APPLIED ISSUES

A method for spatial freshwater conservation prioritization

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SUMMARY

1. Freshwater ecosystems are amongst the most threatened and poorly protected globally. They continue to be degraded through habitat loss, pollution and invading species and conservation measures are urgently needed to halt declining trends in their biodiversity and integrity.

2. During the past decade a suite of decision support tools and computational approaches have been developed for efficient and targeted conservation action in terrestrial or marine ecosystems. These methods may be poorly suited for planning in freshwater systems because connectivity in terrestrial and marine systems is typically modelled in a way unsuitable for rivers, where connectivity has a strong directional component.

3. We modify the conservation prioritization method and software, ZONATION, to account for connectivity in a manner better suited to freshwater ecosystems. Prioritization was performed using subcatchment/catchment-based planning units and connectivity was modified to have directional upstream and downstream components consistent with the ecology of our target species.

4. We demonstrate this modified method for rivers and streams in the southern North Island of New Zealand. Data included predicted occupancy from boosted regression tree models of species distributions for 18 fish species. The study area covered 2.1 million hectares and included 394 first- to fourth order catchment or subcatchment planning units.

5. Realistic modelling of connectivity had a major influence on the areas proposed for conservation. If connectivity was ignored, recommended conservation areas were very fragmented. By contrast, when connectivity was modelled, high priority conservation targets consisted of entire river basins or headwater subcatchments.

6. The proposed method serves as a starting point for the implementation of reserve selection methods in river ecosystems.

Keywords: boosted regression trees, boundary quality penalty, connectivity, reserve selection, site selection algorithm

Introduction

Freshwater ecosystems are globally poorly protected, and continuing declines in their condition demonstrate an urgent need for increased conservation measures (Abell, 2002; Rodrigues et al., 2004; Kingsford & Neville, 2005; Revenga et al., 2005; Dudgeon et al.,...
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2006). Freshwater areas are impacted by several distinct but frequently simultaneous processes including water pollution, over-fishing, flow alteration, invasive species, climate change and human-mediated habitat loss (Richter et al., 1997; Abell, Allan & Lehner, 2007). Freshwater ecosystems provide both unique biodiversity and substantial ecosystem services (Schroeter et al., 2005), creating a strong imperative for their protection and restoration. Even so, the scientific literature about freshwater protected areas is scant, and according to Abell et al. (2007) only 14 relevant publications were to be found from the Web of Science in late 2006.

Considerable effort has been put into the development of methods for designing terrestrial or marine protected area networks (e.g. Margules & Pressey, 2000; Cabeza & Moilanen, 2001; Williams, ReVelle & Levin, 2004; Moilanen, 2005; Knight, Cowling & Campbell 2006 for references). Although one would naturally hope that these methods would also be applicable to freshwater systems (Dunn, 2003; Abell et al., 2007), there is one major drawback. In terrestrial and marine prioritization, connectivity is typically assumed to be both distance dependent and non-directional. Generally, highly aggregated terrestrial reserve networks are presumed to perform better than dispersed networks because of decreased edge effects and improved potential for metapopulation persistence (Moilanen, 2005; Williams, ReVelle & Levin, 2005; Moilanen & Wintle, 2006; Nicholson et al., 2006). This assumption clearly does not apply in freshwater ecosystems, where water flow is directional and species movement is generally restricted to existing river and stream channels. As a consequence, conservation of particular features may require protection of parts of river systems (e.g. headwaters) that are geographically distant from the biological features of interest. It also means that connectivity measures based on Euclidean distances are unrealistic—distance measures that take into account the asymmetry of water flow and to a lesser extent, species movements are needed instead (Lake, Bond & Reich, 2007; Peterson, Theobald & Ver Hoef, 2007). Important components of freshwater conservation that are related to this connectivity include catchment-scale management, maintenance of the natural flow regime and exclusion of invading species (Saunders, Meeuwig & Vincent, 2002; Fitzsimmons & Robertson 2005).

In this study, we address the challenges posed by the distinctive connectivity requirements of freshwater systems by adapting an existing method developed for terrestrial and marine studies. Our overall approach provides a quantitative method for conservation prioritization using observed or modelled species distributions in a complementarity-based reserve selection approach. The key concept with complementarity-based planning is that areas are selected that complement each other in the biodiversity features they contain. An area is selected if it provides a high marginal gain in biodiversity protection with respect to what is already protected. The calculations of biodiversity benefit can be based on gains of individual units such as species, or on broader pattern-based measures such as species turnover (Faith et al., 2003). Complementarity-based planning contrasts with assessments based on individual site scores. In these, protected area candidates are evaluated independently from each other using multiple criteria related to naturalness, uniqueness and species composition, with scores then combined into an index (score) of the conservation value of each candidate river (Boon, 2000; Dunn, 2003 and references therein). Site-scoring approaches currently dominate the assessment of conservation value in freshwaters. For example, Filipe et al. (2004) combine habitat modelling and species weighting to rank catchments for the purpose of conservation prioritization on the Iberian Peninsula. Areas to protect were then selected from the top scoring units on the list, and connectivity between prospective protected areas was only induced qualitatively by using catchments as the unit of interest, and by considering corridors.

By contrast, in complementarity-based reserve selection (sometimes referred to as site selection, area selection, reserve network design or area prioritization) the goal is to find an optimal set of areas that are jointly as valuable as possible by taking into account differences, similarities and connectivity between candidate sites. Such methods are now widely used in terrestrial settings, but applications to freshwater systems have started appearing only recently. In one example, Abellán et al. (2005) compared complementarity-based planning with other methods, for water beetles in rivers of the Iberian Peninsula, but their algorithms included no measures of the connectivity or coherence of the proposed reserve network. In another study in Victoria, Australia, Linke et al. (2007) used modelled species distributions with selection criteria of condition, vulnerability and irreplaceability. Connectivity requirements were enforced on solutions
by always protecting the headwaters of any high-value down-stream targets; an area part way down a river could not be protected unless its headwaters were protected as well. Other studies have focussed on estimates of condition and habitat classification, enforcing connectivity by excluding dams (Thieme et al., 2007) or by treating rivers and their tributaries as planning units (Nel et al., 2007).

In this study, we describe how the reserve selection framework and software, ZONATION (Moilanen et al., 2005; Moilanen & Kujala, 2006; Moilanen, 2007) was adapted to accommodate the connectivity requirements of freshwater systems. ZONATION was originally developed for large-scale planning on grid-based predictions of species distribution in terrestrial settings. The key modifications we implemented for application in freshwater ecosystems are: (i) prioritization was based on planning units (subcatchments/catchments) instead of individual grid cells and (ii) the definition of connectivity was modified to represent more realistically the highly directional and asymmetric nature of connectivity in river systems. We demonstrate the approach using a case study based in the southern North Island of New Zealand, prioritizing areas for conservation based on their ability to protect 18 fish species in a spatially coherent manner. We then discuss key features of the results, and explain how these techniques could be integrated with other important considerations for freshwater planning.

Methods

Adapting ZONATION to river systems

ZONATION is a framework and software for spatial conservation prioritization using species distributions defined on large grids, which allows direct linkages from GIS-based environmental information to statistical species distribution modelling to conservation prioritization (Moilanen et al., 2005; Moilanen & Wintle, 2007; Moilanen, 2007). The ZONATION meta-algorithm starts from the full landscape and proceeds by iterative removal of units (usually grid cells), at each step removing that which results in the smallest marginal loss in conservation value (Moilanen et al., 2005; Moilanen, 2007). As shown later (eqn 1), conservation value is defined ecologically, by integrating the local occurrence levels, weights and original distribution sizes of species occurring in each cell. Use of weights and cost layers allows emphasis of high-priority species and cost-effective locations. The structure of the removal process means that the most important parts of the landscape are retained until last, and a nested hierarchy of conservation priority is produced, where the most important 2% is within the most important 5%, which is in the top 10% and so on.

Output from ZONATION includes: (i) a map with ranks of conservation priority for the landscape of interest; (ii) performance curves that describe the proportion of the original distribution of each species remaining as a function of fraction of the landscape reserved and (iii) species-specific distributions of site quality in a given top fraction of the landscape. Additional features of ZONATION include options for: taking into account variation in costs of protection; weighting of species to reflect their varying conservation priorities; species-specific methods for handling connectivity (Moilanen et al., 2005; Moilanen & Wintle, 2006, 2007); uncertainty analysis to take account of uncertainty in species predictions (Moilanen et al., 2006a,b); and estimation of replacement costs (Cabeza & Moilanen, 2006) allowing evaluation of the importance of existing or proposed conservation areas. Version 1.0 of the ZONATION software and its user manual is downloadable from the web (Moilanen & Kujala, 2006).

We modified the existing terrestrial/marine version of ZONATION by first altering the software to allow it to work with planning units rather than individual grid cells. This change allows use of catchment or subcatchment-based planning units (Peres & Terborgh, 1995; Allan, Erickson & Fay, 1997), enforcing an initial degree of connectivity between grid cells and preventing the removal of isolated cells, i.e. a planning unit is either completely protected (selected) or it is left vulnerable to anthropogenic (mis-)use. Secondly, we adapted the software to accommodate the connectivity inherent in river systems, describing this with a network topology (tree hierarchy) of river segments, which reflects the flow of water. This latter feature was implemented using the planning units, which were linked into a tree hierarchy. A more detailed description of the ZONATION conservation prioritization framework is given in online Supplementary material.

Modifying connectivity in ZONATION Connectivity is a critical component of any reserve network design,
because it influences dispersal, colonization and population sizes at sites. It is generally accepted that a very fragmented reserve system would be both awkward to implement and biologically unreasonable (Possingham, Ball & Andelman, 2000; Moilanen & Wintle, 2006). According to a fundamental tenet of spatial (meta)population dynamics, of two sites with otherwise identical features, the one with higher connectivity would have higher population densities (Hanski, 1998). Three methods have been used to implement connectivity requirements in ZONATION, i.e. boundary length penalties (e.g. Possingham et al., 2000; Önal & Briers, 2002; Fischer & Church, 2003; Cabeza et al., 2004), distribution smoothing (Moilanen et al., 2005; Moilanen & Wintle, 2006, 2007) and boundary quality penalties (Moilanen & Wintle, 2007). The boundary length penalty technique is not species-specific, and it requires assumptions to be made about both the perimeter and boundary length of the proposed reserve. These measurements are largely irrelevant as descriptors of the essentially linear components that make up river networks. Distribution smoothing corresponds structurally to the use of a species-specific metapopulation connectivity measure (see Moilanen & Nieminen, 2002), but it is unsuitable for use in rivers because it fails to take into account the directional, channel-constrained nature of their connectivity. Boundary quality penalties provide the most realistic description of connectivity from the above alternatives, but they are not directly applicable to river systems for the same reason as distribution smoothing, because they fail to realistically represent directed hydrological connection.

The boundary quality penalty concept can however be extended to apply to river systems by redefining the concept of neighbourhood to accommodate its meaning for aquatic species. Here, it is natural to assume that a site (segment of river) is connected both upstream and downstream within the same river. The neighbourhood of the site is the river and all its tributaries upstream and the main river stem downstream from the focal site. Thus, we call the general method of handling connectivity that we use here the *neighbourhood quality penalty*. In a river context, loss of a particular river segment results in both a local loss, plus losses in both the upstream and downstream neighbourhoods of that segment. Upstream and downstream losses can be species-specific, reflecting the different ecological and life history requirements of species, including the need to migrate to the sea for diadromous species, sensitivity to water quality as determined by the state of the upstream catchment or connection to upstream breeding habitat.

We define the responses of species to connectivity loss via two functions, one each for responses to upstream and downstream loss (Fig. 1). The $x$-axis of the function describes the fraction of original connectivity lost (upstream or downstream) for the location, while the $y$-axis describes the fraction of the original local value remaining as upstream or downstream connectivity is lost. The overall loss for any species is calculated as the product of the respective upstream and downstream losses. We explain the ecological basis for the different curves (1–6) in a later section that details the case study. Whatever the functional cause of a negative effect from lost connectivity, it would be modelled with the species-specific loss functions, under the assumption that if a location is left vulnerable to anthropogenic degradation, benefits of connectivity to species may in the future be completely lost. Note that some species might even benefit from lost connectivity (the function would go above one), but such species would probably be of little conservation concern.

Technically, the neighbourhood quality penalty technique for including species-specific connectivity responses into quantitative conservation prioritization can be described by the following equation:

![Fig. 1](image-url) The neighbourhood loss response functions used in this study (Table 1). The different curves (1–6) represent a range of ecological responses to lost connectivity; these are discussed, with examples, in the text.
in which \( p_{ij} \) is the occurrence level of species \( j \) in cell \( i \).

Equation (1) describes the fraction lost from original distribution of species \( j \) following the removal of site \( i \).

The loss consists of three components, local loss, loss upriver and loss downriver. The assumption is that everything remaining locally is lost if a cell is removed, and that loss accrued upriver and/or downriver will depend on the size of unit \( i \) for species \( j \). \( A_{ij} \) – loss of a larger unit implies greater influence on connectivity nearby. The influence of connectivity on occurrence levels is mediated via functions \( h_i \) (upriver and downriver), which are the functions of Fig. 1 with the \( x \)-axis reversed. When the full landscape remains, and nothing has been lost, \( h_i(1) = 1 \). Importantly, when calculating the loss, the equation accounts for the degradation that already has occurred. This implies that if no local value remains according to the connectivity responses, further loss of connectivity has no influence.

One important feature of this approach is that connectivity in eqn (1) is modelled separately upriver and downriver. Quantities \( r_{ij} \) and \( o_{ij} \) (up and down) are the remaining and original connectivities of unit \( i \) for species \( j \) both upriver and downriver, respectively. Loss of planning unit (river segment/catchment) \( i \) influences the downwards connectivity of sites upriver from it, which is the component of the equation having the summation across neighbours \( k \) upriver from focal site \( i \), \( k \in N_{up}^i \). Similarly, loss of unit \( i \) influences the upwards connectivity of units downriver from it. Note that we used species and unit-specific predictions of occurrence \( p_{ij} \) and that connectivity responses \( h_i(\cdot) \) were species-specific. However, hydrological connectivity upriver and downriver was based directly on the numbers of grid cells in planning units in a non-species-specific manner, meaning that \( r_{ij}, o_{ij} \) and \( A_{ij} \) were taken as the same for all species.

Equation (1) is simply a fraction of distribution lost, which does not account for how lost representation is translated to lost conservation value. When deciding which cell can be removed with smallest loss of conservation value, the \( \delta_i \) is aggregated across species according to the cell removal rule, which for core-area ZONATION is

\[
\delta_i = \frac{1}{c_i} \max_j \frac{w_j \delta_{ij}}{q_j},
\]

(2a)

and for the additive benefit function ZONATION

\[
\delta_i = \frac{1}{c_i} \sum_j [V_j(q_j) - V_j(q_j - \delta_{ij})],
\]

(2b)

in which \( w_j \) is weight of the species \( j \), \( c_i \) is cost of cell \( i \), and \( q_j \) is the fraction of distribution of species \( j \) remaining before removal of cell \( i \), and \( V(\cdot) \) is a function translating increasing representation into increasing conservation value (see Arponen et al., 2005; Moilanen, 2007). In all our analyses, we set costs proportional to the river length, but alternatively these could be varied spatially to reflect monetary costs of protection.

Quantifying connectivity responses A remaining question is how to get the connectivity loss responses for species. Expert knowledge would suffice for an approximate answer, as knowledge of the life cycle and water quality requirements of species can be used to give an indication of how sensitive they are to loss of downstream and upstream connectivity. Two other alternatives would provide more quantitative solutions. First, if connectivity-related variables are used in species modelling, then their response functions can be calculated via the procedure described in Moilanen & Wintle (2007), which involves re-prediction of species occurrences under artificially reduced connectivity values in the habitat model. For example, loss of upstream habitat could cause both loss of breeding areas and deterioration in water quality, which would translate into a local loss. Another alternative is to use something akin to the reference
condition approach (Wright et al., 1984; Hughes & Larsen, 1986; Bailey et al., 2006), and recognizing that high-quality locations are the ones most important for conservation. It thus follows that an approximate response function can be obtained by taking a typical high-quality location. Then one asks, what relative occurrence would one expect if 10%, 25%, 50%, 75% or 100% of headwater areas are degraded because of various anthropogenic causes? This information would be used to construct approximate connectivity response functions.

**Study area, species modelling and connectivity**

The study area used for our demonstration includes rivers and streams located within the area administered by the Wanganui-Manawatu Regional Council in the southern North Island of New Zealand (175°E and 40°S, Fig. 2). It covers approximately 2.1 million hectares of land that is predominantly alluvial floodplain, hill country or volcanic plateau. Environmental and biological descriptions of these rivers are available as part of a comprehensive spatial database in which rivers and streams are represented as a network topology. Each river section between adjacent confluences is represented by a unique segment, and upstream catchments and downstream segments can be identified for any site. Environmental conditions relevant to the river biota have been characterized with environmental and spatial predictor variables that describe the local reach and segment, and their related upstream and downstream conditions. These are described in detail in Leathwick et al. (2005); in review). Briefly, downstream predictors quantify conditions affecting the ability of diadromous fish to migrate to and from the river segment; segment-scale predictors describe temperatures, flow, shading and local habitat factors and the upstream predictors describe flow characteristics, presence of lakes and glaciers, climate, land use and geology in the relevant catchments.

In previous distribution modelling, species presence-absence records from 13 369 sites that span the major environmental gradients in New Zealand’s rivers were combined with the environmental data, using statistical modelling methods that can predict the probability of presence of each species in each river segment throughout New Zealand (J.R. Leathwick, J. Elith, L. Chadderton, D. Rowe and T. Hastie unpublished data). The modelling technique – boosted regression trees – is a modern form of logistic regression that is able to capture the complexity of the species’ responses to the environment, including interactions between predictor variables (J. Elith, J.R. Leathwick and T. Hastie, unpublished data). The resulting models provide ecologically realistic descriptions of the drivers of the species distributions, and have good predictive performance, explaining 39.0 ± 7.6% (mean ± SD) deviance in the testing data, and high discrimination of presences from absences (area under the receiver operating characteristic curve, AUC = 0.92 ± 0.03) (Table 1, and see Leathwick et al., in review for full details).

In this study, we used predicted distributions of 18 freshwater fish species for each river segment as input to the conservation planning algorithm. Of these, 15 are diadromous species, spending at least some part of their life cycle in the sea, while the remaining three species are non-migratory. Catchment-based planning units were defined by splitting all rivers greater than fourth order into their fourth order subcatchments plus their main stem, whilst all catchments of fourth

![Fig. 2 Map of the North Island of New Zealand, with the black line outlining the study area.](image-url)
order or smaller were treated as individual planning units (Leathwick & Julian, 2007). This resulted in the identification of 394 planning units in the region (Fig. 3a), which were parts of 67 spatially distinct rivers (Fig. 3b). To accommodate ZONATION’s requirement for data to be presented in raster (grid) format, we converted the species predictions and planning unit identifiers for each river segment into grids in which individual cells were 100 \( \times \) 100 m. Line work describing the river topology was used to indicate which grid cells held data for each river segment, i.e. each river segment was represented by a contiguous string formed from those grid cells that it intersected.

Connectivity response functions for species were based on expert knowledge. Six different curves that represent different responses were created, and species were assigned to one response for their upstream requirements, and one for downstream (Fig. 1, Table 1). The curves display the vulnerability of species to the removal of adjacent habitat. For example, we allocated species varying degrees of sensitivity to degradation of upstream habitat, based on our analyses of their distributions with respect to catchment land use and stream nitrogen load. Angaus was assigned the lowest sensitivity to upstream catchment degradation, reflecting its tolerance of high nitrogen loads and persistence in rivers with highly modified catchments. Conversely, Angdie, Galarg, Galbre, Galfas, Galpos and Gobhub were treated as more sensitive, reflecting their occurrence mostly in rivers and streams in good condition. With respect to downstream connectivity, we treated all non-diadromous (non-migratory) species as having no requirement for maintenance of downstream habitat (curve 6, Fig. 1). Eels and estuarine species were assigned a relatively high tolerance of downstream habitat loss (curve 2), diadromous species breeding in situ with larval fish washed to sea were treated as moderately tolerant (curve 3), and species whose adults migrate downstream to breed in estuarine conditions (Galmac, Retret) were assigned the highest sensitivities (curve 4).

### Table 1: Details of species, model performance and connectivity responses

<table>
<thead>
<tr>
<th>Code</th>
<th>Species name</th>
<th>Prevalence in NZ</th>
<th>% deviance explained</th>
<th>AUC</th>
<th>Upstream connectivity</th>
<th>Downstream connectivity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Angaus*</td>
<td>Anguilla australis</td>
<td>0.200</td>
<td>36.9</td>
<td>0.90</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Angdie*</td>
<td>A. dieffenbachii</td>
<td>0.497</td>
<td>32.0</td>
<td>0.86</td>
<td>4</td>
<td>2</td>
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<tr>
<td>Chefos*</td>
<td>Cheimarrichthys fosteri</td>
<td>0.094</td>
<td>40.5</td>
<td>0.92</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Galarg*</td>
<td>Galaxias argenteus</td>
<td>0.029</td>
<td>32.5</td>
<td>0.91</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td>Galbre*</td>
<td>G. brevipinnis</td>
<td>0.109</td>
<td>35.5</td>
<td>0.90</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>Galdiv</td>
<td>G. divergens</td>
<td>0.026</td>
<td>50.0</td>
<td>0.97</td>
<td>3</td>
<td>6</td>
</tr>
<tr>
<td>Galfas*</td>
<td>G. fasciatus</td>
<td>0.123</td>
<td>46.2</td>
<td>0.94</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>Galmac*</td>
<td>G. maculatus</td>
<td>0.103</td>
<td>36.4</td>
<td>0.91</td>
<td>2</td>
<td>4</td>
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<td>G. postvectis</td>
<td>0.026</td>
<td>38.1</td>
<td>0.95</td>
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<td>3</td>
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<tr>
<td>Geoaus*</td>
<td>Geotria australis</td>
<td>0.024</td>
<td>26.4</td>
<td>0.89</td>
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<td>3</td>
</tr>
<tr>
<td>Gobbas</td>
<td>Gobiomorphus basalis</td>
<td>0.054</td>
<td>47.9</td>
<td>0.95</td>
<td>3</td>
<td>6</td>
</tr>
<tr>
<td>Gobbre</td>
<td>G. breviceps</td>
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<td>50.8</td>
<td>0.95</td>
<td>3</td>
<td>6</td>
</tr>
<tr>
<td>Gobcot*</td>
<td>G. cotidianus</td>
<td>0.163</td>
<td>29.6</td>
<td>0.87</td>
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<td>3</td>
</tr>
<tr>
<td>Gobgob*</td>
<td>G. gobious</td>
<td>0.012</td>
<td>30.8</td>
<td>0.94</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>Gobhub*</td>
<td>G. hubsi</td>
<td>0.049</td>
<td>49.5</td>
<td>0.95</td>
<td>4</td>
<td>3</td>
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<tr>
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<td>G. huttoni</td>
<td>0.173</td>
<td>45.3</td>
<td>0.93</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Retret*</td>
<td>Retropinna retropinna</td>
<td>0.038</td>
<td>37.7</td>
<td>0.93</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>Rhoret*</td>
<td>Rhombosolea retaria</td>
<td>0.006</td>
<td>35.1</td>
<td>0.95</td>
<td>2</td>
<td>2</td>
</tr>
</tbody>
</table>

AUC, area under the curve measure of model performance.
*Diadromous species; prevalence reports the proportion of the 13 369 sites at which the species were recorded.

Overview of the flow of analyses in this study

In summary, the overall computational approach applied in this study comprises:

1. Obtain a sample set of species occurrences across the study area. Obtain GIS data describing environmental quality across the study area.
2. Use best available spatial habitat modelling techniques to model species occurrence across the study area. If observational data are available from everywhere, this step can be skipped.

Fig. 3 (a) Division of study area into 394 planning units. Each unit has been coloured a random shade of grey. Boundaries of the catchments of three large rivers are indicated on the map. (b) Division of study area into 67 complete river basins (hydrologically linked planning units). Each basin has been coloured a random shade of grey. (c) Grid cell-based core-area ZONATION for landscape. A light shade of grey corresponds to cells with low priority. Cells of high priority are shown in dark grey/black. (d) Landscape ZONATION using the additive benefit function cell removal rule.
3 Define catchments that will be used as planning units. Describe the hierarchy of flow through catchments.

4 Give weights to species and specify their connectivity responses.

5 Use both core-area and additive benefit function ZONATION to obtain priority maps for the landscape. Differences between these maps tell us about locations that are important due to species richness, rarity or both (accounting for complementarity in the process). Species-specific performance curves tell of protection levels achievable with different amounts of habitat protected.

6 Evaluate proposed conservation areas, or areas that must be excluded via a replacement cost analysis.

Results

Use of core-area and additive benefit function ZONATION on the species distribution grids, without using catchment planning units, identified high-priority areas (dark shaded in Fig. 3c,d) that were scattered throughout the study region. Even though there are some clusters of high-priority cells, delineating conservation areas from this solution would be difficult, and the resulting protected areas would have poor connectivity. Such an analysis is of course rather unrealistic, as it assumes that grid cells can be selected independently from each other, which is not true for logistic reasons, and ignores all connectivity effects between selected and lost cells.

In our first step towards a more realistic analysis, we divided the landscape into catchment/subcatchment-based planning units, producing a far more aggregated result (Fig. 4) that reflected the manner in which entire planning units were removed at each step. However, high priority areas were still scattered around catchments, and few complete river catchments were given high priority through their entire course, i.e. from headwaters to the sea. This can be seen by comparing the distribution of high-rank planning units with the spatial extents of the entire catchments (Fig. 3b). We call this the non-spatial planning unit ZONATION from here on, to differentiate it from the following spatial analysis that also takes into account connectivity.

![Fig. 4](image-url) Core area (a) and additive benefit function ZONATIONs (b) of the landscape when using catchments (Fig. 3a) as planning units.

Results from our analysis in which we used planning units together with expert-derived upstream and downstream connectivity responses produced a much more satisfactory result (Fig. 5), capturing more robustly the ecological functionality requiring consideration when planning conservation strategies for freshwater ecosystems. Two phenomena are now apparent: (i) headwater planning units were generally given higher priority than in the previous analyses and (ii) there was a tendency to favour entire river catchments. These changes reflect the manner in which connectivity now influences the value of a location to a species, so that isolated sections of rivers cannot be chosen (or lost) without incurring impacts on neighbouring river sections.

Whilst the maps for core-area and additive benefit function analyses look superficially similar, there are subtle differences which mean that the spatial overlap between the top 10% landscape fractions of the two analyses of Fig. 5 is only 49%. The areas of overlap occur mostly where high-quality locations of rare species (core area) coincide with generally species-rich areas (additive benefit), and these areas should have highest conservation priority. However, in the south-east of the study area additive benefit function (Fig. 5b) and core-area analyses (Fig. 5a) suggest a clearly different allocation of high-priority areas. Obviously, management delineation of conservation areas here would require decisions about tradeoffs between different species.

So far the results have only shown rank priority maps, which are one-third of the relevant ZONATION output. In addition to the priority maps, performance curves (Fig. 6) give valuable insights into the relative protection accorded to different species, as follows. First, weighting influences the protection levels that species would get at any level of landscape protection, i.e. increased weighting for high-priority species results in a higher fraction of their individual ranges being protected (Fig. 6; solid lines). Secondly, results from the non-spatial cell-based ZONATION are apparently better than those from the non-spatial planning.
unit based ZONATION, which are in turn apparently better than the spatial planning unit ZONATION – this result is completely illusory and it is important to understand why. The apparently inferior performance of the planning unit based method occurs because ZONATION is constrained to select groups of cells that may include combinations of both high and lower value cells, reflecting the degree of heterogeneity in species occurrence levels that is inherent in virtually all planning units. Thus, the cell-based analysis is able to target good cells and taken on this criterion alone, is apparently better able to retain species distributions.

The apparently superior performance of the non-spatial planning unit ZONATION compared with the spatial ZONATION is more complex, and reflects the failure of this assessment to account for the loss in value occurring at any location as surrounding cells or groups of cells are removed (Fig. 6). When the spatial pattern generated by the non-spatial planning unit analysis is re-evaluated using the spatial connectivity responses (Fig. 6, dashed line), the non-spatial analysis is revealed as clearly inferior. Species have at 20% of the landscape an apparent mean protection level of 0.51 (dotted line), but when evaluated using the connectivity response, only 0.21 of the distributions remain (dashed). For comparison, the connectivity-based ZONATION achieves protection levels of 0.24 across all species at 20% of the landscape (dashed–dotted line). This indicates that conservation gains might have been badly over-estimated by the non-spatial analysis.

As a final analysis, we show how to perform an exclusion cost analysis (sensu Cabeza & Moilanen, 2006), evaluating the importance of planning units that are designated for some other uses (e.g. power generation, effluent discharge) that preclude them being accorded conservation protection (areas A & B in Fig. 5a). Here we ran two constrained analyses, in each of which we removed one area at the outset of the process. We then compared average species performance curves in say the top 10% of the landscape from the constrained analyses with the equivalent curves from the unconstrained analysis, the difference between these indicating the replacement cost of the withheld area (Fig. 7). If the conservation value lost from the withheld area can be replaced by rearrangement of the solution elsewhere, then its replacement cost is zero or near-zero. However, if the area includes conservation values that cannot be replaced from elsewhere except with

significant cost, then the replacement cost of the area will be much greater. In our example, the replacement cost of area A is more or less zero, despite being given a high ranking in the priority map of Fig. (5a), indicating that its exclusion can be compensated for by rearrangement of the solution elsewhere. By contrast, exclusion of area B, which is of an approximately similar size to A and of similar priority to it in the complete analysis, results in a substantial reduction in the conservation value derived from protecting the top 10% of the landscape (Fig. 7), indicating that compensation by rearrangement of the solution elsewhere is not possible.

Discussion

We have described an extension of the ZONATION conservation prioritization method suitable for use in rivers and streams, demonstrating its use in a case study with freshwater fish data from New Zealand. The key features of our method centre on its handling of connectivity via its allowance of catchment/sub-catchment-based planning units, and the explicit rules it uses to represent the asymmetric linkages that occur between these units. A major practical advantage of our method is its ability to allow a direct workflow from GIS environmental layers to species distribution modelling to conservation prioritization. The approach is applicable to relatively large landscapes, with the software able to handle hundreds of species and landscapes with millions of elements of informative data.

Despite the progress that we have made, we acknowledge that the method does have some shortcomings, particularly in the simplified technique that it uses for handling connectivity. While the distribution modelling used to predict species distributions can be as complex and numerically refined as possible, the calculation of connectivity effects in ZONATION is presently restricted to two heuristically defined response functions per species. More accurate estimation of these responses could be achieved within the statistical models used to predict species distributions. However, this would require implementation of one or more of the wide range of the currently used modelling methods (e.g. Elith et al., 2006) inside the prioritization software, and this would be an arduous and error-prone task. The present workflow allows use of any habitat modelling framework, but connectivity is modelled in a somewhat approximate but still species-specific manner.

Although the present study uses fish distribution data for the conservation prioritization of rivers, this method could also be adapted to allow simultaneous prioritization for both terrestrial and aquatic species, as suggested by Abell et al. (2007). To achieve this, different species would need to be assigned different terrestrial or aquatic connectivity responses. As a probably outcome, and assuming that connectivity is important to species, semi-continuous areas would be selected so that rivers are surrounded by terrestrial conservation areas. Alternatively lakes, embedded within the river system, could also be accommodated in a robust and logical fashion.

ZONATION can also be applied to inputs other than species distributions, including layers showing the distributions of valuable habitat types, naturalness, productivity or other variables that would be indicative of high conservation value in river systems (Boon, 2000; Allan, 2004; Abell et al., 2007). The purpose of such an analysis could be for example to select optimal habitats by using locations known to provide high-quality habitat. Similarly, ZONATION could be used to evaluate options for restoration, in which case the data used would describe species distributions conditional on specific restoration or protection actions performed across parts of the landscape. This would allow robust evaluation of the potential returns from different restoration options, while taking into account the known importance of connectivity in determining restoration outcomes in rivers (Jansson, Nilsson & Malmqvist, 2007).

The present analysis is mainly based on core-area ZONATION. Additive benefit function ZONATION protects on average higher proportions of species distributions, but when examining minimum performances (worst-off species), core-area ZONATION does better than the benefit function variant (not shown). This result arises from the different way these two methods weight richness and rarity (Moilanen, 2007), making it important to perform both core-area and additive benefit function analyses. The first one identifies a solution that includes high-quality core-areas for all species. The latter identifies solutions that give relatively higher value to species richness. If both analyses agree, then different measures of conservation priority indicate the same locations, which is
convenient for planning. If not, then further priority choices will be needed between which is a better conservation strategy: protection of species-rich areas, or better coverage of individual species having relatively distinct distributions in otherwise species-poor areas.

Use of results such as these to design on the ground networks of protected areas would clearly require exploration beyond that which we have presented here. In addition to the priority maps and fractions of species distributions remaining shown here, ZONATION can also generate analyses of the quality-distributions of species habitat in the areas selected, allowing investigation of the spatial distribution of habitat quality of individual species in a selected landscape top fraction. Finally, before making operational decisions, we would recommend the use of replacement cost analysis on a comprehensive set of high-priority catchments and/or planning units to enable identification of those with the highest conservation priority, as opposed to those for which there is a high degree of inter-changeability. Areas with high replacement cost are the ones to obtain first.

In practical terms, the sequence of analyses that we present provide increasingly sensible prioritizations of areas for conservation protection in the Wanganui-Manawatu Region. Results from the first analysis (Fig. 4) identify sites that provide protection for a full range of species, including both coastal habitats supporting a diverse range of diadromous species, and more montane habitats containing only two or at most three species that are relatively restricted in range. However, the very high level of fragmentation in this result would not only make implementation difficult, but also risks the loss of upstream and/or downstream values critical to the long-term viability of the priority locations that have been identified. The non-spatial planning unit analysis produces a more sensible solution, identifying catchment-based units that would be straightforward to implement. However, several planning units in larger river systems, e.g. the Wanganui and Manawatu, are accorded high priority without recognition of the need to protect their upstream and downstream linkages, and only a few smaller catchments receive high priority across their full range of subcatchments. These shortcomings are addressed in the spatial analysis, where rivers such as the Manawatu and Wanganui (Fig. 3a) are now assigned similar levels of high priority throughout large parts of their course, indicating connected sequences of high conservation value planning units from the headwaters to the coast. Conversely, the Wangaehu, parts of which support low fish populations because of natural geothermal discharges, is now ranked as a low priority, reflecting the linkages between affected and less-affected parts of this river system.

Natural extensions of the present work could include applications in habitat restoration and more detailed implementation of methods for accommodating hydrological connectivity. Here, we assumed that loss of an area from a reserve system implied total loss of its biodiversity values, but in reality unserved areas can still contribute to biodiversity and may indeed have a low likelihood of degradation, particularly in environments where conditions are unsuitable for intensive land uses such as agriculture. Another component not explicitly modelled here is lateral movements and connectivity to spawning and nursery areas. At present, maps of spawning areas can be entered as separate layers to ZONATION to ensure that the species has both spawning areas and parts of the rest of the distribution covered. In a forthcoming version of ZONATION it will be possible to calculate the connectivity layer of a species to a resource (prey, spawning area etc), which would enable explicit linkage of fish distributions to spawning areas.

The methods we have developed are a step towards making quantitative conservation prioritization methods and software applicable to river systems. We intend to further develop the software to include options that deal with freshwater connectivity in an even more realistic manner than here. Wider use within New Zealand using a larger set of species, and with an extended set of study sites is also planned.

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References


Appendix S1: Expanded description of the Zonation method and framework.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2427.2007.01881.x (This link will take you to the article abstract).

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