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ADDRESSING LONGITUDINAL CONNECTIVITY IN FRESHWATER SYSTEMATIC CONSERVATION PLANNING.

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ABSTRACT

1. Freshwater conservation has received less attention than its terrestrial or marine counterparts, despite freshwater systems containing a considerable amount of the earth´s biodiversity. Given the accelerated rate of change and intensive human use that freshwater ecosystems are submitted to, it is urgent to devote some attention to them. The application of existing conservation planning tools - such as Marxan - to riverine planning needs some adaptations to account for the special nature of these systems. Connectivity plays a key role in freshwater ecosystems – threats are mediated along river corridors and the health of the entire catchmemt influences. This needs to be considered in conservation planning approaches.

2. The probability of occurrence, obtained from MARS-GLM models, of nine native freshwater fish species in a Mediterranean river basin was used as features to develop spatial conservation priorities. The priorities accounted for complementarity and spatial design issues.

3. To deal with the connected nature of rivers, we modified Marxan´s boundary length penalty, hence avoiding the selection of isolated planning units and forcing the inclusion of closer upstream areas. We introduced ‘virtual boundaries’ between non-headwater stream segments, and added distance-weighted penalties to the overall connectivity cost (CP) when stream segments upstream of the selected planning units are not selected.

4. This approach to prioritising connectivity rule is concordant with ecological theory, as it considers the natural and roughly exponential decay of upstream influences with distance. It allows accounting for the natural capacity of rivers to mitigate impacts when designing reserves. With a small emphasis on connectivity, Marxan prioritised natural corridors for longitudinal movements. In contrast, whole sub-basins were prioritised when connectivity was emphasized. Changing the relative emphasis on connectivity causes substantial changes in the spatial prioritisation; our conservation investment could move from one basin to another.

5. Our novel approach to dealing with directional connectivity enables managers in charge of freshwater systems to set ecologically meaningful spatial conservation priorities.

KEYWORDS: Biodiversity, irreplaceability, MARS-GLM, Marxan, Mediterranean, native fish species.

INTRODUCTION

Despite containing a considerable amount of the Earth´s global biodiversity (Allan & Flecker, 1993), and being exposed to higher pressures and threats than adjacent terrestrial ecosystems (Malmqvist & Rundle, 2002; Nel *et al.*, 2007), freshwater ecosystems have received less attention by the conservation community (Abell, 2002). There has been little emphasis on declaring protected areas for the primary purpose of conserving freshwater ecosystems and biodiversity (Saunders, Meewing & Vincent, 2002). Rivers have generally been inadequately dealt with in most assessments of terrestrial ecosystems unless they were considered important for terrestrial biodiversity patterns and processes (Nel *et al.*, 2007). Indeed, one of the primary uses of rivers in terrestrial reserves is to define reserve boundaries. We urgently need better conceptual frameworks and tools for freshwater conservation planning.

The protection of all places which contribute to biodiversity conservation is impossible, since conservation usually competes with other human interests (Margules, Pressey & Williams, 2002). Representativeness (adequate representation of all the targeted biodiversity attributes) and persistence of biodiversity are two main goals in reserve design (Margules & Pressey, 2000). Once established, reserves should promote the long term survival of the biodiversity they contain by maintaining natural processes and viable populations and by mitigating at least some of the proximate threats to their biodiversity (Margules & Pressey, 2000; Margules *et al.*, 2002; Wilson *et al.*, 2005a). Before systematic conservation planning, the acquisition of land for reserves traditionally involved either the use of a subjective judgment of biodiversity value, or the use of other completely extraneous criteria to biodiversity conservation such as scenic value, wilderness quality and inaccessibility, low primary production potential or simply availability (Margules, Nicholls & Pressey, 1988; Pressey, Possingham & Margules, 1996; Sarkar, 1999). These approaches lead to *ad hoc* conservation strategies focused on areas easiest to reserve, sometimes with least need for urgent or immediate protection (Pressey, 1994; Knight, 1999; Pressey *et al.*, 2000). In general, these kinds of approaches have not realised the benefits to biodiversity that they could have, as (i) they do not address representativeness (Pressey & Tully, 1994) and (ii) often force misallocation of limited resources into areas containing relatively few diversity surrogates (see later). To overcome these pitfalls, an explicit framework for systematic conservation planning has emerged (Margules & Pressey, 2000) in the last two decades.

Systematic conservation planning work tries to attain biodiversity conservation goals by identifying important areas where conservation efforts should be focused (priority areas hereafter) to facilitate the effective use of the limited resources intended for conservation issues (Knight *et al*., 2007).

Given the accelerated rate of land use change and because biodiversity protection competes with legitimate alternative human uses, methods for identifying priority areas need to be explicit, efficient, cost-effective and flexible (Margules *et al*., 2002; Possingham *et al*., 2006). While traditional conservation tools relied on crude scoring approaches based on different criteria such as species richness, rarity value, naturalness, or size (Williams *et al*., 1996), modern conservation planning methods use complementarity-based algorithms and proper problem definition. Complementarity is defined as the gain in representativeness of biodiversity when a site is added to an existing set of areas (Possingham, Ball & Andelman, 2000). Algorithms which incorporate complementarity lead to a more efficient representation of biodiversity features and better cost-effective solutions than ad-hoc (Pressey & Tully, 1994), scoring or ranking strategies (Margules *et al*., 2002; Pressey & Nicholls, 1989). After defining clear objectives (such as biodiversity targets), they look for areas that add as many under-represented surrogates (taxa or any other conservation feature) as possible to a network of protected areas (Pressey, Possingham & Day, 1997), achieving the efficiency goal by selecting as few areas as possible that together reach the representativeness goal (Pressey & Nicholls, 1989). However, the identification of single reserve solutions is a rigid strategy which gives no indication on the importance of each area in terms of their potential to be replaced by other available areas in the region (Pressey, Watts & Barret, 2004) and the value of unselected areas (Cabeza & Moilanen, 2006). To include flexibility in systematic conservation planning, quantitative conservation tools often incorporate measures of irreplaceability – calculated by estimating the likelihood that an area will be required to meet a given set of targets (Pressey *et al*., 1994; Ferrier *et al*., 2000).

Most conservation planning approaches have so far overlooked freshwater biodiversity, because incorporating freshwater species and habitats adds several layers of complexity to an already complicated task (Abell, 2002). Nevertheless, systematic conservation planning studies specifically targeting freshwater ecosystems have started to emerge (Nel *et al*., 2007; Linke *et al*., 2007; Moilanen, Leathwick & Elith, 2008).

These studies apply all the principles developed for terrestrial ecosystems, but recognize the need for some refinements to consider the special characteristics of freshwater ecosystems (Dunn, 2003). Freshwater conservation planning must deal with the connected nature of rivers, which is a key factor for the structure and conservation of freshwater biodiversity - even more important in this context than for terrestrial ecosystems (Ward et al., 2002). Riverine systems are characterised by multiple longitudinal, lateral and vertical boundaries (Ward & Stanford, 1989). All these boundaries are more efficiently connected than in terrestrial ecosystems given the density and viscosity of water and its directional flow (Weins, 2002). This strong connectivity has important ecological consequences (Vannote et al., 1980) and clear effects leading the spread of perturbations and threats along freshwater ecosystems. Despite the crucial role that connectivity plays in riverine ecosystems, it has not received the attention that it deserves (Pringle, 2001; Ward et al., 2002). Reserves located in middle or lower watersheds often suffer the cumulative effects of hydrologic alteration and pollution originated in both upstream and downstream, imposing high threats to the conservation of its biodiversity.

Here we adapt Marxan - an extensively used tool in terrestrial and marine systematic conservation planning - to the peculiarities of rivers, aiming to attain more effective reserve design principles for freshwater systems. We account for the connected nature of rivers by introducing a penalty for not conserving upstream areas which could have impacts on downstream reserves. In this way we specifically address one of the components of spatial riverine connectivity, such as longitudinal connectivity, in freshwater systematic conservation planning. At the same time, we simulate the decay in spatial influence along water courses to reflect the natural capacity of rivers to mitigate impacts.

METHODS

Study area

The Guadiana River basin is located in the South-Western Iberian Peninsula draining a total area of 67039 Km^2 to the Atlantic Ocean (Fig. 1). It features a typical Mediterranean climate, with high intra and inter-annual discharge variation, with severe floods and droughts (Gasith & Resh, 1999). Mean air temperature ranges from 13 to 18.1 ºC, with a strong intra-annual variation in extreme temperatures. Mean annual precipitation ranges from 350 to 1200 mm (with a mean of 450 mm).

Although the Guadiana basin is not an overpopulated area (28 hab/km^2), agricultural activities have deeply transformed the landscape during the last century. Almost half of the basin (49.1%) is currently used for agriculture - 30.6% occupied with intensive agriculture as irrigated lands and 18.5% occupied with extensive agriculture, like olive groves or fruit trees. As a consequence, about 8.3 10^9 m^3 of water is retained in 86 big reservoirs (>10^6 m^3) and more than 200 small ones (<10^6 m^3) for water supply. This has resulted in the modification of natural riverine flow regimes and has fragmented fish habitat in the basin. Other common human perturbations are channel modifications due to river channelization and degradation and even complete depletion of the riparian forest. About 3,150 Km^2 (5.2% of basin´s area) are formal reserves and subject to special management regimes, though most of them arose from *ad hoc* or terrestrial planning.

Guadiana's freshwater fish fauna is especially important within the circum-Mediterranean context. Its high species richness is only comparable to that found in the Po River basin in northern Italy and the lower Orontes in southern Turkey (Smith & Darwall, 2006). All of these river basins contain between 11 and 17 native fish species.

Planning units

While in terrestrial systematic conservation planning equal sized grid cells are often used as planning units, subcatchments are a more appropriate option for freshwater environments. This spatial approach accounts for the connected nature of rivers and natural boundaries of areas of influence (Linke et al., 2007; Klein et al., *in press*). We derived 2170 planning units from a 90 m digital elevation model (Jarvis et al., 2006) through ARC Hydro (Maidment, 2002) within ArcGIS 9.1 (ESRI, 2002).

Environmental and biological data

Presence/absence of fish species was determined by electrofishing in 151 sites, each in a different planning unit. These sampling sites were homogeneously distributed through the whole basin, ensuring an adequate characterization of natural variations and human perturbations in the basin. Sampling was conducted once at every site without block-nets in stretches of 100 m (when possible). This protocol is recommended for obtaining an accurate characterization of species´ presence-absence in the same area (Filipe et al., 2004). The sampling stretch was representative of all the habitats present in the area, including pools and riffles where available. All fish were released once they were identified to species level.

Habitat data was used to build a predictive model with which relate freshwater fish community and habitat characteristics. Then this model could be used to infer freshwater fish communities from habitat data in unsampled planning units. The set of environmental variables listed in Table 1, included a combination of both natural and disturbance descriptors, to model actual probabilities of occurrence. We used two different spatial scales to characterize the environmental attributes of our planning units to portray both local influences and catchment scale effects, (i) subcatchment and (ii) catchment scale. The mean value of each environmental variable in every planning unit and across the whole upstream catchment area were considered respectively. Only remotely sensed data was used in both approaches, to enable complete predictive coverage. All the variables were tested for normality and appropriately transformed when necessary before analysis.

Prediction of biological data

Lack of complete survey coverage is a common problem in conservation planning (Margules & Pressey, 2000; Van Teeffelen, Cabeza & Moilanen, 2006; Linke *et al.*, 2007). This is usually dealt with by building predictive models of the distribution of conservation features throughout the landscape (Wilson et al. 2005b). A Multivariate Adaptive Regression Splines (MARS) model developed on the 151 sampled planning units was used to predict the probability of occurrence for each species in the unsampled planning units. MARS is a method of flexible non-parametric regression modelling (Elith & Leathwick, 2007). It is useful for modelling complex non-linear relationships between response and explanatory variables with similar levels of complexity to that of a Generalized Additive Model (GAM) (Hastie, 1991). MARS fits a nonlinear function to the relationships between dependent and predictor variables by breaking the range of each predictor into a subset of portions or “knots”, and fitting linear relationships for each of them (basis functions). MARS allows the slope of the fitted linear segments between pairs of segments to vary while ensuring that the full fitted function is without breaks or sudden steps (Elith & Leathwick, 2007). The predictive function is finally composed of a series of connected straight line segments, rather than the smooth curve of a GAM. Two interesting features made MARS models useful for the present work. 1) It allows exploring interactions between predictors (Leathwick, Elith & Hastie, 2006), and 2) is able to fit a multi-response model which can simultaneously relate variation in the occurrence of all species to the environmental predictors in one analysis (Olden, 2003). Multi-response models facilitate the modelling of rare species occurrences, which are important in conservation planning exercises.

The model was fitted using a code provided by Elith & Leathwick (2007) for the MDA (Mixture and Flexible Discriminant Analysis) library within the free statistical software R, Version 2.1.1 (R Development Core TEAM, 2004). The common function provided in R for MARS uses least squares which works appropriately for data with normally distributed errors. With binomial data this results in the range of predicted values being expanded beyond the acceptable range [0-1] (Leathwick *et al.,* 2006). To solve this problem the cited code fits a MARS model using the standard R code, extracts the basis functions, and computes a Generalized Linear Model (GLM) which uses the basis functions as predictors of each species´ presence-absence. This procedure constrained predictions between of occurrence probabilities to between zero and one. We allowed first order interactions between predictors in the models, since previous analysis showed a significant improvement in model performance when they were included. For more statistical details see Leathwick *et al*. (2005).

Model performance for each species was assessed through both measures of deviance and the area under the receiver operating characteristic curve (ROC) (Fielding and Bell, 1997). The area under the ROC curve (AUC) was assessed through a k-fold cross validation procedure (Hastie, Tibshirani & Friedman, 2001). The data was randomly divided in 10 exclusive sub-sets and model performance was calculated by successively removing each sub-set, re-fitting the model with the remaining data, and predicting the omitted data. The average error when predicting occurrence in new sites can then be calculated by averaging the AUC across each of the subsets (Leathwick *et al*., 2005). An AUC>0.6 is usually defined as acceptable model performance (Fielding & Bell, 1997). Deviance complements AUC because it expresses the magnitude of the deviations of the fitted values from the observations. Analogous to Elith & Leathwick (2007) the full information given in the predictions (raw probabilities of occurrence) were used in both the AUC and deviance analysis, rather than transforming this data into presence-absence estimates with a threshold.

Prior to model construction a Principal Component Analysis was carried out on the environmental data to extract a reduced number of independent predictors for MARS models. The presence-absence of 10 species in the whole biological data set was used for fitting the models (n=151 planning units).

Reserve design

The best reserve system, and irreplaceability for each planning unit, were calculated using the simulated annealing selection algorithm (Possingham *et al*., 2000) within the Marxan software package (Ball & Possingham, 2000). Marxan aims to find an optimal reserve network by minimizing an objective function where feature penalties, spatial design and cost tradeoffs are considered (Equation 1).

$$Objective\ function = \sum_{planning\ units} Cost + SPF \sum_{features} Feature\ \ Penalty + CP \sum ConnectivityCost$$

Equation 1

The mathematical objective in Marxan is therefore:

Minimise: The cost of all the sites in the reserve system plus a penalty of each feature that does not reach its conservation target plus the cost of absent connections weighted by CP, the "connectivity parameter".

After creating a random initial reserve system, planning units are added or discarded from the reserve system in an attempt to minimise the objective function (equation 1). The final aim is to adequately represent a set of targets (species in our case) by selecting as few planning units as possible. In Equation 1, cost represents the cost of preserving each planning unit. Since we lacked objective estimates of the economic cost for the preservation of each planning unit, we assumed a homogeneous cost for all of them.

The feature penalty (FP) is a penalty for not fully representing all the features (fish species in this case) in the final reserve solution at the targeted level. Marxan considers features as objectives rather than constraints so the final solution might fail to meet adequate conservation for a feature if the weighting for the feature penalty is set too low. We set the weight of the feature penalties for unmet targets high (SPF=100), so all species targets were met. Species occurrences within the planning units were formulated as probability of occurrence (*p*). Similar to Wilson et al. (2005), we did not transform the probabilities into presence/absence, but treated the targets as expectations. Hereby, if a target was 10, this target is fulfilled both by ten presences of p_i=1 being reserved, as well as 20 presences of p_i=0.5 being reserved (cf Game et al. 2008). We set a general target of 10 planning units, which roughly equates to 70 km of habitat for each species.

In terrestrial applications, the spatial design of the reserve is determined by a boundary length penalty that forces reserves to be compact. We modified the concept of the boundary length penalty in Marxan to account for the connected nature of rivers (see Linke *et al*., 2007; Possingham *et al.* 2005). While Klein et al (in press) only consider adjacent subcatchments, we introduce 'virtual boundaries' between non-headwater subcatchments by adding penalties to the overall connectivity cost when subcatchments upstream of the selected planning units are not selected (Fig. 2). Hereby, the penalty for each planning unit decreases by a factor proportional to the reciprocal of the distance between the planning units. A planning unit that is 1 km away from the selected subcatchment incurs a penalty of 1, while a planning unit 2 km away incurs a penalty of 0.5 (= 1/2). Hence, the importance of an upstream subcatchment decays over the distance to the planning unit containing the targets (Fig. 2).

How much emphasis we place on upstream connectivity can be adjusted using the connectivity penalty (CP). A CP of 0, means that a planning unit can be chosen for biodiversity protection without any incurring penalties for not including upstream subcatchments. We tested the sensitivity of the reserve design outcomes to different levels of the CP in order to find a reasonable value that balances connectivity with total area to reserve. Ten different CPs where used (0, 0.001, 0.05, 0.1, 0.3, 0.5, 0.7, 1, 2, and 3). Finally, irreplaceability was assessed as the frequency of selection of each planning unit by running the algorithm 100 times.

RESULTS

Predictive models construction and performance

The environmental variables with the highest loading for the 9 first Principal Components (PC) of the environmental PCA were selected as predictors for the MARS-GLM model (Table 2). These 9 PCs accounted for more than 76% of the original variance and ensured high tolerance values (variance in each predictor not explained by the remaining) for the variables used as predictors, avoiding redundancies.

Presence/absence of 9 out of the 10 species was successfully modelled with at AUC>0.6 and an average explained deviance of 29% (Table 2), comparable to previous studies (Leathwick *et al*., 2005). The model only failed fitting *Cobitis paludica* data, which is a ubiquitous species with high prevalence values which probably led to a random distribution at least in relation to the selected predictors. This model was then used to predict the probability of occurrence of each species in the unsampled planning units.

Reserve design

As we increased the connectivity penalty (CP), we observed an exponential decay in the ratio of boundary length to area needed (Fig. 3). This relationship was used to identify a compromise setting of CP (CP = 0.01) at which there was a significant gain for the reserve configuration in boundary length terms while keeping the total reserve area reasonably low. In this way we prioritised for the most cost-efficient clustered reserve (considering area as a surrogate for reserve cost).

Most species were overrepresented in the network for CP = 0.01 (Mean target representation for all the species at CP = 0.01 was 13.7, although some species such as *Iberocypris alburnoides*, reached a representation of 23.0, while others such as *Luciobarbus comizo* and *Salaria fluviatilis* just reached the targeted level,10). Both these species had the highest probabilities of occurrence at downstream reaches. By increasing the emphasis on upstream connectivity representing these two species forces the inclusion of more planning units than necessary for the remaining species, hence raising their representation within the reserve. Moreover, there was a roughly linear increase in the area of the reserve system with increasing target levels (Fig 4).

Clearly, a high CP increased hydrologic connectivity of selected planning units (Fig. 5c), since only headwater or whole upstream sub-catchments were included in the best solution when a high CP was used. In contrast, isolated stream reaches, some even located in the main Guadiana River channel, were selected in the best solution when the CP was set at 0 (Fig. 5 a). Irreplaceability values, or frequency of selection of each planning unit in 100 runs, followed a similar pattern with high values for isolated planning units when using no CP (Fig. 5d) and more clustered solutions with the highest irreplaceability values when setting a CP at higher values (Fig. 5 e and f). At increasing CP values whole sub-basins were included in the best solution. Using a medium CP (0.01) strings of planning units got selected (Fig. 5 b and e) – analogous to movement corridors. At the higher setting (CP=3), entire subcatchments were included (Fig. 5 c and f). Interestingly, the sub-catchments selected in 'corridor mode' (at an intermediate CP, moderate upstream connectivity) were not the same as the sub-catchments prioritised with a very high emphasis on upstream protection. When needing to protect the entire basin, the solutions changed to a smaller basin – the Chanza River basin.

DISCUSSION

Systematic conservation planning aims to select a set of areas to efficiently ensure the long-term persistence of targets (Margules & Pressey, 2000). The simulated annealing optimization algorithm within Marxan increases efficiency in systematic conservation planning. It is widely used by managers and discussed in the scientific literature (Wilson *et al.*, 2005b; Oetting, Knight & Knight, 2006; Carwardine *et al.*, 2007). However some adaptations were needed to account for the connected nature of rivers in freshwater systematic conservation planning. This is the first application in which planning for upstream protection has been realized in Marxan, using freshwater fish communities as surrogates.

Spatial connectivity is an issue of major concern in systematic conservation planning (Cabeza, 2003), especially in freshwater applications due to the connected nature of this environment. Pringle (2001) refers to four main patterns which have important implications for the location and management of freshwater reserves, such as (i) deterioration of lower watersheds, (ii) deterioration and loss of riverine floodplains, (iii) deterioration of irrigated lands and connecting surface waters and (iv) isolation of upper watersheds. All of these threats are connectivity-related. Hence, the consideration of connectivity and its importance in maintaining natural ecological processes and biodiversity in freshwaters is a key for systematic conservation planning in these systems (Fausch et al., 2004; Ward, Malard & Tockner, 2004). With this purpose, we modified the static rule proposed by Linke *et al.* (2007) - which requires all the upstream river stretches to be included in the reserve - going beyond the optimization of size, shape and other spatial issues of traditional conservation planning practices and providing Marxan with a practical approach to tackle longitudinal connectivity. Although connectivity penalties have been shown to affect the reserve configuration and extent (see Carwardine *et al*., 2007; Klein *et al*., *in press*), there is a general agreement in the benefits of this approach (Cabeza *et al*., 2004). However, as commented above, issues with riverine connectivity go beyond longitudinal aspects, having at least two additional dimensions - lateral and vertical (Wiens, 2002). These should be addressed in future approaches to fully consider river connectivity and ecological processes.

Increasing the connectivity penalty showed interesting and unexpected effects on reserve design: at a value of CP around 0.01, the best solutions tended to be corridors down a few river valleys. More emphasis on upstream connectivity forced the prioritization of whole sub-basins. Moreover, both solutions were not nested. When selecting full catchments, the Chanza river basin was chosen, while in ‘corridor mode’ (lower CP at 0.01), the main conservation corridor was in a catchment further north. This is an unusual response of Marxan, contradicting the linear responses to increasing spatial reserve exigencies when enhancing the importance of reserve clustering. Stewart, Noyce & Possingham (2003) found a nested pattern with increasing representation, however in our example the focal catchment differed when increasing the CP. The reason for this is that Degebe River has a larger catchment overall. Thus, cost for whole-of-basin protection favours the smaller Chanza basin. At lower CPs in which the entire basin does not need to be protected to get a good solution, the longer stream network provides a better solution as a corridor. This fact is important to acknowledge in the planning stage, as planning for corridors with a low CP will result in a completely different reserve configuration to the whole-of-basin planning.

By introducing decreasing virtual boundary penalties towards upstream catchments, we also simulated the natural decay in the influence of river segments on lower reaches. The decay we included ensures an appropriate weighting of the potential effect of upstream disturbances by their distance to the targeted area. This resembles the behavior of natural systems (Prenda & Gallardo-Mayenco, 1996; Wiens, 2002), and is a vast improvement to the rigid rule proposed by Linke et al. (2007). The selection of all the upstream catchment is often unrealistic when dealing with conservation of lowland reaches. Our approach has important implications for future consideration of threats to the conservation in freshwater conservation planning, since reserves could be selected accounting for weighted distances to the main perturbations (such as centers of exotic species populations or highly human perturbed environments). Dealing with natural processes has been flagged as a key issue for an effective systematic conservation planning in the present changing world (Pressey *et al.*, 2007). The connectivity rule addresses it not only through the selection of longitudinally connected reserves which mitigates the drawbacks of present freshwater reservation highlighted by Pringle (2001) and Oetting *et al.* (2006), but also accounting for the natural capacity of rivers to mitigate impacts with distance along longitudinal gradients.

A common problem in conservation planning is that species distribution data is often incomplete. To fill the gaps, predicted species distributions can be used (Cabeza, 2003; Cabeza *et al.*, 2004; Linke *et al.*, 2007). Two different approaches have been previously followed at this stage: using direct probability of occurrence or transforming them into presence-absence data through arbitrary thresholds. The latter approach has been tested and used in previous studies (see Polasky *et al.*, 2000; Wilson *et al.*, 2005b). Despite this suppose a more risk-averse approach to conservation planning (Wilson et al., 2005b), it also entails a net loss of information on species distribution data. The threshold used in this transformation influences not only the predicted distribution area for the conservation features, but also the outputs of conservation planning process and has to be carefully set to ensure a suitable use (Wilson *et al.*, 2005b). Moreover, some reserve selection methods based on presence-absence data may fail to consider persistence of targets in reserve selection (Araújo & Williams, 2000; or Teeffelen *et al.*, 2006). We dealt with persistence more thoroughly by using present probabilities of occurrence (see Cabeza *et al.* 2004), instead of potential probabilities of sites used in the reference condition approach (see Linke et al. 2007). This probability of occurrence indicates the likelihood with which a species is present in a planning unit considering different species-dependent factors such as habitat quality requirements or vulnerability to threats (Araújo & Williams, 2000). Instead of using just reference site distributions (Linke *et al.* 2007), our present distribution models were built on the whole dataset - using even sites with perturbed fish communities and including human-influenced environmental variables as predictors. Potential distributions can be unrealistic, since some species may have been pushed out to marginal areas within their original distribution or displaced to new areas due to human impairment (Kouamélan *et al*., 2003; Light & Marchetti, 2007). In this sense, Araújo, Williams & Fuller (2002) showed how the probability of persistence increases if reserve selection algorithms maximize the probability of the current occurrence instead of using a hypothetical niche model. With actual distributions we focused the efforts on identifying the more suitable areas for attaining persistence and optimizing the use of the scarce resources intended for conservation purposes (Knight *et al*., 2007) in conservation areas under current land-use, at least if they remain stable.

An additional benefit of using direct probabilities of occurrence is the ability to better portray the continuous nature of rivers (Vannote *et al*., 1980) in the conservation process. Since biological communities change gradually through natural upstream-downstream gradients in rivers (Allan, 1995; Welborn, Skelly & Werner, 1996; Clavero, Blanco-Garrido & Prenda, 2005) spatial connectivity is better addressed through continuous probabilities rather than through presence-absence data. It also allows the interpretation of the reserve in terms of a trade-off between river length and probability of occurrence. In our approach we ensured selecting 70 river kilometers where the species had a high certainty of occurrence (p_i=1) or larger habitat length at a lower probability. This could then be related to the spatial needs for each species to develop healthy populations and their probability of persistence. A feedback process, where this kind of basic ecological information will guide reserve selection through setting variable representation targets, would have clear beneficial effects for the effectiveness of the conservation plan (Pressey *et al*., 2007). However, as this information is still lacking we have to trust the river habitat length included in the present best reserve to be enough for preserving all the targeted species.

A whole basin approach has been followed in this study while previous efforts in the same area were only focused on the Portuguese (Filipe *et al*., 2004) or Spanish (Hermoso *et al*, *submitted*) portions of the basin while cross-boundary conservation management seems a more effective practice. The most irreplaceable area and the best solution when setting the CP at high values were especially focused on a single sub-basin (Chanza River). This solution highlights the importance of tributaries for conserving freshwater biodiversity (see Nel *et al*., 2007). The same area had previously been included in a set of priority areas for conservation through an alternative method based on the reference condition approach (Hermoso *et al.*, *submitted*). However this is the first time that a complementarity-based algorithm has been applied to this basin in particular. Algorithms which incorporate complementarity ensure representativeness, in addition to persistence, which is the other major goal in systematic conservation planning, (Margules & Pressey, 2000; Margules *et al.*, 2002). This guaranties the adequate representation of each species within the reserve, overcoming uncovered deficiencies in other reserve selection methods based in scoring and ranking approaches (Williams *et al.*, 1996; Margules *et al.*, 2002).

This study introduces substantial innovations to freshwater systematic conservation planning. We have modified Marxan to specifically deal with longitudinal connectivity in freshwater conservation through the inclusion of our virtual boundaries between planning units. A flexible connectivity penalty allowed the consideration of the natural decay by distance between stream reaches. At different penalty strengths Marxan was able to identify either longitudinal corridors or whole sub-basins (at increasing CPs). All of these advances contribute to improved realism when dealing with freshwater conservation issues.

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Table 1. GIS data used to characterize the planning units in the Guadiana River basin at the catchment scale (the whole upstream drainage area excluding itself) and the subcatchment scale (only the stretch within the planning unit in question). SD denotes Standard Deviation.

Catchment scale	Subcatchment scale
% Land uses[1]:	% Land uses[1]:
Urban	Urban
Intensive agriculture	Intensive agriculture
Extensive agriculture	Extensive agriculture
Naturalized	Naturalized
% Geology[2]:	% Geology[2]:
Actual alluvial deposits	Actual alluvial deposits
Calcareous	Calcareous
Siliceous	Siliceous
Acid volcanic	Acid volcanic
Basic volcanic	Basic volcanic
Mean annual rainfall[3]	Mean annual rainfall[3]
Precipitation seasonality[3]	Precipitation seasonality[3]
Mean annual temperature[3]	Precipitation in the wettest month[3]
Altitude (Average, Maximum and SD)[4]	Precipitation in the driest month[3]
Slope (Average and SD)[4]	Mean annual temperature[3]
FootPrint[5]	Annual temperature range
Population density	Temperature in the warmest month[3]
Drainage area	Temperature in the coldest month[3]
	Temperature seasonality[3]
	Isothermality[3]
	Mean annual evapotranspiration[3]
	Altitude (Average, Maximum and SD)[4]
	Slope (Average and SD)[4]
	Soil Quality Index[6]
	Vegetation Quality index[6]
	Distance to headwater
	Downstream distance to the nearest reservoir
	Distance to Guadiana (main river channel)
	FootPrint[5]
	Population density[6]

Data sources:

1 CORINE Land-Cover 1:100.000. Confederación Hidrográfica del Guadiana.

2 Mapa geológico de España 1:1.000.000. Instituto Geológico y Minero de España.

3 WORLDCLIM, Version 1.4. The data is described in Hijmans et al., (2005).

4 SRTM 90 m Digital elevation model from Jarvis et al., (2006).

5. Human footprint. Center for International Earth Science Information Network (CIESIN) at Columbia University (www.ciesin.columbia.edu/wild_areas/)

6. European Environmental Agency. (www.eea.europa.eu).

Table 2. Principal Component Analysis carried out in the environmental data matrix to select the most representative and independent predictors within the study area. The variance explained by each Principal Component (PC) is showed in addition to their respective eigenvalues (in parentheses). The variable with the highest loading within each PC was selected as representative of each of them and used as predictors. * Denotes sub-catchment measured variables in opposition to catchment variables.

	Variance explained	Environmental variable	Factor loading
PC1	24.9 (12.9)	Coldest temperature*	-0.95
PC2	16.2 (8.4)	Average slope*	0.83
PC3	8.5 (4.4)	Average Evapotranspiration*	-0.65
PC4	7.6 (3.9)	Altitude (SD)	-0.79
PC5	6.3 (3.3)	Warmest temperature*	-0.65
PC6	4.2 (2.2)	Area	0.53
PC7	3.5 (1.8)	Siliceous	-0.56
PC8	2.8 (1.4)	Extensive agriculture*	0.41
PC9	2.7 (1.4)	Siliceous*	0.40
Total	76.7 (39.9)		

Table 3. MARS-GLM model performance. The deviance explained indicated the reduction in deviance for each species with respect a null model. The proportion of total deviance accounted for is shown in brackets. The discriminatory power of the model for each species is given through the AUC of the ROC curve (calculated by K-fold re-sampling with its SD in brackets).

Species	Author	Deviance explained	ROC	Prevalence (n=151)
Anaecypris hispanica	Steindachner, 1866	33.6 (0.41)	0.72 (0.11)	0.05
Luciobarbus comizo	Steindachner, 1864	44.7 (0.27)	0.75 (0.15)	0.24
Luciobarbus microcephalus	Almaça, 1967	46.6 (0.25)	0.70 (0.20)	0.31
Luciobarbus sclateri	Günter, 1868	34.6 (0.34)	0.79 (0.21)	0.10
Iberochondrostoma lemmingii	Steindachner, 1866	42.9 (0.30)	0.73 (0.15)	0.28
Pseudochondrostoma willkommii	Steindachner, 1866	53.2 (0.24)	0.70 (0.20)	0.17
Cobitis paludica	Buen, 1930	32.2 (0.02)	0.57 (0.08)	0.66
Salaria fluviatilis	Asso, 1801	47.8 (0.42)	0.69 (0.28)	0.13
Iberocypris alburnoides	Steindachner, 1866	3.8 (0.18)	0.66 (0.12)	0.66
Squalius pyrenaicus	Günter, 1868	25.5 (0.42)	0.69 (0.16)	0.13
Average		36.5 (0.29)	0.71 (0.16)	0.27

Figure 1. Location and water courses network of the Guadiana River basin. The main river channel is identified with a thicker line.

Figure 2. Decay in upstream connectivity penalties incurred if planning units are not selected.

Figure 3. Trade-off between minimizing boundary length and total area to reserve for different Connectivity Penalties (CP) values. We set the optimal CP (pointed out with an arrow) at a value where a substantial gain in the reduction of reserve´s boundary was get for a minimum increase in total area to reserve.

Figure 4. Total area (Mean ± SE) included in best solutions after 100 runs in Marxan for different target levels. For each target level 10 different Connectivity Penalties (CP) where used (0, 0.001, 0.05, 0.1, 0.3, 0.5, 0.7, 1, 2, and 3) to reduce the potential effect of changes in optimal CPs for each targets on the results.

Figure 5. Effect of Connectivity Penalty (CP) on reserve design. It is shown the best solutions (a-c) and irreplaceability values (d-f) for a target of 10 when setting the CP at three different levels (0, 0.01 and 3). Planning units included in the best solution found after 100 runs in Marxan, are pointer out in grey (a-c). Higher irreplaceability values are drawn in darker colours (d-e). Irreplaceability represents the frequency of selection of each planning unit by running the selection algorithm 100 times. It is only represented the portion of the basin where the best solutions and irreplaceability values appeared. The figure in the middle corresponds to the trade-off CP value set in Fig. 3.

Fig.1

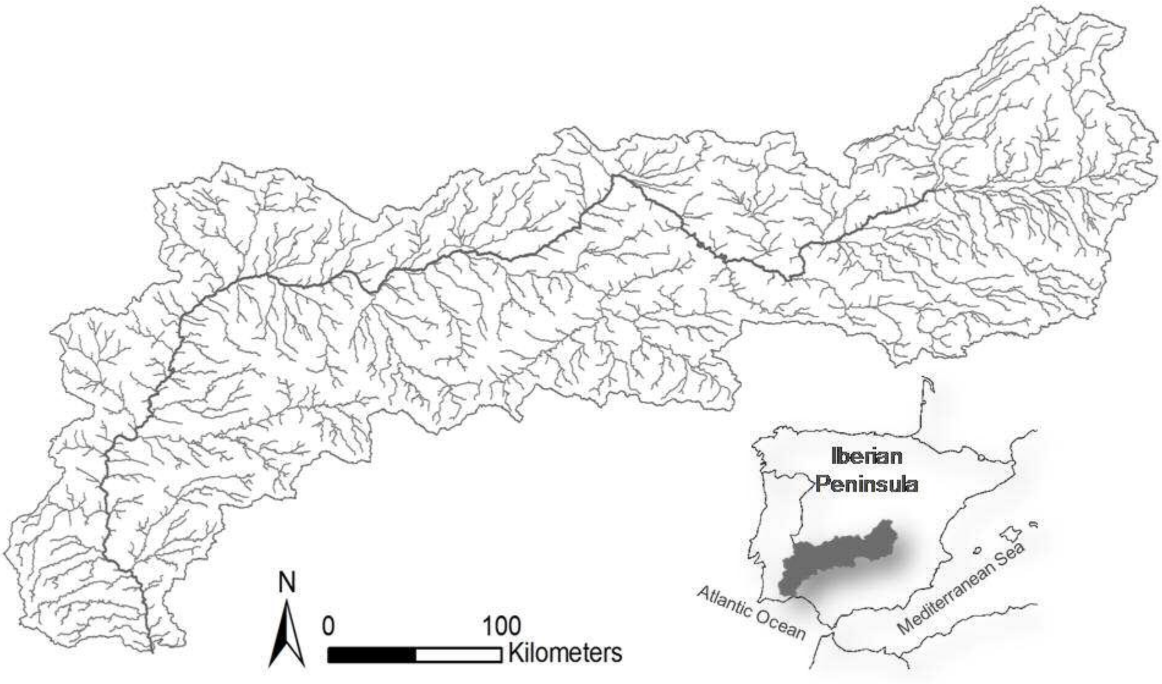

N
0
100
Kilometers
Iberian Peninsula
Atlantic Ocean
Mediterranean Sea

Fig 2

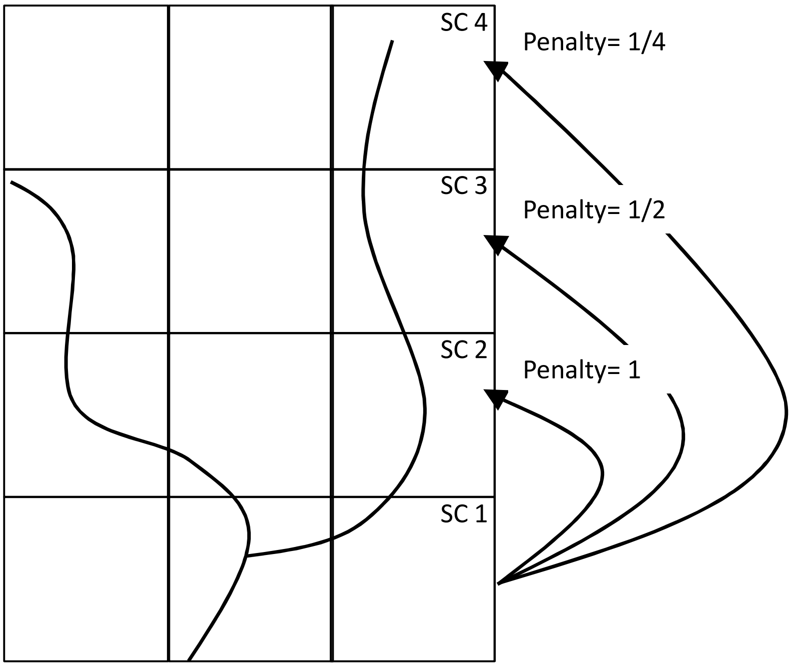


Fig 3

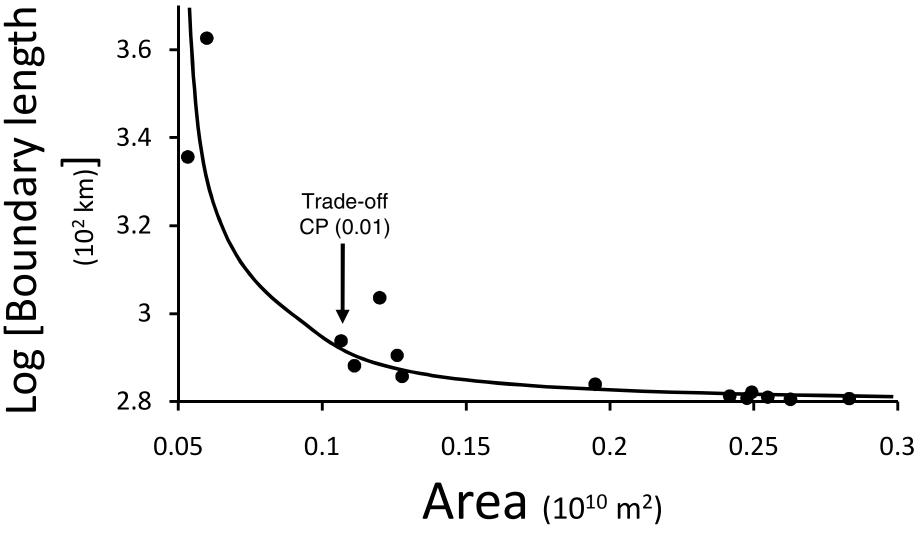

Log [Boundary length (10^2 km)]
3.6
3.4
3.2
3
2.8
Trade-off
CP (0.01)
0.05
0.1
0.15
0.2
0.25
0.3
Area (10^{10} m^2)

Fig 4

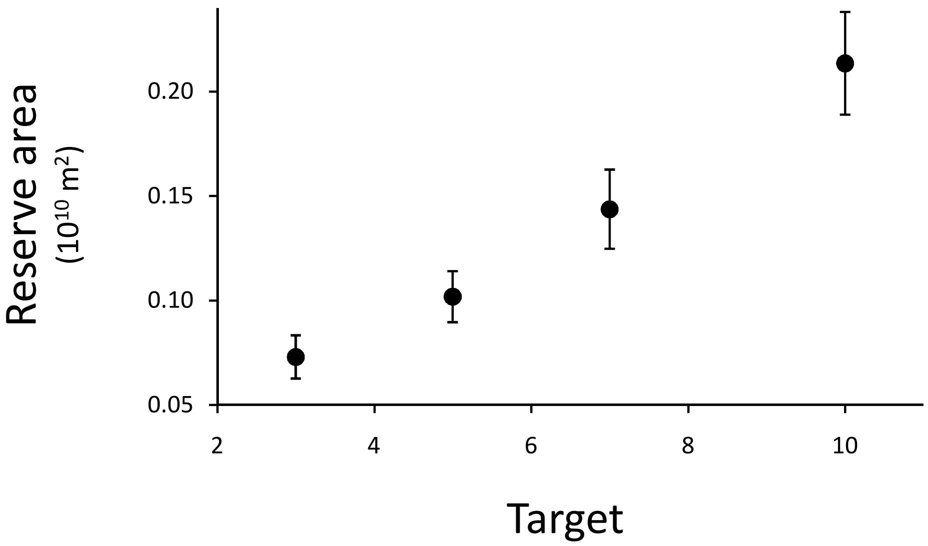
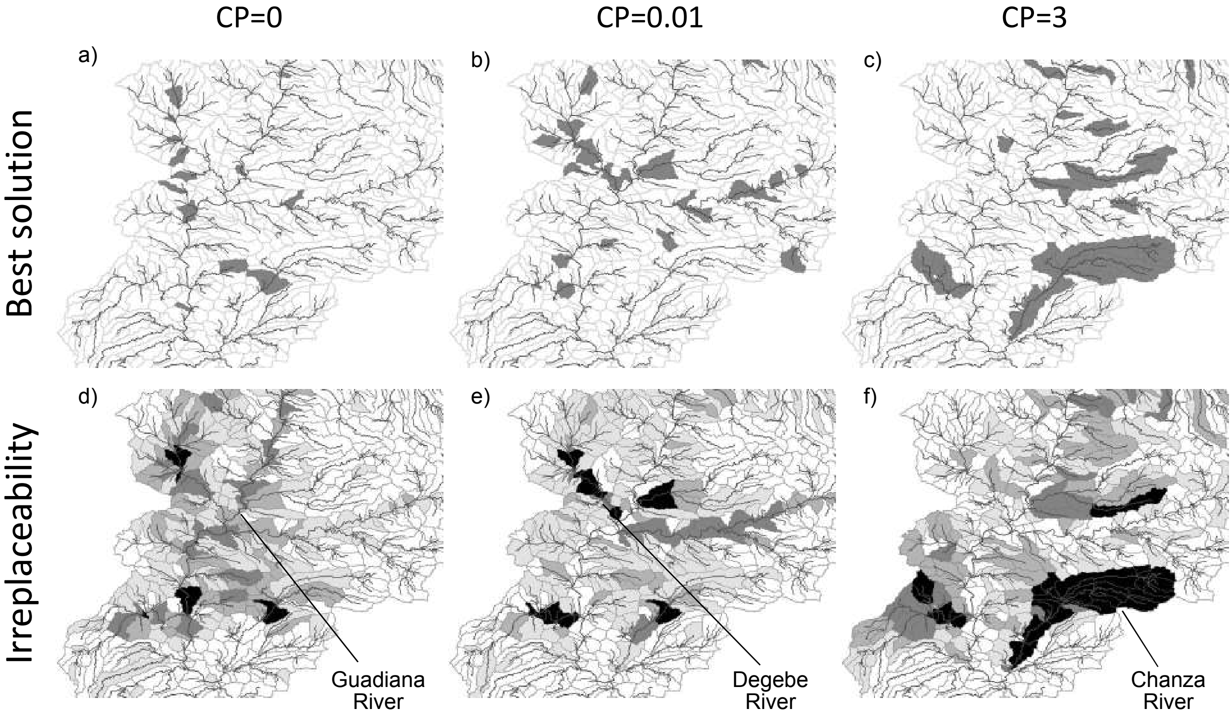


Fig 5


CP=0
CP=0.01
CP=3
Best solution
Irreplaceability
a)
b)
c)
d)
e)
f)
Guadiana River
Degebe River
Chanza River