Biological Conservation xxx (2009) xxx–xxx

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Review

Conservation planning for connectivity across marine, freshwater, and terrestrial realms

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ARTICLE INFO

Article history:
Received 16 March 2009
Received in revised form 26 October 2009
Accepted 7 November 2009
Available online xxxx

Keywords:
Systematic conservation planning
Realm connectivity
Environmental realms
Integrated conservation
Conservation decision-support systems

ABSTRACT

Conservation plans are usually developed for regions that encompass only one environmental realm (terrestrial, freshwater or marine) because of logistical, institutional and political constraints. This is inadequate because these realms often interact through processes that form, utilize and maintain interfaces or connections, which are essential for the persistence of some species and ecosystem functions. We present a conceptual framework for systematic conservation prioritization that explicitly accounts for the connectivity between the terrestrial, marine, and freshwater realms. We propose a classification of this connectivity that encompasses: (1) narrow interfaces, such as riparian strips; (2) broad interfaces, such as estuaries; (3) constrained connections, such as corridors of native vegetation used by amphibians to move between natal ponds and adult habitat; and (4) diffuse connections, such as the movements of animals between breeding and feeding habitats. We use this taxonomy of inter-realm connectivity to describe existing and new spatial conservation prioritization techniques that aim to promote the persistence of processes that operate between realms.

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0006-3207/$ - see front matter
doi:10.1016/j.biocon.2009.11.006

1. Introduction

Rapid global environmental change together with limited conservation and management resources necessitate the targeted conservation management of ecosystems and their dynamics (Moilanen, 2005; Pressey et al., 2007). Because ecosystems do not function independently, there are often important and fundamental interactions among terrestrial, marine and freshwater realms. We must consider these linkages in the systematic conservation prioritization of what actions to take in which places (Lagabrielle et al., 2009; Stoms et al., 2005; Tallis et al., 2008). While theory and analytical tools exist for accounting for connectivity within realms, the necessary characterization of, and planning for, dynamic ecological and biophysical interactions between realms is lacking (Abell et al., 2007; Moilanen, 2005; Pressey et al., 2007; Stoms et al., 2005). Here we provide a framework of methods for integrated conservation prioritization that considers the connectivity between environmental realms.

Ecological and biophysical processes that connect realms, termed 'connecting processes', or 'connectivity' in this study, may link two or more realms and allow for the movement of species (i.e. biological connectivity) and the associated or independent transfer of energy and matter (i.e. geo-physical connectivity). Biological connectivity is mainly concerned with the movement of individuals between habitats diurnally, seasonally, or during their life cycle for feeding or reproduction (for examples, see Table 1). Geo-physical connectivity occurs as a result of gravity, meteorological phenomena, and the water cycle (for examples, see Table 2). Despite this distinction, biological and geo-physical processes are not necessarily independent. The movement of species results in a transfer of matter, as they feed in one realm, and excrete or die in another realm, such as Pacific Coast Salmon transferring ocean derived energy and nutrients as they migrate up rivers to terrestrial and riparian ecosystems (Gende et al., 2002).

The need to integrate conservation management across two realms has been discussed for the interface between marine and terrestrial realms (Banks and Skilleter, 2005; Stoms et al., 2005; Tallis et al., 2008), and between terrestrial and freshwater realms (Abell et al., 2002). Guidelines for freshwater planning highlight the need for integrated planning, but there are few examples of systematic integrated planning across terrestrial–freshwater realms (Abell et al., 2002; Beja and Alcazar, 2003; Hall et al., 2004; Pusey and Arthington, 2003) that go further than setting targets to protect freshwater species or environments in terrestrial reserve systems (e.g. Cowling et al., 2003). Several conservation planning projects have specifically targeted the estuary and mangrove habitats, which are an interesting interface between all three realms (Beck et al., 2001; Drinkwater and Frank, 1994; Edgar et al., 2000; Gillanders and Kingsford, 2002; Ray, 1996), but little progress has been made towards the integration of the adjacent environments. One exception is Mumby (2006), who provided a theoretical example that considered both coral reef and mangrove habitats. At local scales, the theoretical principles of integrating management of terrestrial–marine interfaces are embedded in a substantial body of literature associated with integrated coastal-zone management (Beger et al., 2004; Cicin-Sain and Knecht, 1998; Kenchington and Crawford, 1993; Ray, 1996; Westmacott, 2001). However, few projects have succeeded in creating conservation plans that capture processes that connect realms (Christie, 2005; Forst, 2009; but see Lagabrielle et al., 2009 for a method incorporating biodiversity processes on the marine–terrestrial interface). Within-realm connectivity has, in contrast, received substantial attention (Cabeza, 2003; Calabrese and Fagan, 2004; Fuller et al., 2006; Rouget et al., 2006).

In systematic conservation planning, decision-support systems (DSS) are often used to identify sites for conservation management that achieve explicit objectives while considering constraints on conservation actions (McDonnell et al., 2002; Moilanen et al., 2009). Recent research advocates for incorporating ecological and evolutionary processes that maintain biodiversity (Forest et al., 2007; Lombard et al., 2007; Pressey et al., 2007; Rouget et al., 2006) such as those on realm interfaces (Lagabrielle et al., 2009) or planning for the dynamics of pelagic assemblages (Game et al., 2009). Most conservation decision-support tools operate on a spatially explicit array of planning units that define a landscape, and require the spatial relationships among them to be known (Ball and Possingham, 2000; Game and Grantham, 2008; Stewart et al., 2003). Therefore, considering connecting processes requires different methods depending on their spatial scale, the spatial separation of areas used within realms, and the extent of our knowledge of a process.

Although integrative planning of cross-realm processes in decision-support tools for conservation planning would ensure efficient and effective conservation and management of these processes (Sarkar et al., 2006), conservation planning projects have largely focused on one of the three realms (Stoms et al., 2005) and rarely set quantifiable objectives for integrated planning. This is likely a consequence of several factors:

(1) the management of realm interfaces is typically distributed among several management agencies at local, regional, and national administrative levels (Stoms et al., 2005),
(2) the expertise of scientists, managers and policy makers is usually realm-specific,
(3) conservation planning projects are often based on study regions with administrative or geographical boundaries (Pressey et al., 2002), rather than ecological or functional boundaries, and
(4) the complexities faced by conservation planners in any one realm have focused the evolution of ideas and techniques within a realm and hindered consideration of processes that connect environmental realms.

To overcome these institutional and logistical challenges, and highlight the need to integrate inter-realm connecting processes into spatial conservation prioritization, we require a spatially explicit decision framework with quantifiable objectives. Depending on the spatial scale of inter-realm as well as within-realm connectivity, and the spatial separation of sites important to a process in each realm, radically different data in DSS as well as conservation approaches will often be required. In this review we classify four types of connectivity that represent the diversity of the connecting processes, and describe spatial prioritization techniques that allow for their integration in conservation plans.

Please cite this article in press as: Beger, M., et al. Conservation planning for connectivity across marine, freshwater, and terrestrial realms. Biol. Conserv. (2009), doi:10.1016/j.biocon.2009.11.006

Table 1
Examples of species-specific processes connecting environmental realms. In all these processes, species move among realms, and associated with this movement is the transport of organic matter and/or energy between realms.

	Freshwater–marine	Terrestrial–freshwater	Terrestrial–marine
Narrow interface	The perennial streams on steep volcanic islands such as Maui in Hawaii host unique varieties of endemic fish, shrimp, mollusks and insects (Kinzie and Ford, 1977). The diadromous life cycles of many of these species require movement across the freshwater–marine interface twice: to the ocean as newly hatched larvae and subsequent return from the ocean to the stream as juveniles	Endemic to South American rivers and wetlands, giant river otters (*Pteronura brasiliensis*) are highly dependent on seasonal changes of freshwater systems (Carter and Rosas, 1997). Their reproductive success relies on fish abundance and undisturbed terrestrial habitat conditions, which includes stable river banks	The marine iguana feeds almost exclusively on marine algae by diving for the algae or eating intertidal algae, depending on their body size (Laurie and Brown, 1990). The lizard is sensitive to threats to their terrestrial habitat and to the dynamics of marine algae populations. For example, a high mortality event occurred in 1983, when climatic abnormalities caused a major change in the marine algal flora (Laurie and Brown, 1990)
Broad interface	The mangrove killifish (*Rivulus marmoratus*) is found in North, Central and South America and has an obligate dependence on brackish-water environments, typically associated with mangroves that occur near freshwater (Briggs, 1984)	Australian river red gum are riparian trees that rely on periodic flooding and water exchange between wetlands and the main river channels (Frazier and Page, 2006). Water regulation for irrigation has changed the hydrological regime in much of their habitat, adversely affecting both the gums and other fauna, such as water birds that rely on the same habitats for breeding	Tropical coastal ecosystems often consist of a mosaic of habitat types such as mangroves, seagrass meadows and coral reefs. Access to mangrove nursery habitat can double the standing crop of bluestriped grunt (*Haemulon sciurus*) adults in their coral reef habitat (Mumby et al., 2004). Smells associated with mangrove leaf litter attract settling larvae of the coral reef fish *Amphiprion percula* (Dixson et al., 2008)
Constrained connection	Anadromous fishes spend most of their life in marine habitats then migrate to freshwater to spawn. They are declining in many parts of the world. For example, many of the salmonids (*Oncorhynchus* spp.) in the Pacific Northwest USA. have declined due to habitat degradation of spawning areas along with the impact of over-fishing (Frissell, 1993). These fish play an important functional role by providing prey for many freshwater and terrestrial biota and their spawned carcasses supply nutrients to streams, lakes, estuaries and riparian vegetation (Frissell, 1993). Conservation requires regulation of fishing practices and protection of migration routes from the ocean to spawning habitat	Amphibian species reproduce in wetlands, and move to terrestrial habitats to forage and take refuge during the remainder of the year. On average, terrestrial habitats up to 300 m from the edge of aquatic sites are required by some amphibian species to complete their lifecycles (Semlitsch and Bodie, 2003). Land uses surrounding aquatic habitats can affect amphibians through loss of habitat, fragmentation of populations, diminished dispersal ability, reduced water quality, and increased exposure to toxic substances (Pellet et al., 2004)	The coconut crab (*Birgus latro*) in the Indo-Pacific is almost entirely terrestrial except for a 3 to 4 week marine pelagic larval stage (Lavery et al., 1996). They require an intact connection between their usual rainforest habitat and the sea to release their larvae into the water, but the scale of their movements is not well known. Because of its value as a food source and consequent over-harvesting, combined with slow growth rates, the coconut crab is of high conservation concern with severely depleted or extinct populations on some islands
Diffuse connection	Many coastal diving duck species require both freshwater and saltwater habitats. During winter the North American Redhead (*Aythya americana*) depends on both freshwater wetlands for drinking, and saltwater habitats for feeding (Woodin, 1994). As they can fly between these habitats, many connections are possible. Conservation depends mainly on the persistence of suitable freshwater and saltwater habitats occurring sufficiently close for regular movements	The dispersal of the Great Cormorant (*Phalacrocorax carbo*) is determined largely by the presence of aquatic habitat, since they feed solely by swimming underwater to catch their food. This species therefore breeds and feeds in inland freshwater sites during the wet season and migrates to coastal areas as these breeding sites dry out in the dry season	Marbled Murrelets (*Brachyramphus marmoratus*) feed in near-shore waters but breed in coastal old-growth forest. Logging of breeding habitat is believed to be an important cause of the species' decline along with depletion of prey fish in feeding areas. Conservation planning for this species requires identification and protection of both terrestrial breeding areas and marine feeding areas. The distance between these varies between regions from a few kilometers to about 80 km (Whitworth et al., 2000)

2. A taxonomy of cross-realm connectivity

Our taxonomy of linkages between environmental realms divides connectivity into four types with differing spatial characteristics: (1) narrow and (2) broad interfaces, and (3) constrained or (4) diffuse connections (Fig. 1). Interfaces are spatial entities where elements of two or more realms are intermixed and where the connecting processes occur. In narrow interfaces, realms adjoin with relatively little spatial separation, such as along riverbanks or narrow intertidal zones (Fig. 1a). Matter and organisms move across these interfaces, which themselves often have distinctive physical and biological characteristics (Tables 1 and 2). On broad interfaces, there is a wider mixing zone between realms, often forming distinctive interface ecosystems, such as salt marshes or swamps, with internal zonation, gradients in physical environment, and biological responses (Fig. 1b).

Connections between sites may not require that sites are adjacent. In a spatial context, they involve two or more habitats in different realms that are linked (Tables 1 and 2). The strength of connections usually weakens with increasing distance between habitats, or connections cease functioning at threshold distances of separation. In constrained connections, the link is well defined and, at least over time scales of months or years, spatially stable or subject to only minor movements (Fig. 1c). Constrained connections occur along natural pathways or anthropogenically created corridors that spatially restrict the movement of organisms or material, for example rivers or corridors of remnant vegetation (Chetkiewicz et al., 2006). Diffuse connections vary in space and time and thus are difficult to delineate (Fig. 1d). The movements of sea turtles, for example, create connections between feeding and breeding areas via routes that are variable, hard to quantify, and difficult or impossible to manage (Spotila, 2004).

Table 2
Examples for geo-physical processes connecting environmental realms.

	Freshwater–marine	Terrestrial–freshwater	Terrestrial–marine
Narrow interface	The Fiordland region of New Zealand has deep, steep-sloped fjords with narrow entrances to the open ocean. Low water exchange rates in the fjord and high precipitation rates in the catchments create a layer of fresh water, varying from 1 to 10 m depth, discolored by tannins above the sea water, which darkens the environment below (Gibbs et al., 2000). Below this layer, deep-sea marine organisms live in a dark environment that would normally be found only at great depth, a phenomenon termed "deep water emergence"	Both local point and non-point sources of land-based nutrient pollution contribute to anthropogenic eutrophication of freshwater systems. In particular, phosphorus and nitrogen additions from sewage, agricultural runoff, and disturbance to catchments may shift lakes and rivers from oligotrophic and mesotrophic states to eutrophic conditions where harmful blooms of phytoplankton and benthic macro algae develop, thereby affecting both ecological functions and services (Proulx et al., 1996)	Coastal rivers carry high volumes of sediment to the coast, much of it sand. This sediment is accumulated along the coastal zone, with wave action forming it into sand beaches (Wai et al., 2004). Dams and river dredging have caused a substantial reduction in the volume of sediment delivered to the coast. This reduction, along with a rising sea level, has resulted in extensive erosion of beaches
Broad interface	Estuaries are characterized by a mixing of fresh and salt water. The loss or change in mixing can result in the change of physical and biological processes. Therefore, an important part of conservation planning for this interface habitat is the maintenance of the natural freshwater flow from the catchments	The Pantanal wetland, Brazil, is formed by an alternation of floods and droughts, where most of the 140,000 km^2 of floodplain is an aquatic–terrestrial transition zone. The extent and arrangement of aquatic, semi-aquatic, and terrestrial habitats are determined by changes in flood frequency, extent and duration (Doprado et al., 1994). This wetland system depends on the intactness of key controlling elements such as headwater recharge, natural flow-barriers, water quality and biotic community feedbacks	Mangroves are beneficial on the interface of freshwater and marine realms, because of their function to trap, metabolize and store suspended sediment and organic matter (Alongi and McKinnon, 2005). For example, mangroves can reduce the impact of deforestation on coral reef communities because of their function as a filter for the pollution of river water that results from deforestation
Connections	Organic and heavy metal contaminants frequently enter coastal marine ecosystems from industrial and agricultural effluents occurring upstream in catchments or from atmospheric deposition (see references in Turgeon and Robertson, 1995). Depending on habitat-specific rates of evaporation, dissolution, dispersion, degradation, sedimentation, and transformation, pollutants may be concentrated and bio-accumulated in coastal estuaries and bays. The complex interactions of physical, chemical, and biological gradients at the freshwater–marine interface affect the impact of land-based pollutants on marine ecosystems	The Everglades, USA, is a 10,000 km^2 wetland complex that is threatened by urban and agricultural sprawl. Its network of channels and ponds has suffered severe human interferences and has been heavily modified. Recently, in an effort restore the remainder of the ecosystem; a systematically planned reserve network to protect the Everglades became one of the first cases where the entire catchment was used in a dynamic selection process (Oetting et al., 2006). DSS were used to restore connectivity based on ecological and hydrological networks	The declining reef health of the Great Barrier Reef (GBR), Australia, is critically linked to water quality and therefore land use in the catchment. Increased sediment, nutrients and fertilizer concentrations at an inner reef site in the GBR were shown to reflect land use in the catchment area after European settlement of Australia (McCulloch et al., 2003). A modeling case study in Far North Queensland predicted that restoration of riparian vegetation along a river would reduce sediment load more significantly than land use change from sugarcane to grazing (Hateley et al., 2005)

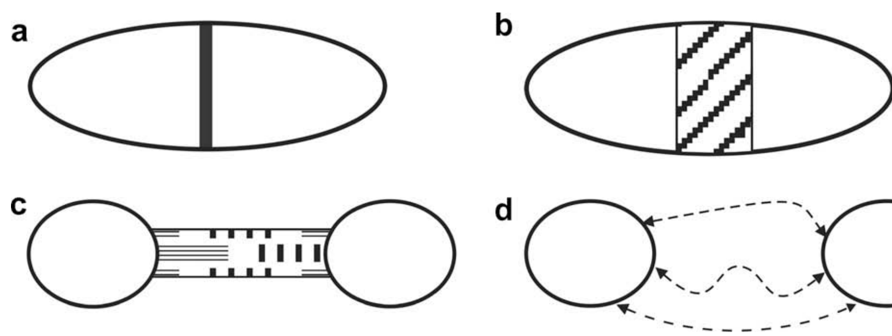

Fig. 1. Classification of processes connecting environmental realms, (a) narrow interfaces where two realms have short, (b) broad interfaces where the boundary between two realms have wider spatial separation, (c) constrained connections where the path between two endpoints is defined by relatively narrow connecting features, and (d) diffuse connections where the path between two endpoints is unknown.

The categories in this classification scheme are defined here to enable us to discuss particular examples and appropriate conservation planning responses, but processes that fall into these classes lie on a continuum of spatial separation. Narrow interfaces may operate on scales ranging from a few meters to several hundred meters and can represent distinctive habitats, whereas broad interfaces are often regarded as specific ecosystems in their own right. Connections, both defined and diffuse, operate over different spatial and temporal scales. For example, while the migration of amphibians from natal pond to terrestrial habitat can operate at a scale of meters (Semlitsch and Bodie, 2003), Marbled Murrelets (*Brachyramphus marmoratus*) can travel up to 80 km between terrestrial breeding and marine feeding sites (Whitworth et al., 2000) and migratory fish in the Amazon travel thousands of kilometers between feeding and breeding areas (Goulding et al., 2003). Transport of sediment and nutrients, likewise, can occur at scales of tens of meters beside streams or on beaches, or tens to hundreds of kilometers through whole river catchments and offshore beyond the edge of the continental shelf.

Although we discuss the taxonomy of connections occurring across different environmental realms to highlight the need for integrated planning, similar conservation problems and solutions apply to interfaces and connections within realms. For example, conservation planners in the Cape Floristic Region, South Africa

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applied a narrow interfaces approach to edaphic boundaries between 'acidic' and 'alkaline' habitat types (Rouget et al., 2003). An example akin to broad interfaces is ecotones, the intermediate zone where two terrestrial ecosystems intermingle gradually (Kark et al., 2007; Ray and Hayden, 1992). These have been addressed previously in conservation site prioritization (Rouget et al., 2006; van Rensburg et al., 2009). Movement of species between habitats within realms can represent a constrained connection if the species depends on specific pathways between different habitats, like vegetated corridors (Chetkiewicz et al., 2006; Minor and Urban, 2008; Saura and Pascual-Hortal, 2007). Within-realm diffuse connections occur, for example, with recruitment and larval dispersal processes in the marine realm which present challenges for management (McCook et al., 2009).

3. Spatial prioritization techniques for different connectivity types

The classification of the processes that connect realms enables us to efficiently summarize methods to incorporate these into DSS for conservation. We provide an overview of approaches using current decision-support tools as well as new formulations that specifically require tool development. Our techniques assume that connecting processes are considered in addition to other objectives. They were developed with the decision-support tool MARXAN in mind (Ball et al., 2009), but generally are applicable to other decision-support tools.

3.1. Narrow interfaces

Narrow interfaces can be incorporated into decision-support tools by (a) including interfaces incidentally by targeting environments around them, (b) representing the interface as a linear feature, (c) configuring planning units specifically to define the interface, (d) apply stratification to conservation features in interface habitats, and (e) use smaller planning units in interface habitats to recognize the higher spatial heterogeneity in features of interest at those interfaces.

When including interfaces incidentally by targeting environments around them, contiguous planning units are deployed spatially across marine, terrestrial, and freshwater realms and information from all realms is incorporated into a single analysis (Fig. 2a). This approach was used in the Puget Trough planning project, and resulted in site selections with bias towards coastline planning units, as these simultaneously contained terrestrial, freshwater and marine features (Floberg et al., 2004; Tallis et al., 2008). This bias presents a problem if planners consider it desirable for selected planning units to lie at different distances from the interfaces.

The simplest method of incorporating a narrow interface into a DSS directly is to represent it spatially as a line or narrow polygon (Fig. 2b), and treat it as a conservation feature with a separate target in the DSS (Banks and Skilleter, 2005). Relatively mobile or seasonal interfaces can be represented as transition zones on either side of the interface line. Where it is desirable to select groups of contiguous units across these zones and adjacent habitats, planning units can be clustered in MARXAN by reducing the total boundary length of selected areas (Banks and Skilleter, 2005; Klein et al., 2009; McDonnell et al., 2002) (compare Broad Interfaces).

When configuring planning units specifically to define the interface, special planning units are delineated to represent the interface and features that meet along the interface (Fig. 1c). Other planning units are then configured around the interface units. This has been used in conservation planning for soil interfaces in terrestrial environments (Lagabrielle et al., 2009; Rouget et al., 2003) but is directly applicable to planning for interfaces between realms.

Stratification is a technique in spatial prioritization where conservation features are allocated to sub-categories. Layers of information (strata) that describe the same feature but at different levels of detail are recorded for each planning unit. The conservation target for this feature is then chosen by setting a larger target for the undivided feature and smaller targets for each fine-scale subdivision to ensure a minimum representation of the feature's internal heterogeneity (Beck and Odaya, 2001). On rocky intertidal shores, for example, the same planning unit can be assigned the following strata: rocky intertidal, exposed rocky intertidal, and lower exposed rocky intertidal. Across the planning region, a

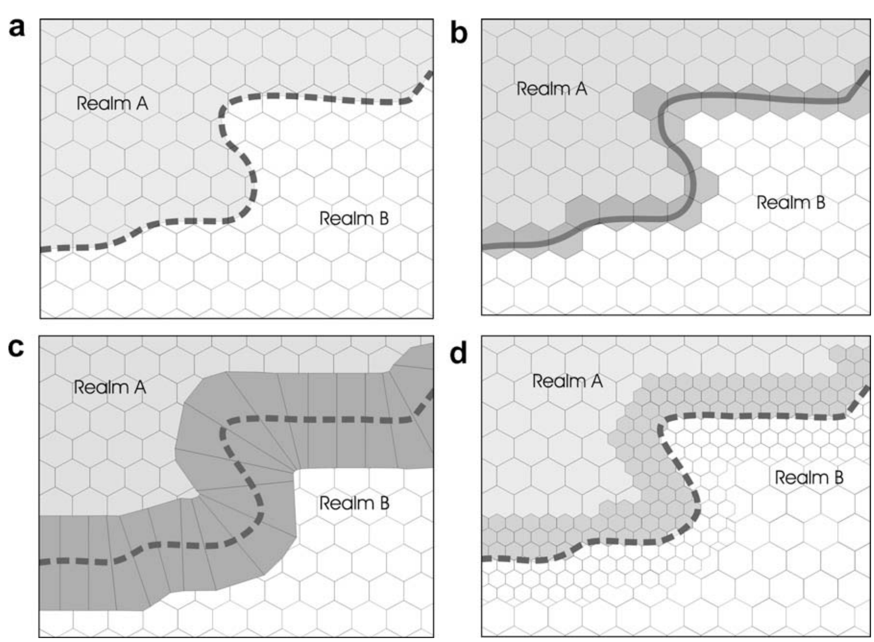

Fig. 2. Planning on narrow interfaces, (a) the interface is included incidentally when planning occurs across the entire planning region; (b) the interface is represented as a distinctive linear feature; (c) a buffer on either side of the interface is composed of specifically configured planning units (also compare Rouget et al., 2003); (d) data are stratified in higher resolution planning units around the interface. Thick dashed lines represent the location of the interface, the full line (b) represent the linear feature of the interface.

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conservation target of 20%, for example, of undivided rocky intertidal might be achieved while missing most or all of some subtypes. To avoid this, the target for rocky intertidal can be supplemented by ensuring, for example, that at least 10% of exposed rocky intertidal and 5% of lower exposed rocky intertidal are included within the overall 20%.

Smaller planning units can ensure the representation of habitat heterogeneity in the narrow interface and adjacent realms by increasing the precision with which particular features can be targeted (Fig. 1d) (Ferdaña et al., 2006), especially if interface habitats are mapped at finer resolution than habitats further out to sea or further inland. Smaller planning units can also represent a narrow interface with less over-representation of interface and adjacent features.

3.2. Broad interfaces

Broad interfaces can be incorporated into conservation plans by treating them as separate conservation features with specific objectives to protect the interfaces themselves and promote the persistence of processes that depend on them (Table 1) (Green et al., 2009). Planning units are therefore defined across the planning region in all habitats, including the interface habitat, to consider connectivity to complementary habitats and proximity to adjacent protected areas (Groves et al., 2000). By setting specific objectives for the interface habitat in addition to other conservation features, it is possible to prioritize broad interface sites that are predominantly adjacent to priority sites in adjacent realms. To define distinct interface habitats, broad interface ecosystems can be subdivided, like the lateral subdivision of habitats in the Amazon floodplain (Hess et al., 2003). A recent US Pacific Northwest Coast ecoregional planning assessment was designed to consider estuarine habitats in the broad interface between terrestrial and marine realms (Table 2) and representation targets were set separately for estuarine features such as benthic substratum, habitat types, and estuarine species (Ferdaña et al., 2006).

3.3. Constrained connections

Constrained connections and the sites they connect should be managed as one system, where the habitats in different realms as well as the connecting link are integrated. Constrained connections can be incorporated into DSS by either (a) assigning values to planning units and their boundaries that reflect their contribution to the connection, (b) setting objectives for habitat features in each realm and managing the connections, and (c) managing the effects of upstream processes in one realm on the persistence of downstream processes in another realm.

Values can be assigned to planning units and parts of their boundaries to reflect their relative importance for maintaining connections. Thus a benefit is associated with conserving two adjacent sites proportionally to the magnitude of a connection between them. In the resulting conservation planning problem the objective is to meet the targets for each feature and additionally maximize the benefit assigned to conserving well-connected pairs of planning units (Klein et al., 2009; Possingham et al., 2005). The value of a pair of planning units for maintaining a connection can be identified by pre-processing that determines, for example, the shortest paths of corridors in a landscape (Rouget et al., 2006), or modeling of flow strengths (for an example, see Supplementary Information). This approach requires pre- or post-processing of data determining which pairs of planning units are functionally related, and then ensuring that if one of these sites is included, there is a strong incentive to include the other.

When the pathway of a constrained connection is known, like a river for anadromous fishes (Table 1), conservation planning can involve setting objectives for the features required in each realm and ensuring that the connection is managed to support the conservation objectives. This is important for large streams, where human use cannot be completely avoided but must be regulated, perhaps by limits on chemical discharges, seasonal fisheries closures, or other limits on harvest.

A method that aims to select terrestrial protected areas with the exclusive purpose of protecting downstream marine features was illustrated for estuaries (Stoms et al., 2005). This approach considers the balance between 'promoters' (activities promoting the persistence of features in downstream marine areas, like retention of native vegetation in catchments) and 'demoters' (activities degrading or eliminating features in downstream areas, like excessive application of agricultural nutrients). This method considers the relative impacts of several kinds of activities in different upstream areas and identifies priorities for protection and restoration in catchments that balance upstream values for biodiversity conservation with the achievement of conservation objectives downstream.

3.4. Diffuse connections

Diffuse connections are difficult to address explicitly in conservation planning because the connection path is unknown, or highly variable. We suggest considering them by either (a) defining cost values of planning units in one realm depending on the distance from corresponding connected areas and (b) assigning boundary costs to promote the selection of functionally connected but non-adjacent planning units.

If species persistence depends on movement between two realms and is related to distance between required areas, the cost of a planning unit in one realm can be defined by its distance to the nearest suitable planning unit in the other realm. This approach was used to determine the value of potential koala (*Phascolarctos cinereus*) habitat patches relative to their spatial configuration (Rhodes et al., 2005). Each potential patch was assigned a colonizing probability that decreased with increasing distance (which could be reflected in higher costs) from known koala habitat given the species' dispersal capabilities. Analogously, if a maximum distance is known at which diffuse connections cease operating (e.g. 80 km traveling distance for Marbled Murrelets, Table 1), any planning units at a distance greater than the threshold can be penalized by giving them a high cost, reducing their likelihood of inclusion in a conservation system.

In DSS that use boundary costs between planning units, pre-processing can determine boundary cost as the strength of a diffuse connection between noncontiguous planning units in different realms, or connectivity cost (Possingham et al., 2005). The overall boundary cost of a planning solution is then reduced by selecting pairs of sites that have high boundary costs individually but not when they are included together, thereby reflecting strong functional connections to promote a process of conservation interest. The method has been described for marine habitats connected by larval dispersal (Possingham et al., 2005) but is adaptable to connections between realms.

4. Future spatial conservation prioritization techniques for inter-realm connectivity

Spatial conservation prioritization techniques are becoming more widely applied and increasingly complex conservation issues are being addressed. Future methods that directly incorporate the cross-interface flows of materials and organisms, and the interdependencies of features contained in planning units include (a) setting objectives for connectivity and (b) managing threatening flows across interfaces.

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Direct consideration of flows requires decision-support tools to deal with vectors that represent the probability, magnitude, and direction of a connection between planning units (Possingham et al., 2005). The greatest challenge of this method might be to quantify these flows, but advances in modeling, empirical data collection, genetics, and ecological and environmental theory make this possible. For example, dispersal flows of two species, American mink (*Mustela vison*) and Prothonotary Warblers (*Protonotaria citrea*) have been evaluated in wetland habitats with graph theory (Bunn et al., 2000). Hydrodynamic and hydrological models are widely used tools to evaluate the flow and dynamics of water, nutrients and sediments within riparian and oceanic systems. Such models can be used to obtain the net flows between planning units (Hateley et al., 2005; Tallis et al., 2008). For example, several strategies exist to derive values for sediment flows, and have associated spatial and technical challenges (Supplementary Information).

The theoretical conservation planning formulation in a minimum-cost framework to incorporate flow vectors directly involves minimizing the expected cost of the entire system, subject to all features meeting their targets, and all flows meeting their targets (Appendix A.1), thus accommodating the fact that the configuration of management or conservation areas influences the flows between any pair of planning units. For some flows it might be necessary to introduce an upper limit on the acceptable amount of the flow in a system (Appendix A.1).

Within coastal catchments, the location and configuration of conservation areas, the features they contain, and management practices within and outside conservation areas influence the persistence of downstream estuarine and marine features (Stoms et al., 2005; Tallis et al., 2008). Based on the example of a tropical coastal environment, we formulate the theoretical basis of the problem of managing threatening flows in decision-support tools, which we believe is not currently implemented in any tool (Appendix A.2). In each planning unit, we assume there are two management options: to apply a conservation action or not. Reefs, inter-reefal areas, and mangroves that are not conserved experience reductions in abundance of species of conservation interest, have reduced resilience to disturbance, and lose their contribution to interactions between realms. Terrestrial planning units that are not protected are developed, and hence contribute to increased sediment and pollutant loads to rivers which adversely affect the reefs. The conservation planning problem formulation remains similar to the minimum set problem (Appendix A, Possingham et al., 2000), but we now want to accommodate the influence of activities in terrestrial and interface ecosystems on the persistence of features at a reef. The probability that a feature is extant generally will be a function of how the reef is managed, how neighboring reefs are managed, and how the terrestrial and coastal systems are managed. That relationship will be complex and include considerations about (a) the impact of fishing on a feature; (b) the net sum of sediment that could flow from the terrestrial planning units to reefs, possibly estimated by a hydrodynamic flow model (Supplementary Information); and (c) the filtering effect of mangroves in reducing sediment flow to reefs. The goal might be to minimize the expected cost of the entire system, subject to non-reef and reef-based features meeting their targets, given the chance that a feature persists on a reef (Appendix A.1). The precautionary principle requires that the explicit consideration of uncertainty associated with such a model will require larger targets than when uncertainty is ignored (Allison et al., 2003).

5. Discussion

Conservation planning for the processes that operate between environmental realms is imperative to promote the persistence of many features of conservation concern, ensure the long-term viability of populations, and maintain many socio-economic values. Nonetheless, conservation planning to date has tended to treat environmental realms separately (Abell et al., 2007; Stoms et al., 2005). Traditional approaches to conservation prioritization have aimed to represent conservation features most efficiently (Possingham et al., 2000) while accounting for uncertainty (Halpern et al., 2006), vulnerability (Wilson et al., 2005), or endangered species protection (Arthur et al., 2004). Although these are important advances, systematic conservation planning must also ensure both that biodiversity features are represented and that supporting processes are protected at a scale relevant and adequate for the processes and associated static features (Possingham et al., 2005). The conservation planning methods described here are early steps towards achieving these goals.

Integrated planning relies on complex data, modeling and conceptualization. When planning conservation actions that aim to maintain ecosystem processes and achieve representation of biodiversity features, socio-economic trade-offs will be required because resources for conservation are limited (Arthur et al., 2004; Rothley, 2006). Maintaining inter-realm processes will often require different sites to be protected than those required to represent biodiversity features in a single realm. Given the complexity of cross-realm connectivity, data that describe it are likely to be relatively uncertain (Krueger et al., 2009). These uncertain data could be given less weight than data that, by comparison, have been more thoroughly surveyed and are relatively well understood. Choices about whether to commit limited conservation resources to aspects of pattern or process are all the more important because unprotected areas face varying risks of losing their natural values (Pressey et al., 2007). Methods for explicitly resolving these choices are poorly developed (Regan et al., 2009).

As in all conservation planning, considering the scale at which processes operate in relation to the scale of planning is crucially important. Some processes, such as the migration of amphibians from their natal pools to their terrestrial hibernation habitat, occur at very fine scales (Semlitsch and Bodie, 2003). Such fine-scale local processes need to be addressed and managed separately at appropriate scales within priority areas identified by regional scale conservation planning. Scale is also important when considering parameter values of flows. Indeed the quantity and direction of flows, including those that govern the transport and settlement of sediment particles, will vary depending on scale (Supplementary Information). Complex hydrological or hydrodynamic models that take these interactions into account can be used to estimate the sediment flow parameters between planning units at the scale of sub-catchments (Anctil et al., 2009; Naik et al., 2009; Velleux et al., 2008). At the scale of a whole catchment, modeling and incorporation of a flow parameter may be irrelevant, and it may be most efficient to measure the actual parameter at the river mouth to evaluate the sediment load that may affect adjacent marine habitats (Nyssen et al., 2006).

The complexities associated with estimating the strength and scale of connections and setting objectives for them present serious challenges to conservation planners. Even if planning units can be allocated estimates of the probability, magnitude and direction of a flow, meaningful objectives or targets need to be determined that will allow the associated process to persist while also accounting for the effects of resource use. For instance, how much sediment or nutrients should be allowed and what are the thresholds around this? There is a critical research need to benchmark key flows in various environmental settings and to understand the natural variability of these flows as well as the responses of natural systems to altered regimes. The modification of terrestrial runoff through catchment alteration, deteriorating water quality, and increasing fishing pressure are likely to have a substantial

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and compounding effect on marine environments (Fabricius, 2005; Jupiter et al., 2008), but this has rarely been quantified (but see Hateley et al., 2005 for an example of modeling sediment input to the Great Barrier Reef). Similarly, the dynamics of beach accumulation and erosion make it difficult to identify strict boundaries of narrow and broad interfaces, suggesting classification approaches such as fuzzy landscape modeling (Cheng et al., 2009). Successful implementation of the spatial conservation prioritization techniques described here requires an integrative, ecosystem-wide scientific approach, based on existing data, measurements, experiments and ecosystem models.

A major impediment to cross-realm conservation planning will be the people involved in planning and how institutions are developed. People tend to create institutions that are specialized in their interests. For example, government departments typically separate marine, terrestrial and freshwater conservation issues. Furthermore, many objectives in coastal and estuarine management are confused because of the difference interests of federal, state/province and regional governments. Finally, scientists often specialize on a particular realm and universities will teach realm-specific courses. These social and institutional factors hamper our capacity for cross-realm conservation.

For all techniques discussed in this framework, identifying configurations of management that best achieve conservation objectives is only part of planning effective conservation systems that maintain processes linking realms. The output from decision-support tools will likely be modified by involving experts and other stakeholders in fine-tuning conservation plans in light of particular constraints and opportunities present in different planning regions (Knight et al., 2006). In this context these tools can quickly process large volumes of data and present planners and managers with indicative sets of areas that achieve explicit conservation objectives, but conservation decisions will require the consideration of many other factors (Knight et al., 2009).

For many of the processes that connect environmental realms, the extent and configuration of conservation areas or actions in each realm are likely to change the parameter estimates for some flows. Ideally, the decision-support tool used for conservation planning should be dynamic and coupled with models that evaluate changes in these processes (Pressey et al., 2007), but this can present serious computational challenges. For example, a hydrodynamic model of sediment transport could dynamically interact with a spatial prioritization tool, whereby in each iteration new configurations of conservation areas could prompt a re-estimate of sediment load values. Planners also need to assess and incorporate explicitly the uncertainty associated with the data used in preprocessing and modeling (Halpern et al., 2006; Regan et al., 2009), which has been explored for spatially explicit conservation applications with bootstrapping methods (Beech et al., 2008), fuzzy set theory (Pyke, 2005; Wood and Dragicevic, 2007), and infogap analysis (Nicholson and Possingham, 2007; Regan et al., 2005). This uncertainty propagates to the modeling results, and affects the selection of notional conservation areas. At the same time, it is important to keep the conservation planning procedure as simple and transparent as possible. The interpretation of results from a dynamic decision-support tool that accounts for uncertainty and error propagation will be complex, and therefore unlikely to satisfy most stakeholders (Knight et al., 2006; Pierce et al., 2005). Under such circumstances, creative ways of communicating models and results to stakeholders will need to be developed.

Integrating processes that connect realms adds complexity and expense to the already complicated procedure of conservation planning. We recognize that planning and management for the major biomes is often segregated for political and bureaucratic reasons, such as the separation of agencies for terrestrial and marine conservation. However, even planning efforts which are primarily designed for either terrestrial, freshwater, or marine objectives can benefit from methods that account for processes connecting environmental realms. Ultimately, integrating processes that connect realms to maintain biodiversity elements and cross-realm habitats in conservation planning will result in more efficient and effective conservation actions, and better use of limited conservation resources.

Acknowledgements

The authors wish to acknowledge all participants of the Heron Island Workshop funded by an Australian Research Council grant to Possingham and McCarthy and The Ecology Centre at The University of Queensland. MB and HSG were supported by a PhD scholarship by The University of Queensland and the Australian Government, and MB was also a member of the ARC Centre of Excellence for Coral Reef Studies. RLP and KAW acknowledge funding from the Australian Research Council and the Commonwealth Environment Research Facilities Programme (Applied Environmental Decision Analysis). RL was supported by The Capes Foundation – Ministry of Education, Brazil and Conservation International. The manuscript was considerably improved by the contributions of seven anonymous reviewers.

Appendix A. Equations to formulate the conservation planning problem to incorporate connectivity

Most DSS tools solve the standard conservation planning problem formulation (Moilanen et al., 2009): minimize the total cost of conserving a set of sites,

$$\min \sum c_i x_i, \tag{A.1}$$

subject to each biodiversity feature meeting a specified target,

$$\sum_{i=1}^{n} a_{ij} x_i \geq T_j, \quad \forall\, j, \tag{A.2}$$

and the constraint that every site is either in the reserve system or not

$$x_i \in \{0, 1\},$$

where $j = 1, \ldots, m$ is the index for the m features for which targets are being set, $i = 1, \ldots, n$ is the index for the n sites each of which could be conserved, c_i is the cost of conserving site i, a_{ij} is the amount of each feature j in site i, T_j is the target for feature j, and x_i is the control variable that determines whether a site is in the reserve system or not. If $x_i = 1$, site i is n, if $x_i = 0$ site i is not in the reserve system. This basic formulation can be extended to address targets for fluxes and the effects of inter-realm flows, below.

A.1. Setting targets for fluxes

Minimize the expected cost of the entire system (Eq. (A.1)), subject to all features meeting their targets T_j

$$\sum a_{ij} x_i \geq T_j, \quad \forall\, j \tag{A.3}$$

where a_{ij} is the amount of feature j in each site i, and subject to all flows meeting their targets T_k

$$\sum b_{ilk} x_i x_l(\underset{\sim}{x}) \geq T_k, \quad \forall\, k, \tag{A.4}$$

where $b_{ilk}(\underset{\sim}{x})$ is the magnitude of the flow of material $k = 1, \ldots, p$ from each site i to every other site $l = 1, \ldots, n-1$, when the set of sites $(\underset{\sim}{x})$ is reserved, thus accommodating the fact that the configuration of management or conservation areas influences the flows between any pair of planning units.

If an upper limit on the acceptable amount of the flow in a system is required, the formulation of the problem is to minimize the expected cost of the entire system (Eq. (A.1)), subject to all features meeting their targets T_j (Eq. (A.3)), and subject to all flows meeting their targets T_k (Eq. (A.4)), while not exceeding upper limits L_k

$$\sum b_{ilk} x_i x_l(\underset{\sim}{x}) \leq L_k, \quad \forall k. \tag{A.5}$$

A.2. Consider the effect of management of features and flows on environments

We formulate a problem where a habitat in one realm is affected by its state, and its management, as well as the state and management of a connected habitat in another realm. Thereby, cross-realm connectivity could be a threatening flow, or a flow that propagates upstream improvements to a cross-realm habitat. We illustrate the approach with the case of a tropical coastal environment. In each planning unit, we assume there are two management options, to apply conservation actions or not. Marine habitats that are not conserved experience reductions in abundance of species of conservation interest, have reduced resilience to disturbance, and lose their contribution to interactions between realms. Terrestrial planning units that are not protected are developed, and hence contribute to increased sediment and pollutant loads to rivers which adversely affect the reefs.

Let p_{ij} be the probability that feature j on reef i is extant. In general, this will be a function of how the reef is managed, how neighboring reefs are managed, and how the terrestrial and coastal systems are managed. Hence p_{ij} is a function of the entire conservation area system $(\underset{\sim}{x})$. That relationship will be complex and include considerations about (a) the impact of fishing on feature j; (b) the net sum of sediment that could flow from the terrestrial planning units to reef I, possibly estimated by a hydrodynamic flow model; and (c) the filtering effect of mangroves in reducing sediment flow to reefs. A formulation of this conservation problem is:

Minimize the expected cost of the entire system (Eq. (A.1)), subject to non-reef features meeting their targets

$$\sum_{i \in NR} a_{ij} x_i \geq T_j, \quad \forall j, \tag{A.6}$$

where a_{ij} is the amount of feature j in site i, NR is the set of non-reef planning units and subject to reef-based features meeting their targets,

$$\sum_{i \in R} a_{ij} p_{ij}(\underset{\sim}{x}\, \underset{\sim}{y}) \geq T_j, \quad \forall j, \tag{A.7}$$

where R is the set of reef planning units, and $(\underset{\sim}{y})$ is a vector of parameters that, along with the conservation plan $(\underset{\sim}{x})$, determine the chance p_{ij} that feature j persists in reef i. Note that $a_{ij}p_{ij}\ (\underset{\sim}{x}\, \underset{\sim}{y})$ is only the expected amount of feature j that persists.

Appendix B. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2009.11.006.

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Please cite this article in press as: Beger, M., et al. Conservation planning for connectivity across marine, freshwater, and terrestrial realms. Biol. Conserv. (2009), doi:10.1016/j.biocon.2009.11.006