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Incorporating ontogenetic dispersal, ecological processes and conservation zoning into reserve design

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ABSTRACT

Computational methods for marine reserve design are frequently used as decision-support tools for the identification of conservation areas. Most reserve-selection algorithms minimise the cost of the reserve system whilst aiming to meet specified biodiversity objectives. Here, we extend a widely-used selection algorithm, Marxan, to incorporate several important considerations related to biodiversity processes and management. First we relax the scorched earth assumption to allow conservation features in non-reserve zones to contribute explicitly to conservation objectives. To achieve this, we generate conservation targets at landscape scales rather than focusing purely on the representation of features within reserves. Second, we develop the notion of spatial dependencies further to incorporate spatial heterogeneity in the value of individual conservation features such as habitat types. We use the example of ontogenetic migrations of fish from mangroves to coral reefs because it nicely demonstrates how spatial ecological processes generate predictable heterogeneity in habitat value that should be considered in the reserve design process. Lastly, we show how habitat value can be disaggregated into ecosystem processes and services. Using a case study for the Belize Barrier Reef we compare reserve networks generated using our new approach with the results of traditional analyses. Consideration of the contribution of different protection zones, connectivity among habitats and more complex management goals resulted in up to a 52% increase in the mean biomass of commercially and ecologically-important fish species represented in the landscape. Our approach strengthens the ecological basis of reserve-design algorithms and might facilitate the uptake of ecosystem-based management into reserve design.

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1. Introduction

Conservation planning often aims to ensure the persistence of natural features, typically by protecting a representative selection of each (Halpern and Warner, 2003; Margules and Pressey, 2000a). One of the most important tools available to achieve these goals is the establishment of networks of reserves (Leslie et al., 2003). The identification of reserve networks, or even the location of individual reserves, is a spatially-complex process requiring consideration of many biophysical and socioeconomic factors such as geographic patterns in 'biodiversity' and the costs of setting areas aside. Ideally, the placement of reserves would be informed by spatially-realistic models of multiple species, capable of incorporating spatially-dependent processes and the response of populations to reserves, but this is rarely practical. To simplify this task, a number of reserve (or site) selection algorithms have been developed that use computational methods to build potential networks from individual planning units (Cook and Auster, 2005; Early and Thomas, 2007; McDonnell et al., 2002; Noss et al., 2002; Possingham et al., 2000; Stewart et al., 2003). These algorithms provide an explicit framework for integrating conservation targets and goals and have the desirable attribute of searching for conservation scenarios that are near-optimal in terms of minimising the cost of conservation management while meeting pre-specified biodiversity objectives.

Reserve-selection algorithms target surrogates of biodiversity such as habitats, but in the absence of information stating otherwise usually assume that these do not vary in space. Yet, in an increasing number of ecosystems, ecological data on spatially-dependent processes and intra-habitat patterns of community structure are becoming available (Condit et al., 2002; Harborne et al., 2006b; Price, 2002; Ries et al., 2004). Incorporating such spatially-dependent information into the reserve-selection algorithms is therefore an important step in improving the ability of such algorithms to represent ecologically-meaningful patterns of diversity,

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community structure, and the distribution of particularly-important flora and fauna. This paper describes the incorporation of two spatially-dependent processes into the algorithm Marxan (Ball and Possingham, 2000), which is routinely used for marine reserve design. We derive these approaches from recent ecological studies of Caribbean coral reef ecosystems and while the resulting algorithms will be directly transferable throughout most of the region, the approach taken here can be used in any ecosystem for which comparable data are available. First, we describe in detail the need to adopt a landscape-scale measure of management goals that combines the contributions of both reserve and non-reserve sites. This approach provides the flexibility to consider the impacts of multi-use zoning and implicitly recognises that populations in reserves are not independent from those outside reserves. Second, we develop the notion of spatial dependencies within the landscape to incorporate spatial heterogeneity in the value of individual conservation features such as habitats. We use the example of ontogenetic migrations of fish from mangroves to coral reefs because it nicely demonstrates how spatial ecological processes generate predictable heterogeneity in habitat value that should be considered in the reserve design process. Lastly, we extend our case study to show how habitat value can be disaggregated into ecosystem processes and services. This approach allows levels of key ecosystem processes to be maximised whilst also minimising losses to certain ecosystem services. As such, we believe the approach is a step towards building ecosystem resilience into reserve-selection algorithms.

1.1. Reserve zoning: integrating reserve and non-reserve contributions to management goals

Many approaches to reserve design make the implicit assumption that the 'earth is scorched' beyond reserve boundaries (i.e., that non-reserve areas do not contribute to biodiversity goals). This might be an appropriate strategy when non-reserve areas are likely to become grossly disturbed or if considering heavily-exploited species. However, this assumption has questionable relevance to situations where habitat might deteriorate in quality, but where species are unlikely to become functionally extinct (Mumby, 1999). Indeed, not only do non-reserve areas contribute to the biodiversity of a landscape – albeit at perhaps lower levels than potential reserves – but the processes of larval dispersal and adult migration ensure that the maintenance of diversity within reserves is at least partly influenced by the status of populations beyond reserve borders (Sale et al., 2005). Moreover, responses to reserve establishment are not necessarily restricted to the reserves themselves. Marine reserves can yield a wide range of benefits outside reserves, including spillover effects (Roberts et al., 2001), increase of aesthetic and recreational values (Bhat, 2003; Bohnsack, 1993) and reduction of the probability of extinction (Grafton et al., 2005). Therefore, reserve design should consider the reserve and non-reserve contributions to management goals explicitly.

Reserve-design algorithms will need a new structure and parameterisation to integrate the contributions of both reserve and non-reserve areas to landscape-scale conservation. Each conservation zone needs to be identified and its associated contribution to management goals estimated. The simplest scenario segregates reserves from non-reserve areas but more complex zonations could be considered, such as a hierarchy of levels of resource exploitation. Estimating the contribution of reserves and non-reserves to conservation also requires a temporal scale. For example, non-reserve levels of a species might decline rapidly after harvesting begins whereas populations in reserves could take many years to recover (McClanahan and Graham, 2005). Importantly, the response of management goals to each level of protection (hereafter referred to as different protection zones) is likely to vary among biodiversity surrogates such as habitat types. Lastly, the spatial heterogeneity generated by differential effects of protection zones and habitat responses requires a convenient framework for integration. Altering the calculation of reserve and non-reserve costs provides such a framework.

Reserve cost is typically measured as a function of area during the reserve-selection process (see McDonnell et al., 2002), under the assumption that larger reserve areas will result in greater economic losses (Balmford et al., 2004). However, measuring the cost of a reserve network by its area alone fails to account for differences in per unit area costs among planning units (e.g., Naidoo et al., 2006). Local differences in productivity, species composition and environmental conditions, all of which will have a direct effect upon the socioeconomic cost or value of a planning unit are thus ignored in this situation. As an alternative, the cost of a reserve network can be expressed as the required financial outlay (Balmford et al., 2004), or as the opportunity cost to alternative uses, such as the foregone benefits from fishing (Richardson et al., 2006; Stewart et al., 2003; Stewart and Possingham, 2005). Here, our first modification of reserve-selection algorithms is to extend the calculation of cost to consider the relative cost of reserve and non-reserve planning units and in so doing assess the ecological and economic potential of management goals in the entire landscape. The approach presented here uses fish biomass as a proxy for economic and ecological value. Whilst this is sensitive to habitat type it should be considered only a step towards the uptake of ecosystem-based management into reserve design. We believe that a combination of optimisation tools and dynamical models of populations (e.g., Kaplan et al., 2006; Walters et al., 2007) and fishing effort will be required to accurately predict the response of populations to different configurations of reserves and the resulting changes in economical costs and ecological benefits. These models would need to be dynamic, structured (by age, size or life stage) and spatially realistic. The development of such models, their parameterisation and incorporation within the reserve selection framework is both theoretically and computationally complex. Despite these complexities, however, we believe this approach will be the way forward in ecosystem-based management.

1.2. Spatial context of planning units in landscape (ontogenetic migration)

One advantage of relaxing the scorched earth perspective and incorporating the contribution of non-reserve areas to conservation targets is that the framework is flexible enough to incorporate the outcomes of spatial processes like spillover of organisms beyond reserve boundaries. This idea can be extended to consider the outcomes of other spatial ecological processes such as the migration of organisms among habitat patches or, in essence, any spatial demographic process of predictable impact on conservation features. We illustrate this principle using the outcome of ontogenetic migrations of fishes among mangroves, seagrass beds and coral reefs.

Many Caribbean coral reef fish utilise mangrove forests as nurseries during their juvenile phase, before migrating to their adult reef habitat (Nagelkerken et al., 2000). The presence of mangroves has been shown to enhance the biomass of both commercially and ecologically-important fish, including parrotfish, on neighbouring coral reefs (Mumby et al., 2004). Insights from a study in Belize were used to generate an algorithm for the identification of connected mangroves and coral reefs (Mumby, 2006). Here, we extend this approach so that the consequences of a habitat patch's connectivity to mangroves are incorporated explicitly into the quantification of reserve costs. Although home range estimates and spillover calculations (Botsford et al., 2009; Kramer and Chapman, 1999) suggest that spillover of fish biomass from reserve to non-reserve

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