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Integrating multi-directional connectivity requirements in systematic conservation planning in freshwater systems.

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Abstract

Aim: Recent efforts to apply the principles of systematic conservation planning to freshwater ecosystems have focused on the special connected nature of these systems as a way to ensure adequacy (long-term maintenance of biodiversity). Connectivity is important in maintaining biodiversity and key ecological processes in freshwater environments, and is of special relevance for conservation planning in these systems. However, freshwater conservation planning has focussed on longitudinal connectivity requirements within riverine ecosystems, while other habitats, such as floodplain wetlands or lakes and connections among them have been overlooked. Here, we address this gap by incorporating a new component of connectivity in addition to the traditional longitudinal measure.

Location: Northern Australia

Methods: We integrate lateral connections between freshwater areas (e.g. lakes and wetlands) that are not directly connected by the river network and the longitudinal upstream-downstream connections. We demonstrate how this can be used to incorporate ecological requirements of some water dependent taxa that can move across drainage divides, such as waterbirds.

Results: When applied together, the different connectivity rules allow the identification of priority areas that contain whole lakes or wetlands, their closest neighbours whenever possible, and the upstream/downstream reaches of rivers that flow into or from them. This would facilitate longitudinal and lateral movements of biota while minimising the influence of disturbances potentially received from upstream or downstream reaches.

Main conclusions: This new approach to defining and applying different connectivity rules can help improve adequacy of freshwater protected areas by enhancing movements of biodiversity within priority areas. The integration of multiple connectivity needs can also serve as a bridge to integrate freshwater and terrestrial conservation planning.

Keywords: adequacy, longitudinal, Marxan, movement, inter-catchment, surrogates, wetland.

Introduction

Freshwater conservation planning is an emerging discipline that has started to receive special attention from the scientific community in the past five years as a response to the lack of effective conservation of freshwater biodiversity (Abell et al., 2007, Linke et al., 2008; 2011; Turak & Linke, 2011). This is despite freshwater ecosystems being among the most diverse and threatened systems in the world (Strayer & Dudgeon, 2010), and being exposed to higher pressures than adjacent terrestrial or marine ecosystems (Malmqvist & Rundle, 2002; Nel et al., 2007). To date there has been little emphasis on declaring protected areas for the primary purpose of conserving freshwater ecosystems and biodiversity (Saunders et al., 2002; Abell et al., 2007). Instead, uninformed opportunism has reigned, whereby conservation of freshwater ecosystems is peripheral to conservation goals developed for terrestrial ecosystems (Olden et al., 2010).

The distinctive characteristics of freshwater ecosystems pose several challenges to conservation practitioners and hinder the implementation of effective conservation plans (Linke et al., 2011). Spatial connectivity plays a crucial role in maintaining natural ecological processes and biodiversity in freshwaters (Pringle, 2001; Fausch et al., 2002; Nel et al., 2011). Designing efficient and effective conservation area networks in freshwaters needs to account for the spatial hierarchies of fluvial ecosystems and the necessity to consider longitudinal, lateral and surface/ groundwater connections (Fausch et al., 2002; Turak & Linke, 2011). This is important because disturbances such as pollution, flow alteration and the spread of introduced species are easily propagated through hydrologic networks and seriously affect the biodiversity apparently protected within the reserved area (Pringle, 2001). Connectivity is also essential in maintaining some key ecological processes in river-floodplain systems. Longitudinal connectivity allows long and short-distance migrations of biota through river networks and is important for dispersal, reproduction and long term population dynamics of many fish species for example. During wet-season inundation, lateral connectivity between the river channel and aquatic habitats (e.g. lakes and wetlands) on the adjacent floodplain is important to maintain exchange of matter and energy (Ward, 1989) and maintain viable populations of many water-dependent species that develop most of the life cycle in the floodplain and use the river channel as a dry season refuge (Welcomme, 1979). Some water-dependent biota are not restricted to water as the medium for movement and may move aerially (e.g. waterbirds and adults stages of aquatic insects) or overland (turtles and some crustaceans) to access nearby or distant freshwater areas (e.g. lakes and wetlands) so spatial proximity of aquatic habitats within and between river catchments may be important to sustain these species. Vertical connectivity is also crucial given the dependence of some surface ecosystems on groundwater or the exchange of biota (Stanford & Ward, 1988).

Several different approaches have been developed to incorporate freshwater connectivity based on modifications of some of the tools originally designed for marine and terrestrial conservation planning, such as Marxan (Ball et al., 2009) or ZONATION (Moilanen, 2006). Longitudinal connectivity in riverine systems has been addressed by attempting to allocate priority areas for conservation while minimising the propagation of threats along the river network or to maintain key ecological processes such as migration pathways for biota (Linke et al., 2007; Moilanen et al., 2008; Beger et al., 2010a; Hermoso et al., 2011b). This is done by using the network topology to link each local subcatchment with their upstream watersheds and the next downstream catchment (Linke et al., 2007; 2008; Moilanen et al., 2008; Hermoso et al., 2011b). This helps allocate priority areas in parts of the catchment where they do not receive negative influences of threats occurring in other sections of the catchment, for example. Lateral connectivity is usually dealt with by planning at the subcatchment scale and incorporating measures of condition or threats (e.g., land uses) as a proxy of the quality of lateral connectivity (Linke et al., 2007; Nel et al., 2007; Turak & Linke, 2011). For example, only zones where dominant land uses at the subcatchment scale does not compromise lateral movement should receive a high priority for protection.

Despite the advances in freshwater conservation planning and the improved capacity to address connectivity, freshwater conservation planning has largely focused on riverine systems with limited consideration of habitats such as floodplain wetlands or lakes (Ausseil et al., 2011). Although many lakes and wetlands are never hydrologically connected (e.g. occur in adjacent catchments) they may have an important connectivity role as part of a broader functional network of freshwater ecosystems (Nel et al., 2009; Olden et al., 2010) and the maintenance of freshwater biodiversity. This additional source of connectivity is especially important when addressing the ecological needs of some water dependent taxa, such as waterbirds, some turtles or insects. The movements of these taxa are not constrained to the submerged portion of the freshwater ecosystem and can or need to move across drainage divides. Providing them with a network of aquatic habitats for resting or feeding which can serve as stepping stones that facilitate movement among sources of permanent water would greatly enhance their future persistence and the adequacy of the conservation plan. Considering this new component of connectivity can also serve as a bridge between freshwater and terrestrial conservation planning, which is a priority in order to advance an integrated terrestrial-freshwater network of protected areas and overcome traditional compartmentalized approaches (Nel et al., 2009; Beger et al., 2010b).

Here, we combine a longitudinal connectivity rule, originally proposed by Hermoso et al. (2011b), with a set of new inter-subcatchment connectivity rules based on the spatial arrangements of sub-catchments not connected longitudinally. By combining longitudinal and inter-subcatchment connections we also show a potential way to overcome the traditional lack of integration of freshwater and terrestrial conservation planning. We demonstrate a practical application of these ideas in a conservation planning example in freshwater ecosystems of northern Australia, based on two taxonomic groups with contrasted connectivity needs (freshwater fish and waterbirds).

Methods

Study area

Northern Australia here defined as spanning all coastal river catchments from the Fitzroy River in the Kimberley regions eastwards to the Jardine river in Cape York Peninsula (Fig. 1A), has a total area of about 1.19 million km^2; encompassing about 15% of the Australian continental area. The region comprises more than fifty major river systems that collectively discharge over 46% of Australia's surface-water runoff (Pusey & Kennard, 2009). The overall climate is tropical, however substantial gradients in landform and climate over this latitudinal range impart a great deal of physical and biological diversity. Landform is characterised by the presence of large seasonally inundated floodplains, steep rocky gorges and upland plateaus. The floodplain wetland habitats of northern Australia are vast and comprise about 25% of the entire area (Pusey & Kennard, 2009) and represent the largest area of unmodified wetlands in all Australia (Woinarski et al., 2007). Most of the rivers, wetlands and estuaries of northern Australia are in good ecological condition (NLWRA, 2002) but poorly protected and under-represented in the

National Reserve System (Hermoso et al., 2011a). The region supports approximately 60% of Australia's freshwater fish diversity Pusey et al., 2011) and 25% of Australia's waterbird diversity (Woinarski et al., 2007).

Biodiversity data

The information on fish and waterbirds species distribution was sourced from Kennard et al. (2010). This database contained continuum predictions of spatial distribution for 89 freshwater fish species and 106 waterbirds across northern Australia. Complete coverage of species distribution was derived from Multivariate Adaptive Regression Splines models (Leathwick et al., 2005) at a fine scale (average area of predictive polygons was 3.6 km^2 for fish and 72 km^2 for waterbirds, respectively). Predictive models were built on a data set of 1609 presence-only plus 115 presence-absence sampling sites and validated in an independent data set of 604 presence-absence sampling sites for fish and 2109 presence only sampling sites for waterbirds (see Supplementary material and Kennard 2010 for more details on predictive models).

Identification of priority areas

Priority areas for conservation were identified using the software Marxan (Ball and Possingham 2000) which finds an optimal set of planning units that minimizes the objective function in Formula 1.

$$Objective\ function = \sum_{planning\ units} Cost + SPF \sum_{features} Feature\ Penalty + CSM \sum Connectivty\ Penalty \quad (1)$$

Hence the mathematical objective in Marxan is to minimise the cost of all the sites included in the solution while accounting for penalties for

- not achieving the conservation target for all the species (Feature Penalty, weighted by Species' Penalty Factor, SPF)
- lacking connectivity (Connectivity Penalty weighted by a Connectivity Strength Modifier, CSM, *sensu* Beger et al., 2010a).

While equal-sized grid cells are often used as planning units in terrestrial and marine conservation assessments, hydrologically-defined subcatchments are more appropriate for freshwater ecosystems (Linke et al., 2007). We derived 5803 planning units from a 9 second digital elevation model (ANU Fenner School of Environment and Society and Geoscience Australia, 2008) using ARC Hydro (Maidment, 2002) for ArcGIS 9.3 (ESRI, 2002). Each planning unit included the portion of river length between two consecutive nodes or river connections (16.6 km on average) and its contributing area (201.5 km^2 on average). We then calculated the total area of predicted occurrence for each species within each planning unit as the sum of the areas of all the predictive units where the species was expected to occur. During the optimization, we applied a high penalty factor for not achieving targets (SPF) to ensure that all the species were adequately represented in the solutions. Finally, given our special interest in exploring the effect of connectivity and the lack of estimates of conservation cost, we used a constant cost across the study area (all the planning units were assigned a cost of 1). If a heterogeneous cost had been used, the Marxan selection processes would have been forced to avoid expensive areas, and it would have been difficult to distinguish between the effect of local patterns in cost and the different connectivity rules applied. We aimed to show the effect of the different connectivity rules rather than producing an accurate conservation plan for northern Australia. However, we acknowledge that better estimates of conservation or management cost would be necessary if these analyses were to be further considered for conservation purposes beyond a demonstration exercise.

Connectivity specification in Marxan

We tested different types of connectivity to account for the importance of connections in freshwater conservation planning (Linke et al., 2011) and the particular needs of fish and waterbirds (Fig. 1B–E). Connectivity in Marxan is specified in a file that contains all the connections between planning units that we consider important. If these are disconnected in a conservation plan, penalties are applied. Whenever a planning unit is included in the solution, a penalty value for all open connections is calculated. For example, if planning unit A and B are connected, and the solution contains A but not B, the connectivity penalty applies. Marxan tries to minimize this connectivity penalty by rejecting all solutions that do not contain connected planning units and that therefore apply high penalties.

To account for the potential longitudinal propagation of disturbances and movement requirements of fish along river networks we included the longitudinal connectivity rule for Marxan described in Hermoso et al. (2011b). Under this rule a penalty applies when the upstream or downstream connections of selected planning units are not included in the solution (Fig. 2A). To avoid forcing the selection of whole catchments, the connectivity penalty is weighted by the distance between the planning units (penalty= 1/ distance^2). Reflecting reality, closer upstream or downstream planning units receive a higher penalty than distant ones, so their inclusion is more important. This component of connectivity ensures that planning units selected are spatially aggregated along the river network (e.g., planning units 1 and 4 in Fig. 2A). The application of the longitudinal connectivity rule is unlikely to adequately reflect the connectivity requirements of waterbirds.

Waterbirds move between habitats within wetland systems, between wetlands within a regional network, and also extra-regionally, not only constrained to within catchment movements (e.g., Traill et al., 2010). To address this additional connectivity requirement, we included all the pairwise connections between planning units not longitudinally connected by the river network to account for lateral movements beyond the planning unit scale both within and between river catchments. This will force connections between neighbouring lakes or wetlands in a conservation plan (Fig. 1D). In order to simplify the boundary file, we only incorporated the connections among planning units that were <50 km apart (geographic distance). Our choice of a 50 km threshold represented a trade-off between an ecologically realistic and meaningful distance (based on expert criteria) and a computationally affordable approach (a higher threshold would increase exponentially the number of connections). The multitude of potential connections even when applying this distance threshold made it difficult to calculate continuum distances for each pairwise connection. This was addressed by categorizing Euclidean distance between planning units into 12 concentric buffers around each planning unit's centroid (<1km, 1-2km, 2-3km. 3-4km, 4-5km, 5-7.5km, 7.5-10km, 10-12.5km, 12.5-15km, 15-20km, 20-25km, and 25- 50 km). We then identified the centroids of planning units within each buffer (note that each planning unit had 12 different buffers). Since distance classes were nested, whenever a planning unit appeared in a lower distance class, it was not further accounted for in the next one. Then we used the upper distance limit of each class to calculate connectivity penalties. In the example provided in Fig. 2, the distance between planning units 4 and 3 is 4.5 km. The penalty included in the boundary file is not 0.05 (1/ 4.5^2), but 0.04 (1/ 5^2). This way all the planning units within a radius of 4-5 km from planning unit 4 would apply the same penalty as planning unit 3.

Large lakes and wetlands may extend over more than one planning unit (Fig. 1C). To account for the high connectivity within these waterbodies we also included all the pairwise connections of planning units occupied by each independent lake or wetland in the boundary file. Given the strength of these connections we used a high penalty in the boundary file which usually forced the selection of entire waterbodies independently of the number of planning units it might spread through. Alternatively, the whole waterbody could be considered a single planning unit, but this would require modifying the predefined set of planning units.

The different connectivity files were aggregated to produce the final integrated Marxan boundary file. Whenever the connection between two planning units was repeated, the highest penalty was retained. We tested the effect of different connectivity rules by running independent analyses for each type of connectivity (either longitudinal only or inter-subcatchment only) and the combination of both in the integrated boundary file. Both, waterbird and fish data were used for this analysis. The relative importance of connectivity in the optimization process used by Marxan has traditionally been controlled by the CSM in Equation 1. When using a high CSM, Marxan is forced to find highly connected solutions. Here, we incorporate an additional parameter to be controlled: the relative weight of longitudinal vs. lateral connectivity. This can be done by pre-processing the boundary file and changing the magnitude of the penalty used for each type of connection. For example, if a high relevance was wanted to be given to inter-subcatchment over longitudinal connections, inter-subcatchment penalties could be multiplied by a k factor (k being a reflection of the prevalence of the lateral connectivity over the longitudinal one). In order to explore the effect of weighting both sources of connectivity differently we ran the same conservation plan (same species, targets and cost) on three alternative scenarios: i) inter-subcatchment = longitudinal, ii) inter-subcatchment > longitudinal and iii) inter-subcatchment < longitudinal. For scenarios ii) and iii) we used a ten-fold increase in the original penalty to lateral and longitudinal connectivity respectively. All the scenarios were run on the combined fish and waterbirds datasets as before. Finally, we compared the spatial allocation of priority areas identified when running separate analyses for waterbirds and fish and using the integrated connectivity rule.

In all the analyses described above, we aimed to represent 30% of each species' predicted area of occupancy as the conservation target. Marxan was run 100 times (1M iterations each time) to find 100 near-optimal solutions. The solution with the lowest value for the objective function was used as the best solution in subsequent analyses.

Results

Systematic conservation planning and connectivity

The results from the systematic conservation planning analyses to represent all fish and waterbird taxa revealed that the spatial distribution of planning units in the best solution was influenced by the type of connectivity rule used when planning for fish and waterbirds (Fig. 3 and Fig. 4). When using the longitudinal connectivity rule alone, best solutions were very efficient at selecting connected planning units along the river network (Fig. 3A and Fig. 4A). This rule focused the selection of planning units within the limits of a few isolated catchments across the study area. Large portions of some catchments were selected due to the medium-high CSM that we applied (Fig. 4A – B). Conversely, when using only inter-subcatchment connectivity, the selection was primarily centered in lowland reaches of several neighbouring catchments along the coast (Fig. 3, Fig. 4C – D). As expected, this approach rarely selected planning units connected along river networks even within the same catchment, but was better at connecting neighbouring lakes and wetlands (see Fig. 4C). The use of the integrated connectivity rule showed an intermediate behaviour, without a significant increase in the selected area (3% more area selected in the integrated connectivity solution compared with the longitudinal-only solution). Groups of planning units from neighbouring catchments were selected, similar to the solution obtained using only the inter-subcatchment connectivity rule. These groups contained either whole small coastal catchment (Fig. 3 and Fig. 4E) or headwaters of neighbouring catchments (Fig. 3 and Fig. 4F). Under the additional influence of the longitudinal connectivity rule, the inclusion of lowland-reaches only (as when applying the inter-subcatchment connectivity alone) was a highly penalised configuration which explains why the selection of planning units shifted to whole small catchments or groups of neighbouring headwaters streams. The key priority areas identified using the integrated connectivity rule included coastal catchments of the Kimberley region, the Darwin-Daly region, catchments within Kakadu

National Park and Arnhem Land, the upper and lower Mitchell River catchment and the tip of Cape York Peninsula (Fig. 3c).

Under the same CMS value, the difference in the weights given to the longitudinal vs. inter-subcatchment connectivity rules and vice versa strongly influenced the spatial configuration of high priority areas (Fig. 5). When maintaining the inter-subcatchment component constant at low-weighted longitudinal penalties (Fig. 5A), lowland reaches of neighbouring catchments were selected in a few spatially isolated clusters. When the weight of the longitudinal penalty was increased (Fig. 5B) whole neighbour catchments were forced to be selected, reducing the selection of neighbour headwaters and forcing more connections to the ocean (Fig. 5B). On the other hand, maintaining the longitudinal component constant and increasing the weight of the inter-subcatchment component resulted in a shift from within catchment connected priority areas (Fig. 5C) to an enhancement of inter-catchments connections (Fig. 5D).

When conservation planning analyses were run separately for fish and waterbirds using the integrated connectivity rule, the distribution of priority areas for each group of taxa showed low overlap (13% of planning units or 17% of total area, Fig. 6). Despite these differences, 71 % of fish species and 84% of waterbird species were adequately represented (at the target level) in the waterbird and fish plans, respectively. The combined total area selected by the separate conservation plans for each group of taxa (261,500 km^2, Fig. 6) was 33% larger than was obtained from the single conservation planning analysis to represent all fish and waterbird taxa (175,800 km^2, Fig. 3c).

Discussion

There is increasing concern among conservation practitioners to quantify and manage processes that support the persistence and functioning of ecosystems and their biodiversity (Meir et al., 2004; Possingham et al., 2005). The ability to integrate ecological connectivity into conservation planning is therefore a research priority as it should enhance the adequacy of conservation solutions (Moilanen et al., 2008; Beger et al., 2010b; Linke et al., 2011). The movement of organisms between different areas is often vital for population persistence and is particularly important for maintaining the ecological integrity of freshwater ecosystems (Pringle, 2001; Fausch et al., 2002; Fullerton et al., 2010). For example, the population dynamics of some waterbirds and turtles requires the use of multiple wetlands even on a daily basis (Haigh et al., 1998; Rea et al., 2009) and many diadromous fish species may move long distances between estuaries, rivers and wetlands to complete their life cycles (e.g., Barramundi, *Lates calcarifer* in the study area; Pusey et al., 2011). Maintaining connectivity is also important to allow re-colonization in temporally dynamic systems after dry periods (Albanese et al., 2009). Connectivity is also an important consideration in freshwater conservation as it determines the propagation of threats through river networks. The presence of dams and deterioration of water quality as a result of wastewater disposals are just two examples of how threatening processes can be propagated along river networks to affect freshwater conservation priority areas potentially situated far away.. Similarly, overexploitation of water resources or transformation of wetlands may not only have local consequences for waterbird populations (e.g. local extinctions), but also in other parts of the catchment or more distant areas (e.g., Kingsford & Thomas, 2011). Despite the importance of considering various aspects of connectivity for adequate freshwater conservation, most previous work has usually been restricted to within-catchment longitudinal connectivity (e.g., Linke et al., 2007; 2008; Moilanen et al., 2008; Hermoso et al., 2011b; Turak et al., 2011). This is probably due to the riverine-focused approach of conservation practices and the poor consideration than other freshwater systems (e.g. lakes and wetlands) and the biodiversity they sustain (but see Aussiel et al., 2011). Hence, conservation practitioners need to consider not only longitudinal (catchment-constrained) processes but also the spatial relationships and proximity of aquatic habitats within and among catchments.

Here we show how to integrate inter-subcatchment connections that account for lateral movement requirements with other traditional freshwater connectivity components (longitudinal and within subcatchment lateral connectivity). We have extended the traditional lateral connectivity in freshwater conservation planning (restricted to the floodplain-river channel connection) beyond the hydrological limits of planning units. Although the concept of inter-subcatchment connectivity that we apply here is not new for conservation practitioners [two-dimensional connections have been extensively used in terrestrial conservation planning], the combination of longitudinal and lateral connectivity within hydrological catchments framework is a novel approach. Klein et al. (2009) used subcatchments as planning units for terrestrial conservation planning in an attempt to account for ecological and evolutionary processes.

However, they only considered connections between neighbouring planning units along river networks (longitudinal connectivity). With the multiple connectivity rule proposed here, we can account for different ecological processes important for the persistence of two taxonomic groups with contrasting ecological needs and movement constraints. When applied together, the different connectivity rules allow the identification of priority areas that contain whole lakes or wetlands, their closest neighbours whenever possible, and the upstream/downstream reaches of rivers that flow into or from them (see Fig. 4E – F). This would facilitate longitudinal and lateral movements of biota within priority areas while minimising the influence of disturbances propagated along river networks. This should improve the persistence of biodiversity and hence the adequacy of identified priority areas while not significantly increasing the overall area requiring protection.

The different components of connectivity addressed here can be weighted according to the type of biodiversity and processes that are being targeted. The connectivity penalties that we applied are distance-based, so the closer two planning units are the higher the penalty applied for missing connections. This allows manipulating and interpreting connectivity penalties according to particular priorities or needs. For example, if longitudinal connections are considered to be more important than inter-subcatchment ones we can apply twice the penalty for the same distance to connections located along the river network than across inter-subcatchment boundaries. Note that this weight to a particular component of connectivity is independent from the CSM. The CSM can be used to adjust the importance of connectivity penalties in the objective function (equation 1) in order to control the level of spatial aggregation of planning units in the solution (the same CSM applies to both components of connectivity). If a high CSM was used in combination with inflated longitudinal connectivity penalties, we would focus the selection of planning units in highly spatially aggregated groups along the river network (see Fig. 4A – B). A similar capability was recently presented by Beger et al. (2010a) in a modification of the software Marxan to account for asymmetric connections between marine planning units. Here, pairwise connections could have been weighted differently in each direction (e.g., upstream connectivity> downstream connectivity) to accommodate the likely asymmetry of ecological connections (see Vuilleumier & Possingham, 2006). For the sake of simplicity, we have used the traditional symmetric connectivity version of Marxan, where connections are equally weighted in both directions. However, whenever enough information is available to estimate the asymmetry in connections, they could be used in this multiple connectivity approach as well. For example, the different components of connectivity could be weighted according to their hypothesised or demonstrated importance to sustaining different ecological processes on which the persistence of the targeted biodiversity depend).

Our results also demonstrate the importance of using multiple groups of taxa when identifying priority areas. The capacity of a single group of taxa to represent other components of biodiversity (surrogacy capacity) has been questioned in freshwater ecosystems (Growns, 2009). In our study, separate analyses for waterbirds and fish produced priority areas with poor spatial overlap and taxon representativeness in the priority areas. This also lead to a decrease in efficiency by 1/3 (a higher area would be needed to represent all species in separate plans) under the same connectivity constraints.

Rivers and floodplain water bodies are influenced by the surrounding landscapes (Fausch et al., 2002) so conserving freshwater biodiversity requires the assessment and management of threats beyond the wetted limits of freshwater ecosystems (Abell et al., 2007; Nel et al., 2007). This should be taken as an opportunity to integrate freshwater and terrestrial conservation planning which have been both targeted independently from the conservation community (Abell et al., 2002). Freshwater priority areas may offer interesting opportunities for terrestrial conservation and vice versa that are being missed when planned separately. For example, when planning for freshwater we do not account for the benefits that terrestrial biodiversity would receive out of the plan (e.g., how many terrestrial species could be also protected). Therefore, targeting both realms independently would be the most efficient way of protecting biodiversity. The integration of freshwater and terrestrial conservation should adequately account for historic patterns in both aquatic and terrestrial biota as hydrological boundaries are unlikely to isolate populations of terrestrial species from one another to the same extent as aquatic species. The use of hydrological catchments as basic units for planning has been proposed as a potential way to bridge the gap between freshwater and terrestrial conservation (Cowling et al., 2003; Klein et al., 2009). With this work we hope to contribute a new approach toward addressing connectivity beyond the freshwater realm that could be helpful in this essential process of integration.

Finally, the application of these new methods is often hindered by the lack of ecological knowledge that should inform the practice of conservation planning. For example, little is known about the appropriate connectivity requirements to ensure the persistence of freshwater biodiversity (Nel et al., 2009). More effort must be devoted to the analysis of the spatial connectivity requirements among habitats to sustain life cycles or among populations to maintain long-term genetic integrity. In addition, further research is required to assess how freshwater biota are affected by the multi-directional propagation of human disturbances in freshwater ecosystems and how this can be used to inform freshwater conservation planning. .

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Supporting information

Additional Supporting information may be found in the online version of this article:

Supplementary material. Development and validation of species distribution predictive models for fish and waterbirds in northern Australia.

Biosketchs

Virgilio Hermoso is a postdoctoral Research Fellow at the Australian Rivers Institute (Griffith University, Australia). His research interest focuses on the study of threats to the conservation of freshwater biodiversity, especially on the interactive effects of habitat degradation and introduced species, as a way to better inform conservation decision making.

Mark Kennard is a Senior Research Fellow at the Australian Rivers Institute (Griffith University, Australia). His research interests include the ecology of freshwater fish, environmental flow management, river bioassessment and conservation planning for freshwater biodiversity.

Simon Linke: Simon Linke is a research fellow at Griffith University, Brisbane. With a background in modeling and bioassessment, he is now one of the leading scientists in the field of freshwater conservation planning.

Figure 1. Northern Australian study region (A) and examples of three different types of spatial connectivity addressed in this work for a portion of our study area (B). Connectivity within lakes and wetlands that may spread over more than one planning unit (C); lateral connectivity between hydrologically unconnected planning units (inter-catchment) to account for movements across catchment divides (D); and longitudinal connectivity(E). Thick black lines show river catchment boundaries and thin black lines show planning unit boundaries. Rivers and wetlands are shown in grey and thick arrows indicate the main direction of movement that is being addressed with each component of connectivity.

Figure 2. Example of different boundary files combined in this work. The longitudinal component of the boundary file (A) is obtained by using the network topology built in ArcHydro (Maidment, 2002). The network topology can be used to route connections along the stream network. The penalty applied for a missing connection (Boundary) is calculated as the inverse of the squared distance between planning units (Hermoso et al., 2011b). The lateral component of the boundary file (B) gathers all potential pairwise connections not included in A. Penalties are also distance-based.

Figure 3. Best solutions for representing the distribution of all fish and waterbird species using (a) longitudinal, (b) inter-subcatchment and (c) integrated connectivity rules. The areas in the squares are displayed in more detail in Figure 4.

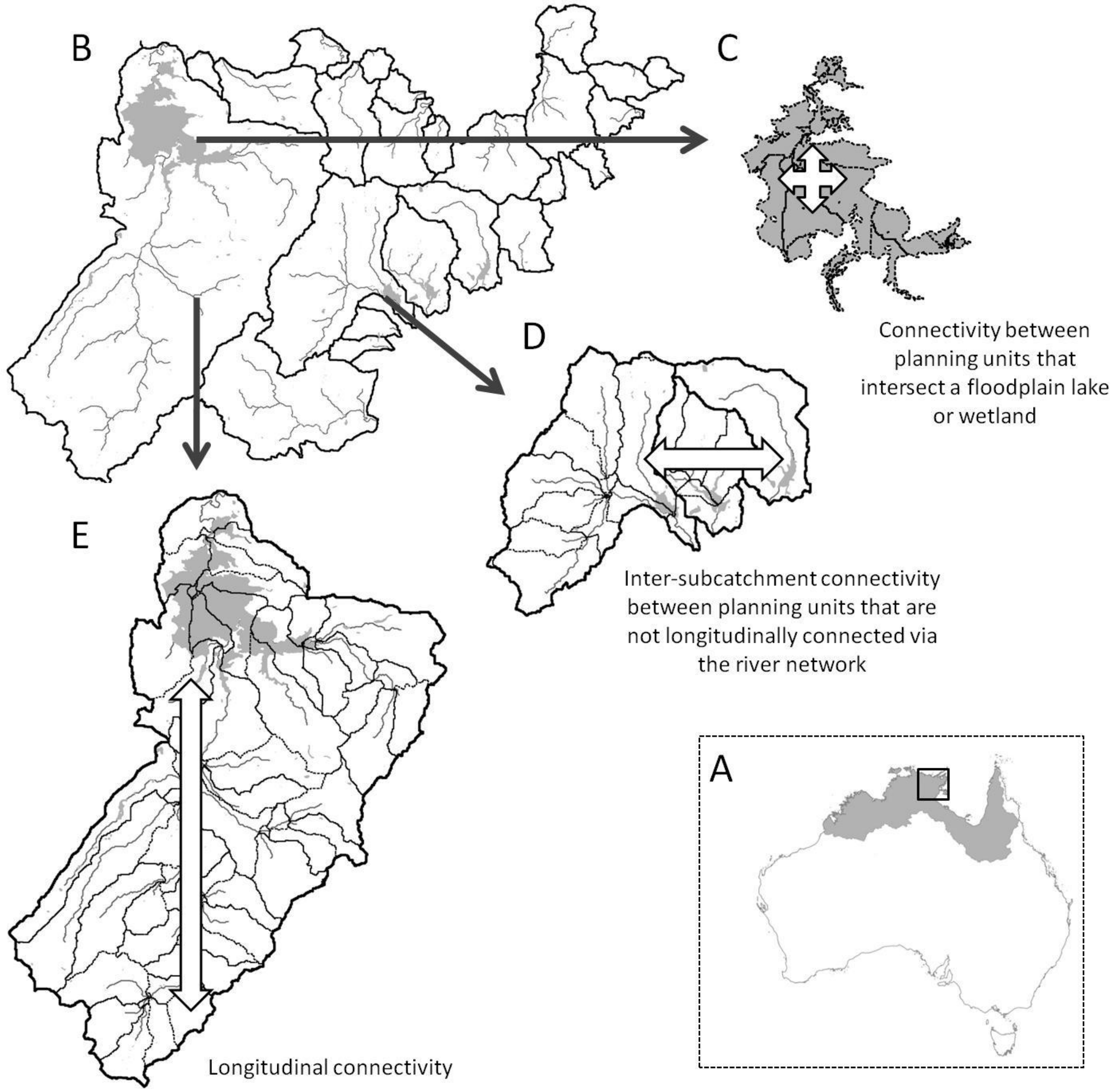
Figure 4. Detail of best solutions obtained using different connectivity rules. When using longitudinal connectivity alone, solutions were focused on the selection of whole catchments (A, B). Lateral connectivity produced solutions that clustered some portions of neighbouring catchments (C), and showed to be very efficient at groping neighbouring lakes and wetlands (D). When including multiple connectivity rules neighbouring catchments (whole small catchments or headwaters) were selected (E, F).

Figure 5. Best solutions for increasing weight on the longitudinal component (from A and B) of the multiple connectivity rule while maintaining the inter-subcatchment component and the Connectivity Strength Modifier (CSM) constant. At low longitudinal penalties (A) lowland reaches of neighbouring clustered catchments were selected. When the longitudinal penalty is increased (B) whole neighbouring catchments or neighbouring headwaters are forced to be

selected. Captions C and D show best solutions for increasing weight on the inter-subcatchment component while maintaining the longitudinal component and CSM constants.

Figure 6. Comparison of best solutions for waterbirds and fish. Different analyses were run for each taxa. Overlap between both solutions (17% of total area in each solution) are shown in black

Figure 1.



B
C
Connectivity between planning units that intersect a floodplain lake or wetland
D
Inter-subcatchment connectivity between planning units that are not longitudinally connected via the river network
E
Longitudinal connectivity
A

Figure 2.

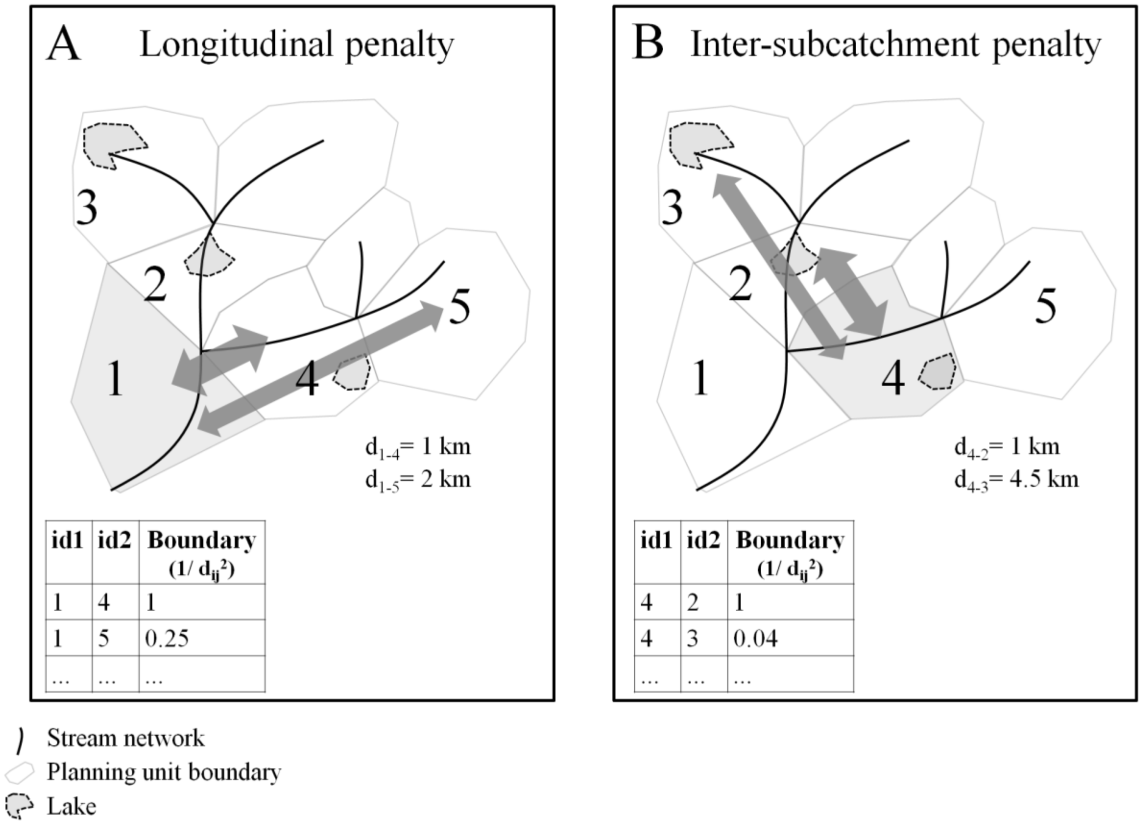
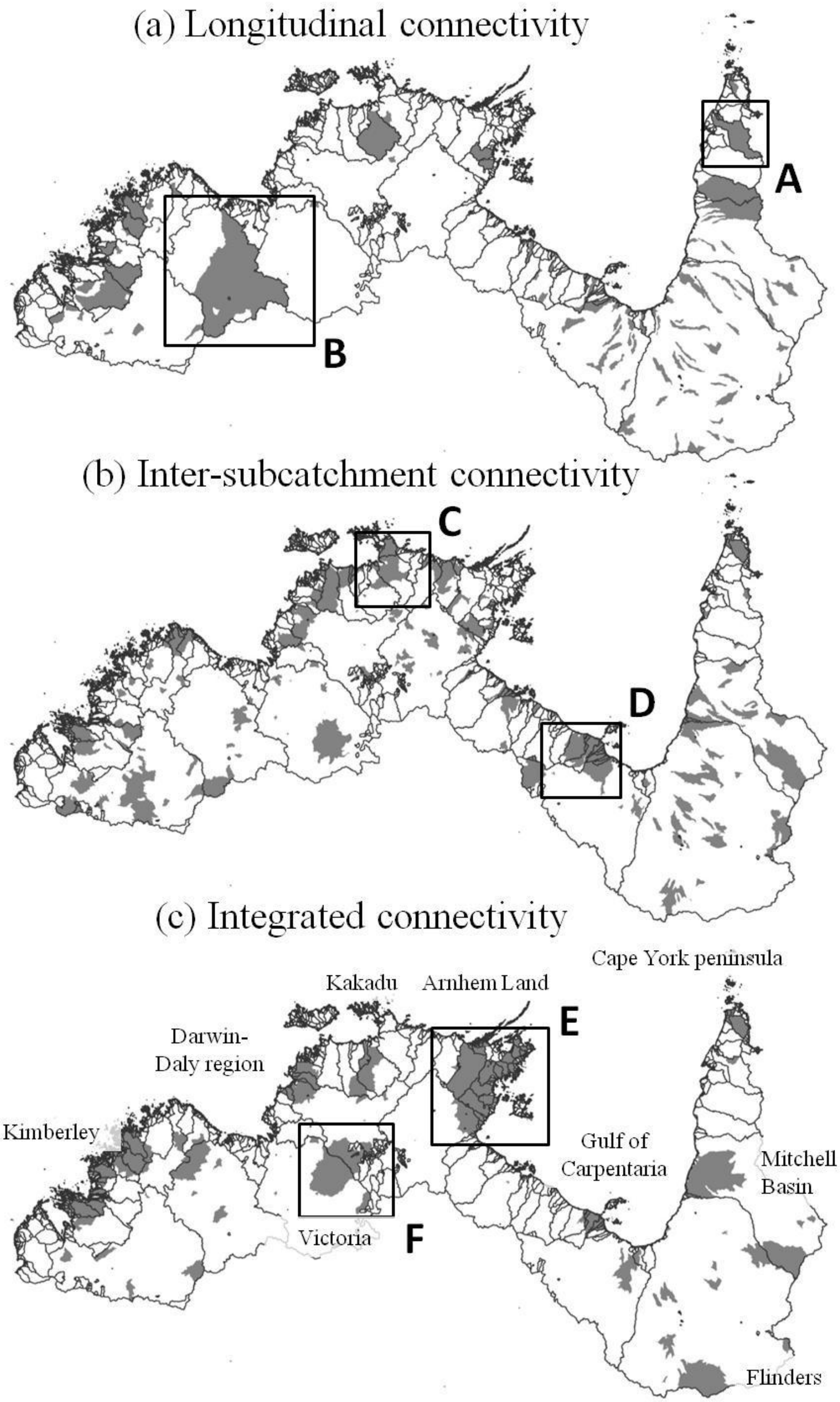

A Longitudinal penalty
3
2
1
4
5
d1-4= 1 km
d1-5= 2 km
id1 id2 Boundary (1/ dij2)
1 4 1
1 5 0.25
... ...
B Inter-subcatchment penalty
3
2
1
4
5
d4-2= 1 km
d4-3= 4.5 km
id1 id2 Boundary (1/ dij2)
4 2 1
4 3 0.04
... ...
Stream network
Planning unit boundary
Lake

Figure 3.



(a) Longitudinal connectivity
A
B
(b) Inter-subcatchment connectivity
C
D
(c) Integrated connectivity
Cape York peninsula
Kakadu
Arnhem Land
E
Darwin-
Daly region
Kimberley
Gulf of
Carpentaria
Mitchell
Basin
Victoria
F
Flinders

Figure 4.

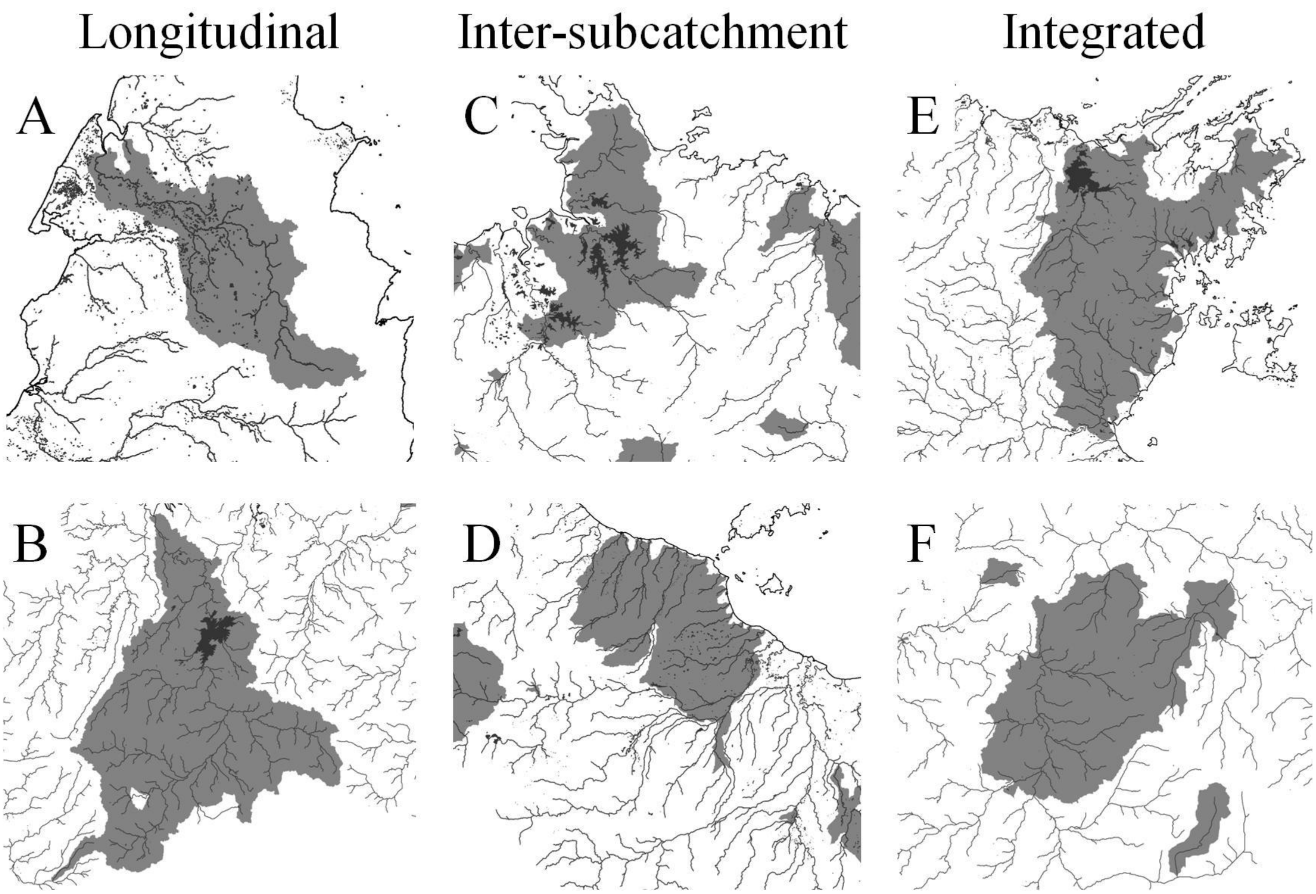
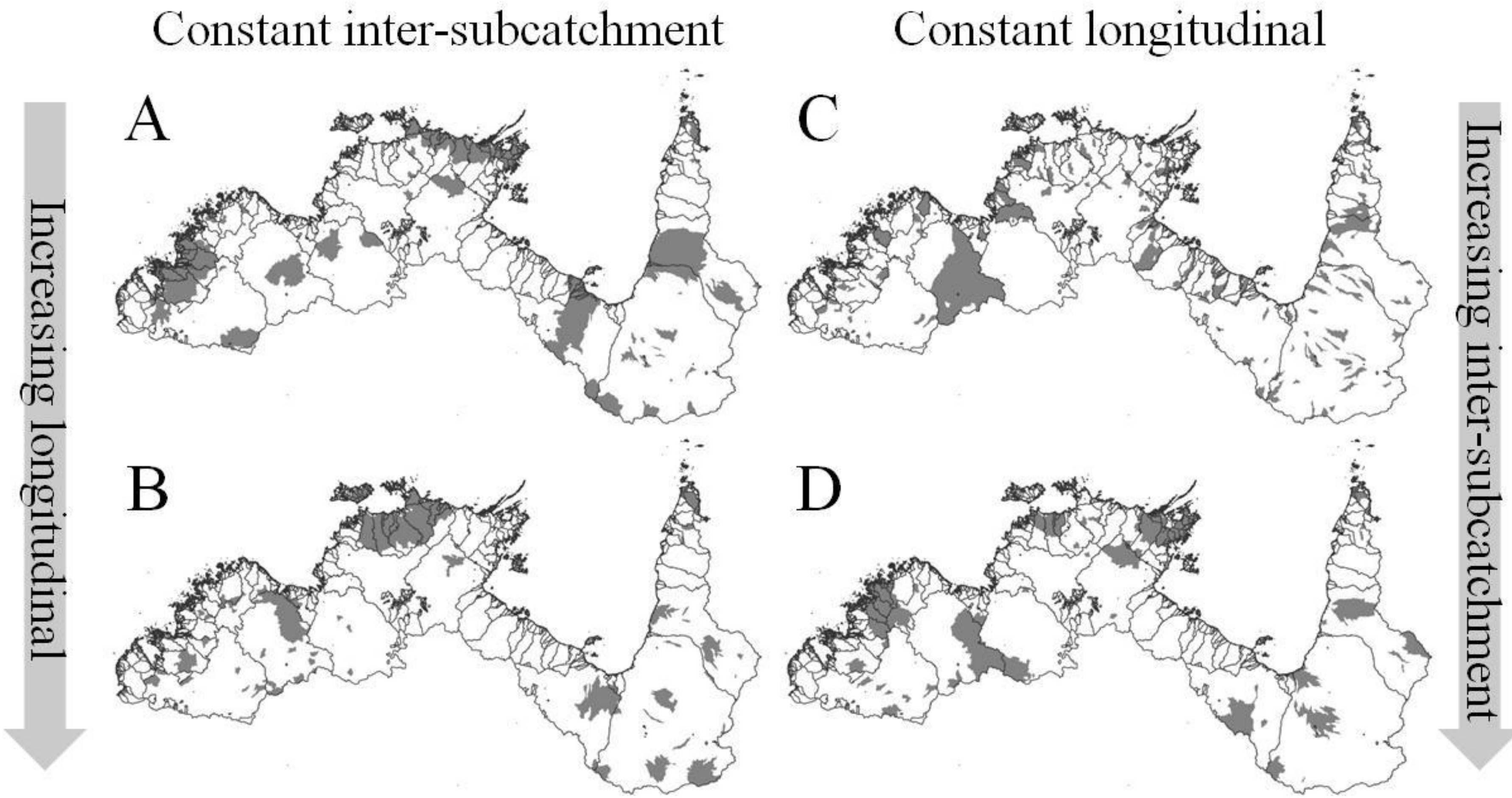


Figure 5.



Constant inter-subcatchment
Constant longitudinal
A
C
B
D
Increasing longitudinal
Increasing inter-subcatchment

Figure 6.