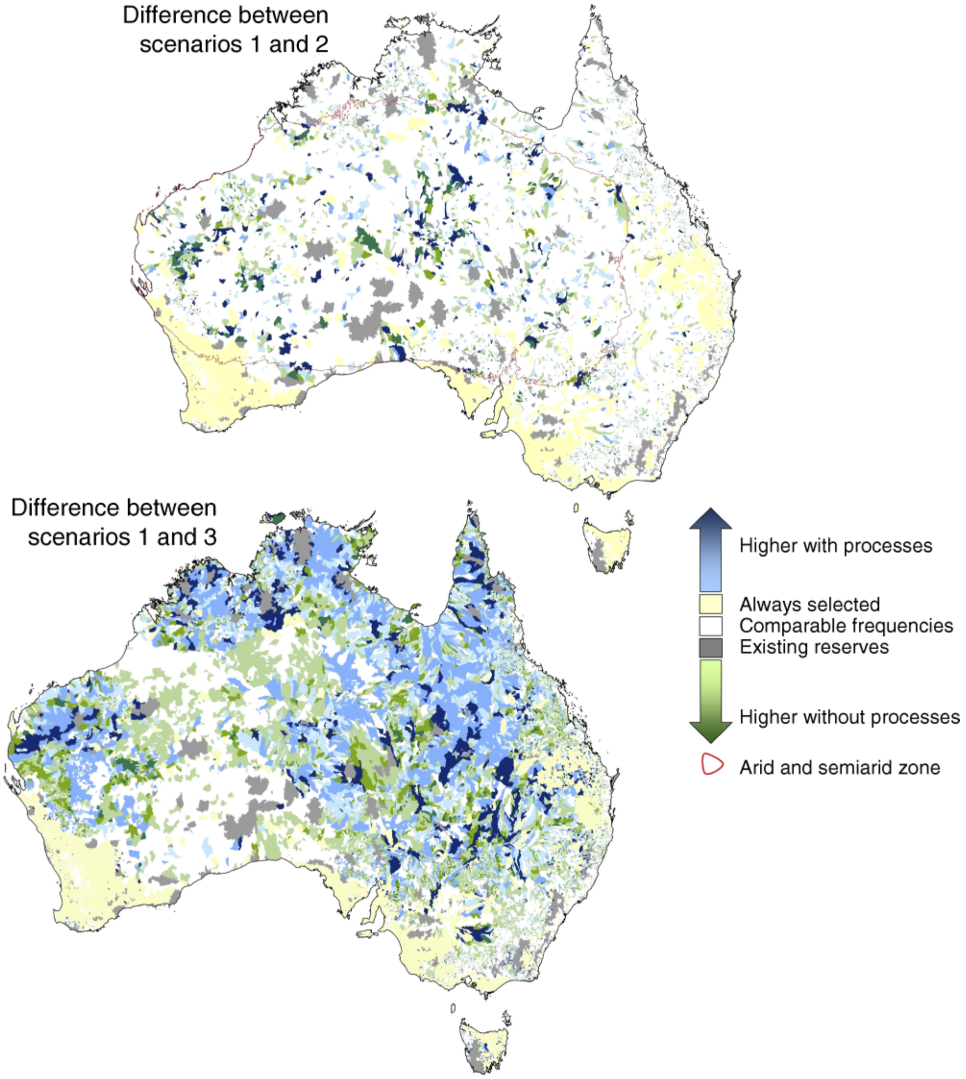

FIG. 2. Difference in selection frequency between scenarios when ecological and evolutionary processes were (scenarios 2 and 3) and were not (scenario 1) considered. This map does not indicate relative priorities across the landscape; instead it shows which sub-catchments have a higher, lower, or comparable selection frequency between two different scenarios. The scenarios represent planning for: biodiversity representation (scenario 1); biodiversity representation and some processes (ecological and evolutionary refugia, scenario 2); and biodiversity representation and all processes (ecological and evolutionary refugia and connectivity along waterways, scenario 3).

of biodiversity process targets (i.e., ecological and evolutionary refugia in each bioregion) in scenario 2 explained the difference in selection frequencies of the other 10% of sub-catchments. When ecological and evolutionary refugia were not targeted (scenario 1), there was no guarantee that 30% of each refugia was represented in each bioregion. However, when they were targeted (scenario 2), 30% of each refugia was always represented in each bioregion. For example, in an efficient solution of scenario 1, at least 30% of ecological and evolutionary refugia per bioregion were included in 62% of bioregions containing ecological refugia and 69% of the bioregions containing evolutionary refugia. In scenario 2, 100% of the bioregions containing ecological and evolutionary refugia achieved the 30% representation target. Therefore, the difference in conservation objectives between scenarios caused the selection frequencies between scenarios to differ for some sub-catchments. There is a negligible difference in the acquisition cost (0.04%) and total area selected (0.24%) of the most efficient solution from scenario 1 compared to the most efficient solution from scenario 2.

We explored the trade-offs between representation targets, costs, and waterway connectivity (Table 1). A higher degree of waterway connectivity can be achieved in two ways: (1) increasing the connectivity parameter, holding the representation target constant; and (2) increasing the representation target, holding the given

TABLE 1. Trade-off between minimizing sub-catchment acquisition cost, waterway connectivity, and representation targets of reserve systems for various values of the connectivity parameter (CP) and representation target.

Connectivity importance	Target	Relative cost	Waterway connectivity
None, CP = 0	10%	1.00	17.3%
	20%	1.07	22.2%
	30%	1.17	28.3%
	40%	1.38	38.9%
	50%	1.63	54.4%
Low, CP = 0.001	10%	1.01	50.4%
	20%	1.08	53.4%
	30%	1.18	57.6%
	40%	1.39	68.6%
	50%	1.67	82.0%
Medium, CP = 0.1	10%	1.27	67.2%
	20%	1.35	68.8%
	30%	1.42	70.1%
	40%	1.69	78.8%
	50%	1.85	85.8%
High†	10%	1.83	100%
	20%	1.84	100%
	30%	1.84	100%
	40%	1.90	100%
	50%	1.96	100%

Notes: Target indicates the minimum amount of each feature representing biodiversity and ecological and evolutionary refugia. Relative cost is the proportional change from 1.0. The waterway connectivity indicates the percentage of sub-catchments along waterways that were prioritized.

† In this scenario, we aimed to include all waterways in the final solution by locking them into the solution with a CP value of zero.

connectivity parameter constant. When importance was placed on increasing connectivity between sub-catchments along vegetated waterways (scenario 3), there was a trade-off between minimizing sub-catchment acquisition cost and waterway connectivity. We identified a point on the trade-off curve where substantial gains in connectivity were made for a minimum economic cost (i.e., acquisition cost), and we use this result to represent scenario 3 in this paper (Fig. 3). For just a 0.74% increase in acquisition cost, 29% more of the possible river connections were made compared to the scenario where connectivity was not considered. A similar level of connectivity can be achieved with different representation targets (Table 1). Scenarios with similar levels of connectivity were generally more costly with larger representation targets.

In Fig. 4, we compare the connectivity of priorities along waterways of solutions from the scenarios that consider connectivity (scenario 3) and do not consider connectivity. Fig. 4A shows that most sub-catchments along the Murray and Darling rivers were allocated a high selection frequency in scenario 2. These areas were prioritized to meet biodiversity and process representation objectives at a minimum cost. When the connectivity objective was incorporated (scenario 3), more sub-catchments along these rivers were allocated a high selection frequency. In contrast, Fig. 4B shows that sub-catchments along the Isaac and Harrow waterways were not allocated a high selection frequency when connectivity is a priority. Because there are trade-offs between acquisition cost and connectivity, an increase in connectivity was not achieved along all waterways. The solutions achieving 100% connectivity are substantially more costly than the trade-off solutions for various representation targets (Table 1).

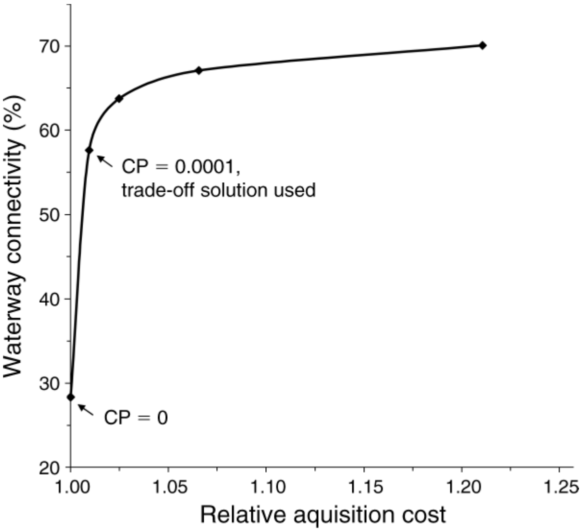

FIG. 3. Trade-off between minimizing sub-catchment acquisition cost and waterway connectivity of reserve systems for various values for the connectivity parameter, CP. We identified a point on the trade-off curve where substantial gains in connectivity were made for a minimum economic cost (i.e., acquisition cost), and we use this result to represent scenario 3.

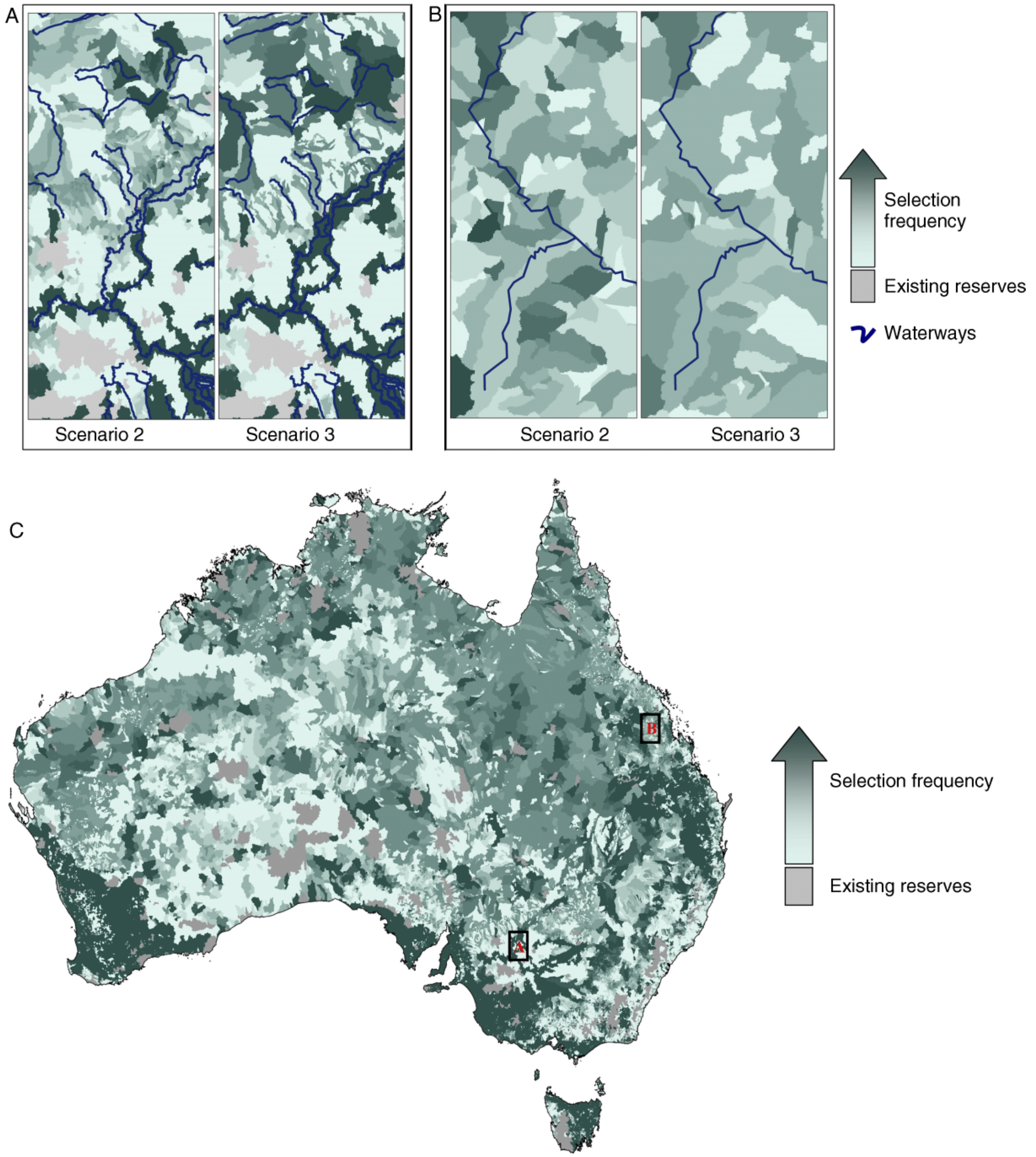

FIG. 4. Change in selection frequency without (scenario 2) and with (scenario 3) the consideration of connectivity of sub-catchments along two major waterways for (A) the intersection of the Darling and Murray Rivers and (B) the intersection of the Isaac River and Harrow Creek (locations are shown in C). (C) Selection frequency of sub-catchments when biodiversity representation and processes are considered. In this scenario we targeted 30% of each feature representing biodiversity and ecological and evolutionary refugia, while minimizing the cost of acquiring all areas of native vegetation within each sub-catchment. In addition, we preferentially selected groups of sub-catchments containing native vegetation along waterways. Boxes A and B indicate location of rivers in panels A and B.

We identified priorities for conservation investment when biodiversity representation and our selection of ecological and evolutionary process approaches were considered (Fig. 4C). Sub-catchments selected frequently are a high priority for conservation investments because they represent areas that are most likely to be required to meet our objectives (i.e., represent biodiversity and a selection of the ecological and evolutionary processes that maintain and generate that biodiversity). Sub-catchments that are heavily cleared but contain a small amount of native vegetation are often selected frequently (e.g., southwestern Australia) because they contain biodiversity features that do not exist in other parts of the landscape and are therefore needed to meet biodiversity representation targets. Only native vegetation within these sub-catchments would be considered for reservation.

DISCUSSION

This study demonstrated how both biodiversity representation and process objectives can be incorporated when identifying cost-effective areas for conservation investment in Australia. We addressed the principles of systematic conservation planning, aiming to identify priority areas in Australia that are comprehensive, representative, efficient, and adequate (Possingham et al. 2006). We addressed the adequacy criteria by ensuring that the spatial arrangement of priority areas encompasses a selection of ecological and evolutionary processes important for the persistence of biodiversity. Explicitly considering ecological and evolutionary processes to address adequacy is a task that is frequently suggested, but rarely undertaken, in the field of systematic conservation planning. The paucity of work in this area is probably due to the challenges associated with understanding processes and identifying spatial data to represent them (Possingham et al. 2005), factors that are magnified when considering a large study region like Australia.

We aimed to identify one type of ecological refugia, drought refugia, in the arid/semiarid region of Australia. Morton et al. (1995) also identified ecological refugia in this region, but used an expert-knowledge approach. If the data were available, however, their preferred method was to use fine-scale gross primary productivity to delineate ecological refugia. The areas that we identified as ecological refugia are suspected to be resource-rich areas that are critical for the persistence of many species during harsh climatic conditions (James et al. 1995). The validity of this hypothesis is unknown. In addition, introduced herbivores may also prefer these resource-rich areas (Pickup and Chewings 1994), causing a decline in native species and a change in the community composition (Wilson 1990). Various ways in which our methods to define ecological refugia could be adapted include: (1) using productivity data at finer spatial and temporal scales; (2) using a different threshold for determining areas with "high" gross primary productivity (cf. we used top 5%); (3) considering the variability of production over time; and (4) qualifying the selection of areas by a measure of ecological integrity in the seminatural vegetations (e.g., landscape leakiness index [Ludwig et al. 2007], distance to water as a surrogate for this [James et al. 1999], or measured grazing gradients [Pickup and Chewings 1994]). Regardless of how refugia are identified, they can be incorporated into priority setting using the methods outlined in this paper. Determining whether or not such places really do provide increased conservation benefits with respect to long-term species persistence would be difficult.

Riparian areas support ecological and evolutionary processes that maintain a large variety and abundance of wildlife (Williams 1994, Bentley and Catterall 1997, Soderquist and Mac Nally 2000, Woinarski et al. 2000, Lynch et al. 2002). However, terrestrial reserve design research rarely considers riparian areas, especially in Australia (Pringle 2001, Cullen 2003, Linke et al. 2007). By using sub-catchments as planning units and emphasizing the importance of protecting catchments along waterways, we make progress at integrating freshwater and terrestrial conservation planning (Abell et al. 2002, Tetzlaff et al. 2007). Another way to do this would be to target additional surrogates for freshwater species and habitats. The protection of entire sub-catchments is likely to promote the protection of ecosystem processes contained within a sub-catchment, with the potential to positively influence the integrity of unprotected ecosystem processes downstream (Pringle 2001, Everard and Powell 2002, Pressey et al. 2003, Nel et al. 2007, Mackey et al. 2008).

In the first scenario, we aimed to represent biodiversity, and in the second scenario, we aimed to represent biodiversity and one type of ecological and evolutionary refugia. Although there were spatial differences between the priorities identified in the first scenario compared to that identified in the second, these differences were not substantial. This can be explained by the meeting of refugia targets in many bioregions, regardless of their inclusion in the objective; suggesting that our biodiversity representation features (i.e., species and habitats) did a reasonable job of capturing some refugia. However, we found that ecological and evolutionary refugia were not represented across all bioregions in arid/semiarid Australia unless the objective was explicitly incorporated into the conservation planning assessment, as we have done in scenario 2. The generality of these results to other planning regions is unknown.

By placing importance on connected sub-catchments along waterways (scenario 3), spatial priorities are more likely to contain whole-river systems (Fig. 4A, B). Previous research aiming to protect the processes associated with protecting connected waterways included entire riverine corridors (Cowling et al. 2003). Although this would be the best way to protect ecological processes occurring in these areas, the cost of acquiring these areas may be prohibitive, given a limited conservation budget. We developed a unique method for identifying priorities along a waterway by incorporating a connectivity parameter into the objective function that allows trade-offs to be made between planning unit acquisition cost and waterway connectivity. We demonstrated that large gains in waterway connectivity can be made for a minimal economic cost, but we emphasize that various trade-offs between connectivity, acquisition cost, and representation can be identified by varying the connectivity parameter and representation target. Although more connected spatial priorities were not substantially more costly than less connected priorities, they required more area to ensure that biodiversity goals were met. As a result, many of the priority areas identified were large because groups of adjacent sub-catchments were selected, an outcome that may be important for some ecological processes (e.g., predator–prey interactions) (Cowling and Pressey 2001, Cowling et al. 2003, Pressey et al. 2003, Rouget et al. 2003).

In this paper, we give preference toward the selection of groups of sub-catchments containing native riparian vegetation because there is no conservation benefit of prioritizing heavily cleared sub-catchments that are adjacent along a waterway (Catterall et al. 2007). However, our method can be applied using different connectivity costs between sub-catchments (adjacent as well as nonadjacent). This modification can account for the situation where the connectivity of some waterways is more important than other waterways due to the dependence of particular species and ecosystem properties on specific environmental attributes, such as water flow or quality. For example, impact of dams of water flow could be taken into consideration.

We recognize that this work only addressed a limited number of ecological processes and evolutionary processes. We did not attempt to replicate the selected processes using dynamic simulation models. Rather, the processes were captured by spatial features that reflect their "footprint" in, or that are correlated with their flows through, the landscape. The bioregions and environmental domains also served as features that account for certain evolutionary processes. Mackey et al. (2008) argued that environmental domains can serve as surrogates of evolutionary processes in the absence of molecular data. Significant environmental differences between bioregions can function as the extrinsic isolating barriers that instigate allopatric speciation and environmental gradients can provide the selective pressures that result in parapatric speciation. Given reliable and comprehensive data across the Australian continent, other processes could be included to promote the persistence of biodiversity and improve the adequacy of protected area design. For example, access to molecular data that can reveal spatial patterns in the genetic structure of taxa, more specific and useful information about phylogenic diversity (Faith et al. 2004, Forest et al. 2007), or reveal modes of species (Mayr 2001, Norman et al. 2007) could provide key insights to setting priorities that capture evolutionary processes. Our aim was to demonstrate methods for identifying priority areas for conservation across the continent of Australia. An analysis of each identified priority at the continental scale could utilize other types of process data not available at the continental scale.

We recognize that setting the same target (e.g., 30%) for each biodiversity feature may not be adequate for protecting all species and habitats. If information on population sizes required for species persistence were available, we could set species-specific targets based on individual species' requirements (Burgman et al. 2001, Carroll et al. 2003). The type of conservation action will also be an important factor in the persistence of biodiversity. Integrating off-reserve conservation actions (i.e., stewardship, restoration) with reservation will also be an important factor in the persistence of biodiversity (Wilson et al. 2007). Pressey et al. (2007) describes the utility of moveable conservation areas to capture species that shift between parts of a planning region through time (e.g., water birds).

By integrating some ecological and evolutionary processes into our conservation plan, we predict that the priorities identified are more likely to maintain and generate biodiversity (Cowling et al. 1999). However, validating the performance of our surrogates at various scales would be challenging, and would require the combined use of land-use simulators, population viability analyses, and process-based species models. Given the large number of surrogates, this would be extremely time consuming. We identified data to represent processes and profile new approaches that help to overcome some challenges associated with incorporating ecological and evolutionary process into geographically extensive conservation plans. We illustrate that ecological processes can be incorporated for minimal additional expenditure. Through their explicit consideration, we can be more confident about the potential long-term benefits to biodiversity of our conservation investments. We hope that this manuscript will help to facilitate freshwater conservation and progress the integration of freshwater and terrestrial conservation efforts. Our methods can be applied and adapted to identify regional, continental, or global priorities that aim to represent biodiversity comprehensively, adequately, and efficiently.

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