Advancing systematic conservation planning for freshwater ecosystems

Thesis submitted by

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To Chuck

Thank you for guiding me to this opportunity.

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Abstract

Freshwater ecosystems and their associated biota are among the most endangered in the world. Key disturbances, such as water extraction, dams, and modifications to riparian and in-stream habitats, invasive species, and impacts on water quality have heavily altered these ecosystems. Escalating human pressure on, and disturbances to, water resources requires well-informed decision making and effective on-ground management to conserve and restore freshwater ecosystems. Systematic conservation planning offers the tools needed to address these issues, providing a strategic and scientifically defensible framework. Systematic conservation planning was pioneered in the terrestrial realm and has, with time, become the most commonly recommended approach to marine planning and management because it can ensure the selection of multiple protected areas that together achieve explicit objectives. However, in comparison to the terrestrial and marine realms, the adoption of systematic methods to inform decision making for the protection and/or restoration of freshwater ecosystems remains in its infancy. The principal focus of this thesis is on spatial conservation prioritisation applied to both protected area and off-reserve management decision making. It focuses on two areas in the field of freshwater systematic conservation planning that have been identified as research priorities: 1) assessing the sensitivity of conservation planning outcomes to different surrogates and objectives; and 2) enhancing applicability of systematic conservation planning to inform on-ground management decisions.

The aim of this thesis is to advance the scientific basis and application of systematic conservation planning for fresh waters. I address key questions in the field of systematic conservation planning in freshwater ecosystems, which are both novel contributions to the field and influential in informing conservation decisions both on and off-reserves, using the Wet Tropics of Queensland bioregion as a case study. My objectives were to 1) determine the occurrence of disturbances, and the incidental protection of fresh waters in terrestrial protected areas; 2) identify the effectiveness of using coarse-filter surrogates for representing freshwater fish diversity in systematic conservation planning; 3) develop methods to evaluate the effectiveness of invasive species management; and 4) integrate management costs into systematic conservation planning for invasive species.

There is a need for assessments that quantify the effectiveness of terrestrial protected areas for representing freshwater ecosystems and their dependent species, and that determine areas of vulnerability from human-induced disturbances. In Chapter 3, I used data on the spatial distribution of freshwater ecosystems and fish, human-induced disturbances, and the Wet Tropics protected area network to assess how well freshwater ecosystems and fish species are protected within this network. I identified human-induced disturbances likely to influence the effectiveness of freshwater protection measures and I evaluated the vulnerability of these ecosystems to human-induced disturbances within and outside protected areas. The representation of freshwater ecosystems and species in the protected areas of the Wet Tropics is poor: 83% of streams, 75% of wetland types, and 89% of fish species have less than 20% of their total lengths and areas in IUCN category II protected areas. Higher-order streams and their associated wetlands are influenced by the greatest number of human-induced disturbances and are also the least protected. My results indicate poor representation of freshwater ecosystems and fish species in protected areas, and high numbers of human-induced disturbances impacting on these systems both within and outside of protected areas despite the high level of protection of terrestrial areas in the Wet Tropics. My findings demonstrate the need for greater consideration of protection status and off-reserve management of freshwater systems.

Abiotic and biologically informed classifications are often used in conservation planning as coarse-filter surrogates for species. The relationship between these surrogates and the distribution of species is commonly assumed, but rarely assessed by planners. In Chapter 4, I derived four abiotic and eight biologically informed classifications of stream reaches to serve as surrogates for biodiversity patterns in the Wet Tropics. I used stream reaches as planning units and, as conservation targets for each surrogate, I used two percentages – 10% and 30% – of the total number of stream reaches occupied by each class. I then derived minimum sets of planning units to meet targets for each surrogate and tested the effectiveness of the surrogates by calculating the average achievement of the same targets for predicted distributions of 28 fish species. My results showed that neither abiotic nor biologically informed classifications were good at representing freshwater fish species; in fact none of the surrogates led to average representation of species better than randomly selected planning units. There were two main reasons for this poor performance. First, none of the surrogates had high classification strength or informativeness about compositional change in fish species within the study region. Second, frequency distributions of probabilities of occurrence for most fish species were strongly right-skewed, with few stream reaches having high probabilities. Combined, these results meant that selection of stream reaches to achieve surrogate targets were effectively random with respect to probabilities of fish species occurrence, leading to poor representation of fish species.

Often ecologists and natural resource managers can easily access data on invasive species occurrence across a region. Yet, collecting species abundance data over a large area is arguably more important for decision making, but inherently costly, so methods which can provide robust information at low-cost are particularly valuable. In Chapter 5, I tested the relationship of environmental suitability with local abundance of an aquatic invasive species, olive hymenachne (*Hymenachne amplexicaulis)* in the Wet Tropics. Least squares and quantile regressions revealed a positive relationship between environmental suitability and local abundance of olive hymenachne. I used the relationship between environmental suitability and local abundance to quantify the effectiveness of management (reduction in local abundance) under four different management investments. I showed that the upper limit of abundance can be used to evaluate management effectiveness based on varying investments, and that ongoing management is the most effective at reducing local abundance.

The successful management and eradication of invasive species is often constrained by insufficient or inconsistent funding. Consequently, managers are usually forced to select a subset of infested areas to manage. In Chapter 6, I present a spatially explicit decision method that can be used to identify actions to manage invasive species while minimizing costs and the likelihood of reinvasion. I apply the method to a real-world management scenario, aimed at managing an invasive aquatic macrophyte, olive hymenachne (*Hymenachne amplexicaulis*).

The approaches I developed in this thesis allowed me to overcome several challenges related to the conservation and management of fresh waters, advancing the field of freshwater systematic conservation planning by: 1) quantifying conservation gaps for fresh waters, 2) identifying the effectiveness of surrogate methods and invasive species management investments, and 3) advancing the application of systematic approaches to address resource allocation questions for invasive species management. I was able to achieve these outcomes by integrating systematic approaches and spatial models of native and invasive species distributions. The results of my work can be used to inform conservation decision makers about the limitations of 1) protection afforded to fresh waters and their dependent species and 2) surrogates for representing freshwater biodiversity in regional scale conservation plans. Further, using the method I developed for monitoring the effectiveness of invasive species management, and implementing actions at the sites that I identified as priorities for weed management, would provide more cost-effective solutions to managers in the region..

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Publications produced during my PhD Candidature

*indicates those publications that are derived wholly or in part from this thesis

Peer-reviewed literature

Foale, S., Cohen, P., **Januchowski-Hartley, S.**, Wenger, A. and Macintyre, M. 2011. Tenure and taboos: origins and implications for fisheries in the Pacific. *Fish and Fisheries*. DOI: 10.1111/j.1467-2979.2010.00395.x. In press.

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Chapter 1 Introduction

The need for freshwater conservation

It is known that only a small fraction of the world's freshwater ecosystems remain unimpacted by humans (Vörösmarty et al. 2010). It is probable that freshwater ecosystems are the most endangered in the world, with species extinction rates in freshwater environments estimated at four per cent per decade (Ricciardi & Rasmussen 1999), far greater than in the most impacted terrestrial ecosystems (Sala et al. 2000; Dudgeon et al. 2006). Freshwater ecosystems are particularly susceptible to habitat and biodiversity loss because they occupy only 0.8% of the Earth's surface, but support over 6% of the species known to science, making them disproportionately species-rich. In addition, conservation efforts might be more problematic for fresh waters. These ecosystems and their supported species are subject not only to the effects of localized disturbances but also to disturbances elsewhere in their catchments. These more distant impacts can contribute to increases in habitat modification, poor water quality, flow modification and the spread of invasive species (Dudgeon et al. 2006; Light & Marchetti 2007). Levels of disturbance from these stressors typically increase downstream, with an accumulation of disturbances, generated upstream, meeting dense human populations downstream near the river mouth and along the coastal zone (Vörösmarty et al. 2010).

Stream ecologists have long recognized the strong influence of surrounding terrestrial environments on streams and the important role that landscape condition has on fresh waters (Harding et al. 1998). Efforts to conserve freshwater ecosystems and their species have largely focused on structure and habitat, with processes being a secondary benefit (Roni et al. 2008a). To date there has been poor transfer of knowledge about human-induced disturbances affecting freshwater biodiversity (Dudgeon et al. 2006). Human-induced disturbances include habitat loss (Revenga et al. 2005), habitat fragmentation (Clavero & Hermoso 2011), flow alteration (Poff et al. 1997), overfishing (Allan et al. 2005), introductions of exotic species (Light & Marchetti 2007), climate change (Regier & Meisner 1990) and input of contaminants (Malmqvist & Rundle 2002).

While there have been a number of methods developed for conserving freshwater ecosystems, ranging from integrated catchment management to fine-scale restoration of individual habitats, data are usually lacking to evaluate the long-term effectiveness of such strategies. The majority of efforts to conserve freshwater ecosystems have been carried out in an *ad hoc* manner (Linke et al. 2011), or sites have been selected for their aesthetic rather than ecological values, with poor consideration given to the idea that catchments should act as the focal management unit if conservation of fresh waters is to be effective (Harding et al. 1998).

During the late 1990's and early 2000's the idea of integrated catchment management was promoted for freshwater conservation with the Convention on Biological Diversity (CBD 2003) identifying the need to select protected areas within this framework. The limitations associated with previous attempts to conserve freshwater ecosystems and the realisation that terrestrial protected area networks fall short in conserving freshwater biodiversity (Abell et al. 2007) led to a call for the protection of fresh waters in the form of comprehensive, adequate and representative conservation areas – borrowing from the ideas developed for terrestrial ecosystems (e.g. Margules & Pressey 2000). Importantly, conservation researchers called for methods that would not compromise basic freshwater conservation principles, such as the maintenance of connectivity and natural hydrologic processes (e.g. Pringle 2001; Bunn & Arthington 2002). In 2007, the methods and tools that had been developed over the past 25 years for systematic approaches to conservation of terrestrial and marine ecosystems were integrated to inform decision making for freshwater ecosystems (e.g. Linke et al. 2007; Nel et al. 2007; Thieme et al. 2007).

Systematic approaches to conservation

Conservation efforts to support biodiversity are constrained by limited financial resources across all ecological realms. Therefore, decision makers must choose how, where and when to allocate resources to achieve explicit conservation objectives. This was the focus of systematic conservation planning, which was first introduced as a six-stage process by Margules & Pressey (2000) as a way to improve the efficiency of reserve selection for the conservation of species. The six-stage process was further refined by Pressey & Bottrill (2008), who recognised critical social aspects of the planning process.

To be systematic, the prioritisation approach applied to a conservation problem must include: 1) a list of assets to be targeted for conservation (e.g. fish species, habitats); 2) clearly defined objective/s stating the desired outcome (e.g. represent 30% of each habitat type); 3) a list of areas and their spatial dependencies; 4) a list of management actions (e.g. restore 100 hectares of native riparian vegetation) and an understanding of how they contribute towards achieving the defined objective/s; and 5) financial information specifying the cost of implementation of each action and, preferably, a budget (Figure 1.1). Other factors that should be considered in a systematic approach to conservation include: 1) regional and local goals; 2) additional constraints and opportunities such as disturbance, willingness of stakeholders, access to the land or water and condition of the existing landscape; and 3) local priorities that may not be identified during the planning process but that are identified once the spatial priorities are implemented (sensu Pressey & Bottrill 2008) (Figure 1.1). Information flow is a critical part of the process of systematic conservation planning (Figure 1.1): it starts with available data (boxes within black outline) that can be used to establish measures (boxes within grey outline) for each component (assets, spatial dependencies, constraints and opportunities and management actions) of the planning process.

There are two approaches to the issue of resource allocation. In the maximal coverage approach the objective is to maximize the amount of biodiversity protected given a pre-defined budget or resource constraint (Possingham et al. 2006). The alternative set-covering approach is to meet all specified objectives while minimizing the resources expended (Pressey et al. 2002). In addition, the principle of complementarity underlies the selection of areas or actions in systematic approaches (Pressey et al. 1997; Justus & Sarkar 2002). Kirkpatrick (1983) demonstrated the first assessment of conservation value that had the principle of complementarity as the central role. Complementarity-based selection algorithms look to add as many under-represented areas (e.g. habitat types) or management actions as possible to pre-existing conservation areas (e.g. network of protected areas). The principle of connectivity ensures efficiency in the selection of areas or actions, avoiding bias. The persistence of most freshwater ecosystems is, directly or indirectly, maintained through longitudinal, lateral and/or vertical connectivity, as well as a temporal dimension linked to flow regimes (Poff et al. 1997; Pringle 2001). These dimensions are interdependent, emphasizing the importance of considering all types of connections when planning for conservation (Nel et al. 2011). Systematic approaches to conservation planning can account for these different dimensions through decision-support tools (e.g. Marxan, Ball et al. 2009). Using these tools planners can allocate a spatially explicit arrangement of planning units to define a landscape and the spatial relationships among them (Beger et al. 2010). Therefore, with both complementarity and connectivity, systematic approaches to conservation planning can produce spatial solutions that are more than the sums of their parts (Margules & Pressey 2000).

Approaches to conservation planning are being progressively refined. While much emphasis in systematic conservation planning has been on protection and reserve design, a wide variety of actions for protection, management and restoration are relevant and can be addressed with systematic approaches (e.g. McBride et al. 2010). In addition, the success of systematic conservation planning within terrestrial and marine realms has precipitated a call for similar action from freshwater scientists, planners and catchment managers (Linke et al. 2011). In the last ten years, systematic approaches to freshwater conservation have been flagged as the way forward for local to global conservation (e.g. Abell et al. 2007; Vance-Borland et al. 2008; Barmuta et al. 2011).

Freshwater systematic conservation planning

Freshwater habitats are typically located on a spatial continuum that is sustained by the hydrological cycle of precipitation, surface and groundwater storage, and surface and groundwater flow. Fresh waters are thus typically influenced by longitudinal (upstream-downstream), lateral (land-water) and vertical (surface-subsurface-groundwater) connections which can facilitate the movement of energy, materials or organisms (Ward & Stanford 1995). Connectivity in fresh waters, influenced by the timing, frequency, and duration of flow, maintains natural patterns that are vital to many species. The loss of any level of connectivity between freshwater ecosystems, or between fresh waters and the terrestrial and marine realms, can lead to isolation of populations, failed recruitment and local extinctions of native species (Bunn & Arthington 2002), although natural lack of connectivity between systems can facilitate evolutionary processes.

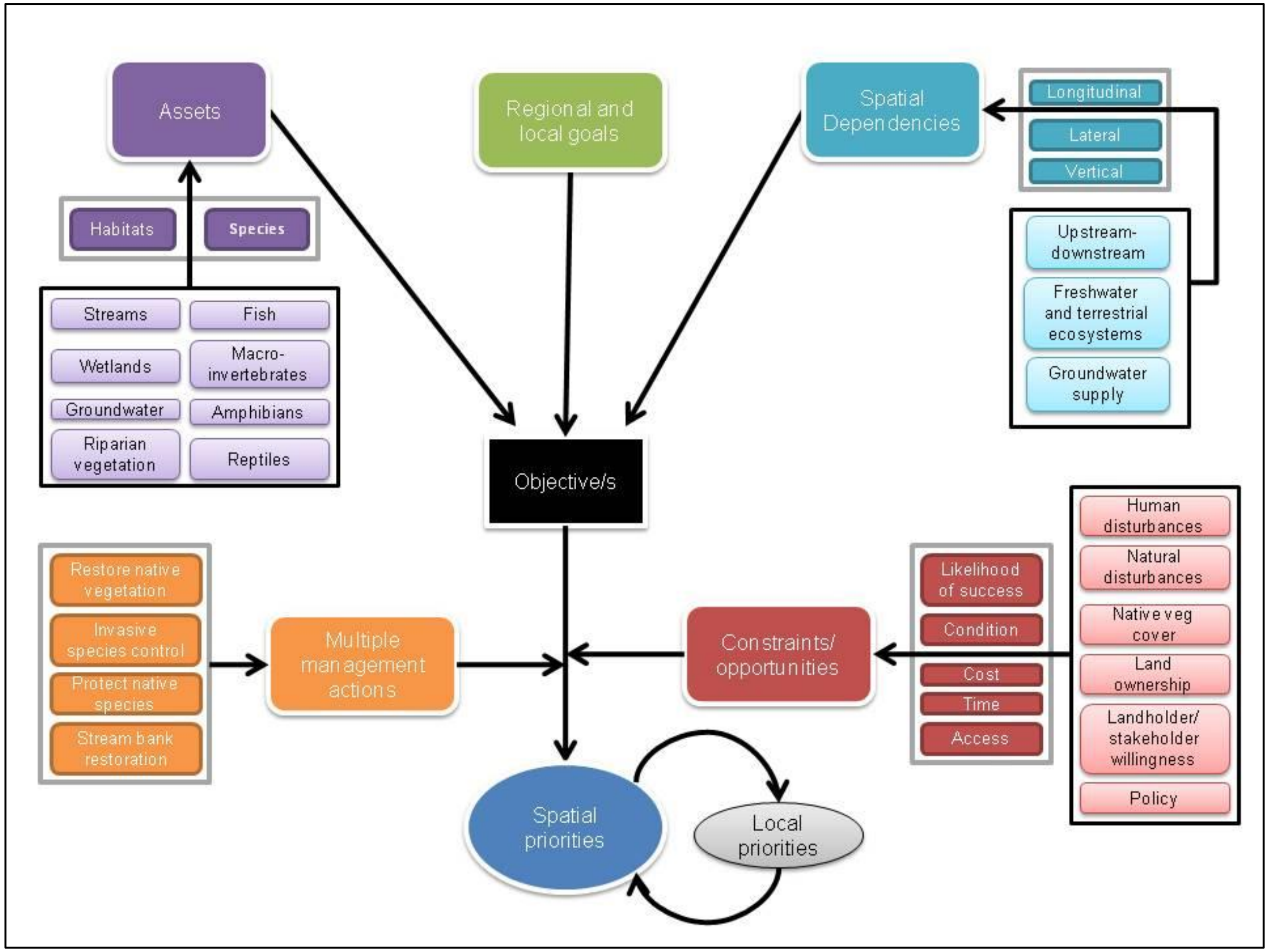


Figure 1.1 The process of developing a systematic conservation plan. Boxes with a black outline are data inputs, and boxes with a light grey outline are measures that can be considered for each component (assets, spatial dependencies, management actions and constraints and opportunities).

Connectivity plays a critical role not only in the persistence of many species, but also in the occurrence, movement and distribution of disturbances to these ecosystems (Sato et al. 2010). Therefore, conservation planning for fresh waters needs to consider the role of connectivity in the management of native and invasive species.

Differences in ecological and evolutionary processes among the terrestrial, marine and freshwater realms stem from differences in biophysical characteristics and processes, and from types and patterns of human impacts (Carr et al. 2003). One of the most obvious differences between planning in the terrestrial and freshwater realms is the connected nature of freshwater ecosystems (Linke et al. 2011). While all ecological realms are influenced by spatial and temporal connectivity, the movement of energy and materials in the terrestrial realm is more localized than in fresh or marine waters. The connected nature of fresh waters has posed a challenge to the conservation planning community. In fact, the first integrated framework for the conservation of rivers was not produced until 2007 (Linke et al. 2007). Like Linke et al. (2007), Moilanen et al. (2008) included an *a priori* consideration of upstream and downstream connectivity in their conservation assessment of streams. Similar approaches have now been adopted for wetlands (e.g. Nel et al. 2011) and ground waters (Michel et al. 2009). However, to date, the majority of freshwater systematic conservation planning examples have focused on a single type of connectivity (longitudinal connectivity – upstream/downstream) with few studies (e.g. Roux et al. 2008; Esselman & Allan 2011) addressing lateral or vertical connectivity and few studies accounting for more than a single type of connectivity in a single freshwater conservation plan. This area of research is wide open, with opportunities to improve current approaches by 1) accounting for individual species' dependence on ecosystem connectivity and 2) refining the way conservation planning software can trade off ecosystem connectivity with other constraints such as cost. In the last five years scientists and planners have begun to address the differences between terrestrial and freshwater ecosystems, and the application of systematic approaches to conservation of freshwater habitats and species is rapidly expanding (Barmuta et al. 2011).

While the body of information on systematic conservation planning for fresh waters is rapidly expanding, a number of challenges remain (Linke et al. 2011). In this thesis, I address four of these challenges, as follows.

1. *Disturbance and incidental protection of fresh waters in terrestrial protected areas*

The consideration of human-induced disturbances on freshwater biota is rarely incorporated into conservation planning because of the difficulties in quantifying human-induced disturbances. The general focus of the field of systematic conservation planning has been on the protection of areas to ensure adequate representation and persistence of biodiversity. However, the ecological condition of ecosystems is also an important consideration that is often overlooked in the planning process. Therefore, to improve current approaches to planning for the protection of freshwater ecosystems we require better integration of ecological condition into the planning process (e.g. Linke et al. 2007). Similarly, there have been few quantitative assessments of the role that terrestrial protected areas play in conserving freshwater ecosystems (Herbert et al. 2010). As there are very few protected areas set aside specifically for the protection of freshwater habitats and species (e.g. Ramsar sites), there is a critical need to evaluate how well terrestrial protected areas represent freshwater ecosystems and their threatened biodiversity (Abell et al. 2007). Assessing the spatial extent of incidental representation of fresh waters within protected areas is a prerequisite for identifying and filling protection gaps (Herbert et al. 2010), and has been identified as a priority by the Conference of the Parties' Strategic Plan for Biodiversity 2011-2020 (CBD 2011). Understanding the degree to which terrestrial protected areas confer protection to freshwater ecosystems is complicated by the interconnected nature of aquatic ecosystems, the critical role of hydrological dynamics, and the generally poor state of spatial data describing freshwater ecosystems and species (Abell et al. 2007). Therefore, in regions where adequate data do exist, analyses can be used to inform the general global picture.

2. Surrogate effectiveness for freshwater biodiversity

Systematic conservation planning in all realms relies on surrogates (proxies) that serve as indicators of general biodiversity (Sarkar et al. 2002; Ferrier et al. 2004) and there has been a long history of using biotic and abiotic surrogates to assess the condition of water bodies and their catchments (Van Sickle & Hughes 2000; Snelder et al. 2004). Despite the reliance on surrogates for freshwater systematic conservation planning, especially coarse-filter surrogates derived from quantitative methods, there have been no assessments of their effectiveness. Nevertheless, the availability of ample data for developing surrogates in fresh waters ecology provides conservation planners with several options for predicting the composition of biological assemblages (e.g. statistical models, Simpson & Norris 2000) and developing river classifications (e.g. Turak & Koop 2008). In data-rich regions the opportunity exists to evaluate the effectiveness of surrogate methods. While not necessarily transferable between regions, results from such assessments can inform conservation planners about the benefits and limitations of particular surrogate methods.

3. Management effectiveness

Despite the need to quantify effectiveness of conservation programs, few studies (e.g. Capizzi et al. 2010) have investigated the success of invasive species management. Often, monitoring and quantification of effectiveness by managers has been limited by a lack of straightforward and robust methods (e.g. Palmer et al. 2005; Roni et al. 2008a). In tropical environments in particular, collection of spatial information on the occurrence and distribution of invasive species at a regional scale is expensive and logistically difficult. In addition, management effectiveness and supporting data are often reported in grey literature or are otherwise inaccessible to researchers. Evaluations that have been performed for conservation management in protected areas are often undertaken within institutions and are not accessible or applicable across institutions (Hockings 2003). This is likely to be similar across institutions that also undertake invasive species management outside of protected areas. These limitations make it difficult for researchers to access the information needed to develop and apply quantitative methods to inform managers across institutions.

4. Costs in systematic conservation planning

The problem of identifying effective solutions for the management of invasive species is difficult. In large part, this has been because managers do not give explicit consideration to the costs associated with carrying out management actions, and often do not have access to methods that can identify cost effective solutions or trade-offs between potential solutions to a problem (Buckley 2008). Therefore, the methods developed under the field of systematic conservation planning can offer a solution to complex problems related to resource allocation for invasive species management. A major advantage of systematic approaches is that complementarity-based planning is able to minimize costs of management. However, to date, there have been no examples of freshwater systematic conservation plans that have accounted for the costs of carrying out different types of management, but the field would greatly benefit from such examples (Ban et al. in press).

This thesis addresses these issues in a series of case studies in the Wet Tropics of north-eastern Queensland, Australia. I selected the Wet Tropics as a study area because it is a discrete bioregion for which a substantial amount of relevant data exists. Bioregions are large, geographically distinct areas of land with common characteristics such as geology, landform patterns, climate, ecological features and plant and animal communities. The Wet Tropics bioregion is recognised for its high biodiversity values for which extensive samples of terrestrial ecosystems have been placed under World Heritage listing (UNESCO 1972). It is a region of high freshwater biodiversity (Connolly et al. 2008; Pusey et al. 2008) and is particularly useful for asking questions about conservation and the effectiveness of management for fresh waters because, firstly, there is a substantial knowledge about freshwater biota; and, secondly, while an extensive area of land is under protection, there remain a number of human-induced disturbances that threaten the ecological integrity of freshwater ecosystems in this region.

The Wet Tropics bioregion

The Queensland Wet Tropics bioregion, like other wet tropical regions, has high levels of species diversity across many taxa. It also has very high levels of endemism, reflecting the long isolation of the Australian continent. The region provides habitat for a number of rare and threatened species, including several endemic freshwater fish and invertebrate species (Connolly et al. 2008). This region has high rainfall, concentrated in the summer wet season, but occurring all year round, resulting in perennial streams. Sustained over millions of years, perennial flows have contributed to the development of the unique freshwater fauna of the region (Pearson et al. 1986; Pusey & Kennard 1996).

The Wet Tropics World Heritage Area (WTWHA) was listed on the basis of four criteria: 1) outstanding in its representation of major stages of the Earth’s evolutionary history; 2) representing examples of significant geological processes, biological evolution and ongoing processes in the development of communities of plants, animals, landforms, marine and freshwater areas; 3) containing superlative natural phenomena and combinations of natural and cultural elements; and 4) having the most important and significant natural habitats where threatened species of animals or plants of outstanding values from the point of view of science or conservation still survive (World Heritage Committee 1984). The primary goal of WTWHA management is to fulfil Australia's international duty to protect, conserve, present and rehabilitate the area for future generations (Clarke 2008). The Wet Tropics Conservation Strategy was developed by the Wet Tropics Management Authority (WTMA) to promote coordinated conservation of the Wet Tropics and its World Heritage Area. Management of the WHA and its surrounds involves cross-jurisdictional partnerships between the Australian Government, Queensland State Government, local and regional governments, non-government natural resource-management bodies, Indigenous groups, landholders and the broader community. There is a range of spatial (e.g. protected areas) and non-spatial (e.g. protection of species by legislation) strategies employed by the various agencies to mitigate the impacts of anthropogenic activities on the ecosystems of the WTWHA. For example, "Terrain," the region's natural resource management body, is responsible for monitoring and evaluating resource condition across the region (Dale et al. 2008).

Adjacent to the WTWHA is the Great Barrier Reef World Heritage Area (GBRWHA) which is a complex and diverse collection of tropical marine ecosystems of global significance for their environmental, cultural, social and economic values. Anthropogenic activities that occur in the Wet Tropics bioregion can threaten the values of the GBRWHA, particularly through the input of contaminants transported through streams and rivers. In addition to the range of strategies employed to mitigate impacts to the WTWHA, there are a number of initiatives directed at the mitigation of threats that flow downstream into the GBRWHA. Similar to the WTWHA, the GBRWHA has a multitude of government and non-government agencies responsible for mitigating threats both within the GBRWHA boundaries and in adjacent catchments.

While there are a number of agencies managing, monitoring and evaluating the condition of both the terrestrial and marine ecosystems in the Wet Tropics, there has been little direct consideration of the human-induced disturbances influencing the condition or protection of freshwater ecosystems in the region. The majority of strategies put into place have been to mitigate the impact of land-based activities on marine ecosystems. The case of the Wet Tropics is not unusual across the globe. Fresh waters have been given little consideration in terms of habitat and species protection or mitigation of human-induced disturbances that make these ecosystems so vulnerable (Abell et al. 2007). The urgent need to protect freshwater biodiversity worldwide means that there needs to be prioritisation of areas for conservation action (Linke et al. 2011). There is no single Australian river system that is fully protected by the existing national reserve system, nor does the Ramsar Convention afford protection to many of Australia's most significant wetlands (McComb & Lake 1990).While the WTWHA and GBRWHA offer critically important protection of globally significant terrestrial and marine ecosystems, there is a need for greater consideration of the conservation of fresh waters and dependent species in the Wet Tropics.

Thesis aim and objectives

The overall aim of this thesis is to advance the scientific basis and application of systematic approaches for the conservation of fresh waters. To achieve this aim, and using the Wet Tropics as a case study, I addressed the following objectives:

1) Determine where in the Wet Tropics disturbance to fresh waters occurs, where incidental protection is afforded through terrestrial protected areas, and the extent to which this protection occurs;

2) Identify the effectiveness of using coarse-filter surrogates for representing freshwater fish diversity in systematic conservation planning;

3) Develop methods to evaluate the effectiveness of invasive species management; and

4) Integrate management costs into systematic conservation planning for invasive species.

To achieve these objectives, I carried out four case studies.

Objective 1: Determine the occurrence of disturbances, and the incidental protection of fresh waters in terrestrial protected areas

It is particularly important and informative to identify the occurrence, and to quantify the number of, human-induced disturbances encroaching upon the persistence of freshwater ecosystems and species occurring both within and outside protected areas (Paukert et al. 2011). This is particularly true in highly productive landscapes where land uses such as agriculture and grazing occupy a large part of the landscape, as is the case in the Wet Tropics.

Given the connected nature of fresh waters (Bunn & Arthington 2002), assessment of human-induced disturbances requires quantifying the effects on individual stream reaches and wetlands as well as upstream catchment areas that drain into these areas (Abell et al. 2007; Linke et al. 2011). To date, human-induced disturbances adjacent to and upstream of fresh waters have been poorly accounted for in conservation planning. Given that there are very few protected areas set aside specifically for the protection of freshwater habitats, there have been calls to evaluate how well regional terrestrial protected areas are capturing fresh waters and their imperilled biodiversity (Abell et al. 2007). Even so, the effectiveness of incidental protection from terrestrial protected areas for conserving freshwater ecosystems and species remains uncertain (Herbert et al. 2010). Gap analyses offer insights about how well ecosystems and species are represented in protected areas (Scott et al. 1987). To begin the process of identifying how well fresh waters and dependent species are protected in a particular region there is a need for spatial analyses that quantify levels of protection of ecosystems and species. A number of previous assessments have focused solely on quantifying the representation of freshwater ecosystems and species within existing protected areas networks (Keith 2000; Herbert et al. 2010); however, it is commonly recognized in the freshwater conservation planning literature that accounting for the protection afforded by terrestrial protected areas alone does not ensure adequate protection of fresh waters (Nel et al. 2007; Turak et al. 2011b). In Chapter 3 I address these needs by determining the effectiveness of protected areas and quantified the intensity of human-induced disturbances influencing freshwater biodiversity in the Wet Tropics.

Objective 2: Identify the effectiveness of using coarse-filter surrogates for representing freshwater fish diversity in systematic conservation planning.

Identifying the effectiveness of surrogates for freshwater conservation is another critically important step for achieving well-informed conservation decisions. Compared with most tropical regions, information on freshwater ecosystems and species (e.g. fish) is rich in the Wet Tropics. However, given the heavy reliance on surrogates to inform the selection of areas for conservation, it is important to identify how well they can be used to represent habitats and species. This requires information from regions with rich species datasets, where assessments of surrogate effectiveness can be evaluated. These evaluations not only inform local conservation decision makers about the effectiveness of using surrogates, but can also be used to inform the conservation community about the limitations associated with certain types of surrogates. Chapter 4 examines the effectiveness of coarse-filter surrogates for representing freshwater fish diversity.

Objective 3: Develop methods to evaluate the effectiveness of invasive species management.

Identifying the effectiveness of current approaches and determining more cost-effective solutions to aquatic invasive species management are important considerations if freshwater conservation is to be effective. Currently in the Wet Tropics, local governments are responsible for the management and eradication of aquatic invasive species on both public and private lands. On the protected area estate, the Queensland State Government and the Wet Tropics Management Authority are responsible for control of invasive species. Local government organizations are limited by time and funding. To evaluate the effectiveness of their management programs, managers require access to quantitative methods, which are often not easily accessible. Collaborations between managers and researchers can offer opportunities to explore new methods that advance the theory and application of science that may otherwise not be taken up or applied. These opportunities exist in the Wet Tropics because of the long-standing partnerships between the research and end-user communities (Goosem 2008). To date there have been few examples of quantitative methods applied to address questions about invasive species management effectiveness (but see reviews by Stewart et al. 2007 and Tyler et al. 2006). When applied, these methods can provide the evidence to aid decision-making and identify research gaps (Stewart et al. 2007). In Chapter 5, I address this need using the relationship between environmental suitability and abundance of an invasive plant species to quantify management effectiveness over various investment times.

Objective 4: Integrate management costs into systematic conservation planning for invasive species.

It is not feasible for managers to target every human-induced disturbance because of limited funding and other resources. The Australian government has offered some guidance for local governments through the Weeds of National Significance (WONS) framework, which is the first attempt to prioritise weeds over a range of land uses at the national level (WONS 2009). However, for local governments to achieve effective outcomes for aquatic invasive species management, they require strategic deployment of conservation resources. Systematic approaches to invasive species management can assist managers in identifying priority areas that will deliver cost-effective solutions. Of importance to invasive species management, systematic approaches are transparent, requiring explicit quantitative objectives to be set; they account for connectivity between freshwater ecosystems, which is important in mitigating spread or reinfestation; and they explicitly account for costs of undertaking different management actions. Accordingly, I developed a systematic approach to guide invasive species management in the Wet Tropics.

Thesis outline

In this thesis, I use a conceptual framework (Figure 1.1) to illustrate the steps considered when developing a systematic conservation plan for fresh waters. I use this framework to demonstrate the contributions of my research to the advancement of the theory and application of this field. At the start of each chapter I highlight the steps in the conceptual framework to which the chapter relates.

Chapter 2 describes the Wet Tropics study area.

Chapter 3 is a gap analysis that assesses the extent to which freshwater ecosystems and biodiversity are represented within the current protected-area network in the Wet Tropics. In addition, I identify human-induced disturbances to freshwater biodiversity and discuss how the distribution of these disturbances across the landscape should influence future selection of areas for protection or restoration of freshwater ecosystems. This chapter is in review with *PLoS One*.

Chapter 4 investigates whether coarse-filter surrogate classification methods, commonly used in freshwater systematic conservation planning and bioassessment, represent fish biodiversity at a regional scale. The assessment was carried out on an available fish database for the Wet Tropics I used presence/absence records from this database to model two biotic classifications, and used abiotic data (e.g. rainfall, stream length) to model one abiotic classification. I used all three classification methods to derive classes that I used as coarse-filter surrogates, and modelled fish distributions using the same presence/absence data, as a means for quantifying surrogate effectiveness. This chapter is in press in *Biological Conservation*.

Chapter 5 models the relationship between environmental suitability and the upper limit of olive hymenachne (*Hymenachne amplexicaulis*) abundance using ecological niche modelling and linear quantile regression. This relationship is used to quantify the effectiveness (reduction in local abundance) of different management investments (varying lengths of time) for reducing local olive hymenachne abundance. This chapter is in press in *Environmental Management*.

Chapter 6 takes a spatially explicit approach to identifying actions to achieve objectives related to invasive species while minimizing management costs and the likelihood of reinvasion. The approach is applied to a real-world management scenario, aimed at reducing the adverse effects of an invasive macrophyte, olive hymenachne (*Hymenachne amplexicaulis*) in the Tully-Murray catchment in the Wet Tropics. This chapter has been published in *Biological Invasions*.

Chapter 7 provides a synthesis of the research outcomes and the conservation priorities in the Wet Tropics. I then discuss future research directions for freshwater systematic conservation planning, and discuss how systematic approaches to conservation can be applied to prioritize restoration actions at a regional scale. I conclude by discussing how my research and regional conservation priorities identified for the Wet Tropics align with those broader priorities for conserving fresh waters globally.

Chapter 2 The Wet Tropics study area

The Wet Tropics study area (from here on the Wet Tropics) is a unique region within Australia (Figure 2.1). It is characterized by monsoonal rainfall, dense rainforests and a narrow coastal plain. The Wet Tropics has the highest average annual rainfall in Australia as a consequence of the summer monsoon and mountain ranges that run perpendicular to prevailing south-east trade winds (Stork et al. 2008). Numerous perennial streams flow from these ranges either directly to the east coast, or to the west, eventually reaching the east coast or the Gulf of Carpentaria (Pusey et al. 2000). Mean annual rainfall ranges from 4000 mm near the coast to 1200 mm at the western extremity. Mean daily temperatures range from 18 to 31°C on the coast and from 9 to 28°C in the uplands (Kemp et al. 2007).

Stream flows of the Wet Tropics are predictable, with relatively low monthly variation (Pusey & Kennard 1996). There are nine catchments exclusively within the bioregion (from north to south they are the Daintree, Mossman, Barron, Mulgrave, Russell, North and South Johnstone, Tully and Murray Rivers); a tenth river, the Herbert, has much of its catchment outside this bioregion, but its southern coastal part is included in the Wet Tropics. All nine catchments enter the Great Barrier Reef lagoon, part of the Great Barrier Reef World Heritage Area, draining a total area of 11 862 km^2. I discuss these systems and their conservation status further in Chapter 3.

Three main freshwater palustrine wetland habitats occur on the Wet Tropics floodplains: 1) remnant lagoons, 2) distributaries, and 3) swamps, both permanent and intermittent (Pearson et al. 2010). These habitats are substantially disturbed by land clearing, drainage, irrigation, agricultural chemicals and grazing, which variously affect water quantity and quality, and associated ecology (Pearson et al. 2010). In addition, there are estuaries and brackish wetlands which in the Wet Tropics receive continuous freshwater inputs, sustaining salinity gradients that are typical of estuaries in much of the world. During wet-season high flows the entire river to its mouth can be fresh water. The upper intertidal area is covered in mangroves right through to the rainforest (Sheaves et al. 2010). There are over 90 types of wetland ecosystem occurring in the Wet Tropics, of which 82 are endemic (DERM 2009). A number of these endemic wetlands are highly susceptible to grazing, agriculture/horticulture, urban development, weed infestation, drainage alteration and further clearing. For example, a unique wetland regional ecosystem type that comprises fernlands and sedgelands with emergent rainforest species, has less than 10% of its pre-clearing extent remaining, and is listed to occur only within a single protected area, with most of the remnants in very poor condition due to drainage changes and weed invasion (DERM 2009). Using a broad classification, I present an assessment of how well wetland types are protected, and quantify the human-induced disturbances threatening the integrity of these ecosystems in Chapter 3.

Wet Tropics streams and wetlands sustain a unique and diverse freshwater fauna, including species-rich invertebrate communities (Pearson et al. 1986; Walker et al. 1995), distinctive fish fauna with 11 endemic species (Pusey & Kennard 1996; Pusey et al. 2000) and a diverse freshwater-dependent frog fauna (Rowley & Alford 2007). Fish species diversity (>100 species) and endemism are high for Australia and are driven by two factors: the reliable flow tending towards constancy; and a diverse and reliably available array of lotic habitats (Pusey et al. 2004). Some of the Wet Tropics endemics are restricted to single catchments (Unmack 2001; Pusey et al. 2008). The maximum species richness, 50 species, occurs in the Mulgrave, Russell and North and South Johnstone River catchments, with richness declining south in the Tully and Murray River catchments (Pusey et al. 2008). Although the region is known for its diverse and unique fish fauna there has been little effort towards protecting or restoring waterways that support critical habitats for these diverse fauna. The majority of the landscape surrounding critical habitats for freshwater fish has been modified by humans for agricultural, horticultural and grazing production, or for urban development.

The Wet Tropics landscape below 200 m, including substantial areas of the floodplain, is fragmented by human alteration. One of the major impacts on freshwater ecosystems has been the degradation and loss of riparian forests and wetland/floodplain habitats (Pusey et al. 2008), commonly accompanied by invasions from introduced plant species (e.g. olive hymenachne, *Hymenachne amplexicaulis*). Additional alterations to the landscape such as small dams, weirs and culverts are scattered across the Wet Tropics, and abstraction of water for irrigation and urban supply results in altered flow regimes that influence fish movement and wetland connectivity (Pusey et al. 2000; Arthington & Pusey 2003). Beyond these local and regional impacts on freshwater ecosystems and biodiversity there are several climate-related global changes such as rising sea levels, reduced rainfall and reductions in mountain rainforest cloud interception (e.g. McJannet et al. 2007) that are predicted to influence freshwater habitats, stream flows, species diversity, and endemicity (Pusey et al. 2008).

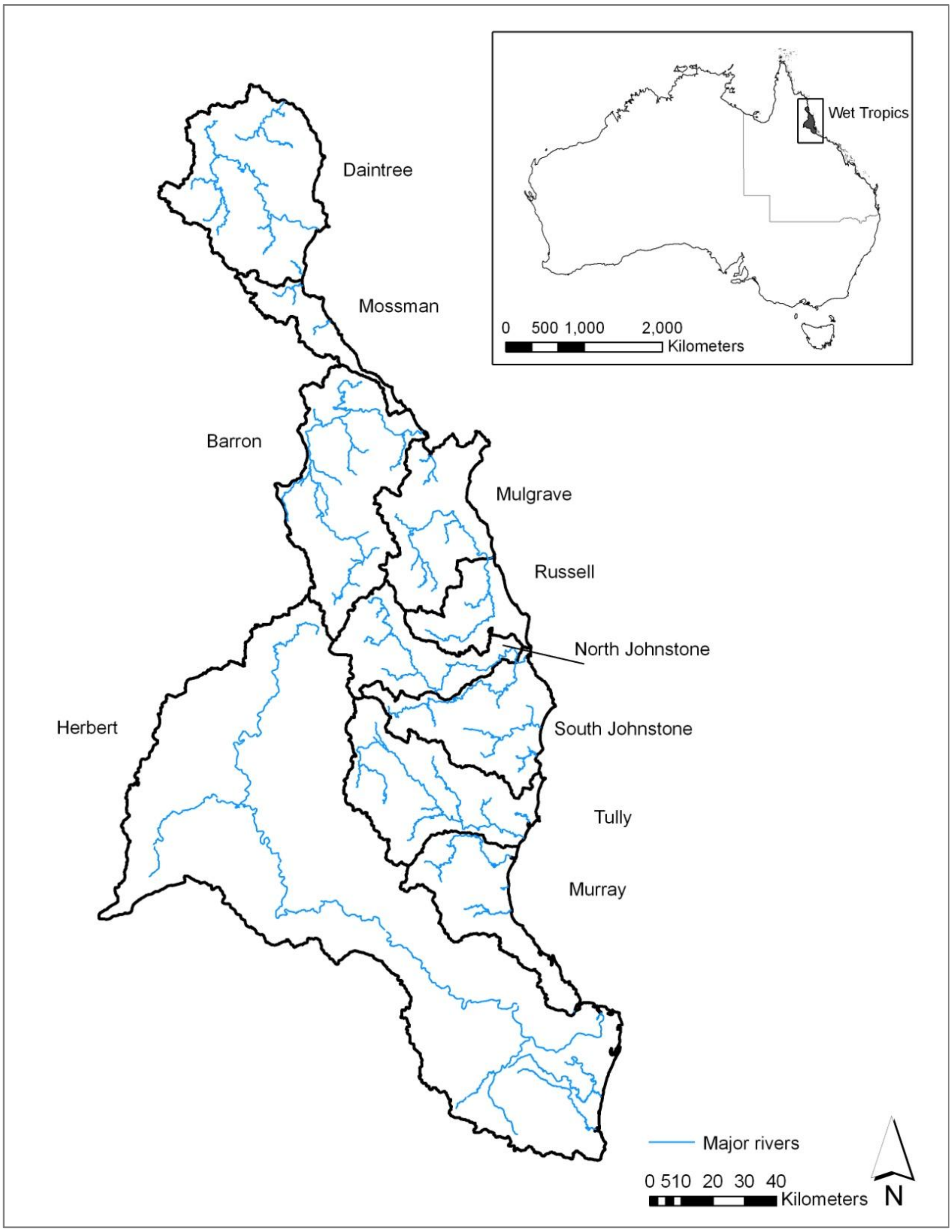


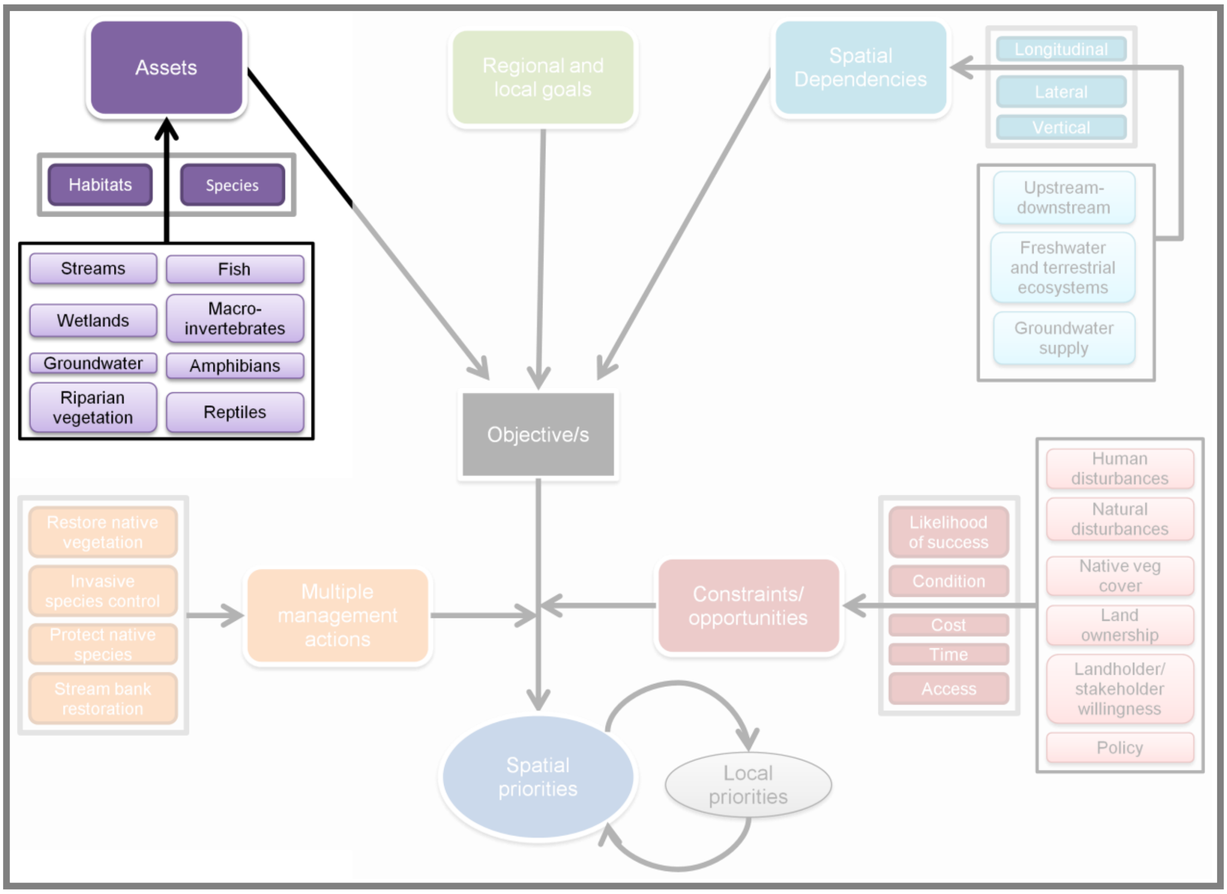
Figure 2.1 The Wet Tropics study area in north-eastern Queensland, Australia, showing the major rivers and their catchments.

Chapter summary

- The Wet Tropics is characterized by monsoonal rainfall, dense rainforests and a narrow coastal plain.
- The Wet Tropics have the highest average annual rainfall in Australia.
- Stream flows of the Wet Tropics are predictable, with relatively low monthly variation.
- The streams and wetlands sustain a unique and diverse freshwater fauna, including species-rich invertebrate communities.
- The majority of the landscape surrounding critical habitats for freshwater fish has been modified by humans, and beyond these local and regional impacts there are several climate-related global changes such as rising sea levels, reduced rainfall and reductions in mountain rainforest cloud interception.

Chapter 3

Freshwater ecosystems and biodiversity: distribution, protection and disturbance in tropical Australia[1]



[1]**Januchowski-Hartley, S. R.**, Pearson, R. G., Puschendorf, R. and Rayner, T. Fresh waters and fish diversity: distribution, protection and disturbance in tropical Australia. *PLoS One*. In press.

Introduction

Fresh waters are the most threatened ecosystems in the world, with high species extinction rates resulting from human dependence on freshwater resources, combined with localized and distant disturbances from upstream drainage networks, and further exacerbated by anthropogenic climate change (Vörösmarty et al. 2010). The poor condition and vulnerability of freshwater ecosystems to human-induced disturbances is further amplified by the poor level of protection afforded to these ecosystems and the species they support (e.g. Keith 2000; Abellán et al. 2007; Nel et al. 2007; Herbert et al. 2010). While protected areas act as a valuable tool in preventing habitat and biodiversity loss (Margules & Pressey 2000), and existing international commitments (CBD 2011) are in place to establish protected area systems that contain viable representations of terrestrial, freshwater and marine ecosystems, freshwater protected areas remain rare (Esselman & Allan 2011).

There have been three reasons given in the freshwater conservation planning literature (e.g. Abell et al. 2007; Nel et al. 2007; Linke et al. 2011) for why these ecosystems have been poorly protected. Firstly, fresh waters are generally only protected incidentally through their incorporation into terrestrial protected areas (Abell et al. 2007; Nel et al. 2007). Secondly, partial inclusion of fresh waters within protected areas does not ensure protection as impacts outside protected area boundaries can have negative consequences (Mancini et al. 2005). Thirdly, the connectedness of freshwater ecosystems has offered unique challenges when it comes to planning and implementing protection (Linke et al. 2011). In regions where there are no freshwater protected areas, these challenges can be addressed through systematic assessments that detail the effectiveness of terrestrial protected areas for representing freshwater ecosystems and biodiversity, and accounting for the limitations of partial inclusion and the connected nature of freshwater ecosystems.

Apart from three studies (Nel et al. 2007; Lawrence et al. 2011; Turak et al. 2011a), previous assessments of freshwater ecosystem representation in terrestrial protected areas (e.g. Abellán et al. 2007; Keith 2000; Herbert et al. 2010) have focused solely on protection *per se*. However, given the interconnected nature of freshwater ecosystems and the limited explicit protection afforded to them, comprehensive evaluations need to take into account the disturbances that might affect them. The identification of disturbances and their proximity to protected areas can further demonstrate the level of effectiveness of terrestrial protected areas for abating threats to freshwater ecosystems and species (Turak et al. 2011a).

This study presents a regional assessment of freshwater ecosystem and fish distribution and protection, and human-induced disturbances to these ecosystems, in the Wet Tropics of north-eastern Australia, a notionally highly protected region. This is the first regional scale assessment of the effectiveness of a terrestrial protected area for freshwater ecosystems and biodiversity at tropical latitudes. This research addresses a large knowledge gap (Wantzen et al. 2006; Boyero et al. 2009; Daam & Van den Brink 2010; Sanchez-Arguello et al. 2010) regarding the mismatch in basing management policies and conservation strategies for tropical streams on research in the temperate zone. To date there have been few studies dealing with the systematic assessment of protection for fresh waters in Australia, with the majority of studies focused in temperate regions (e.g. Linke et al. 2007; Linke et al. 2008; Turak et al. 2011a; Turak et al. 2011b). Apart from the work of Turak et al. (2011a) previous systematic assessments for fresh waters in Australia have either not been focused on protection (e.g. Januchowski-Hartley et al. 2011) or have not given consideration to existing terrestrial protected areas (e.g. Linke et al. 2007; Turak et al. 2011b). Building on the existing network of terrestrial protected areas has been suggested as the most practical approach to improve freshwater ecosystem and species representation in protected areas (e.g. Nel et al. 2007; Nel et al. 2009). These assessments can be used further to guide the selection of additional protected areas to achieve both terrestrial and freshwater conservation objectives (Abell et al. 2007; Nel et al. 2009; Herbert et al. 2010).

I expand on previous assessments of terrestrial protected area effectiveness (e.g. Abellán et al. 2007; Herbert et al. 2010) and disturbances influencing the condition of fresh waters (e.g. Nel et al. 2007) by: 1) including tributaries as well as main river systems in my analysis; 2) accounting for freshwater ecosystems and fish species' (not only rare species) representation in the terrestrial protected area network; 3) assessing the total amount of protection as well as the percent representation of ecosystem length or area, and the distribution of each species, protected entirely within IUCN category II protected areas; and 4) quantifying current adjacent and upstream human-induced disturbances that influence condition of stream reaches and wetlands both within and outside of terrestrial protected areas. I focused on fish species because their taxonomy is well known, they are dependent on stream and wetland ecosystems and because there was sufficient available data to model their current distributions. Protection level of each ecosystem and species was determined for the protected area categories for the State of Queensland and the IUCN, making my results both nationally and internationally relevant. These results are an initial step towards identifying systematic conservation priorities for freshwater ecosystems and biodiversity at a regional scale.

Methods

Stream reaches and wetlands

I compiled available spatial data for freshwater ecosystems in the Wet Tropics, including: stream reaches and wetlands (Figure 3.1a), adjacent sub-catchments, and upstream catchment areas for each stream reach. I derived stream reaches (n = 7210) from a 30 m x 30 m digital elevation model (approximately 1: 100 000 scale mapping) (see Appendix C) using ArcHydro 1.1 (Maidment 2002) in ArcGIS® 9.3 (Environmental Systems Research Institute 2009). I assigned a Strahler stream order to each mapped stream reach using ArcGIS 9.3. For each of the mapped stream reaches (Figure 3.1b) I determined the adjacent sub-catchment and upstream catchment area using ArcHydro 1.1. The wetland types were defined and mapped at a scale of 1: 50 000 by the Queensland Department of Environment and Resource Management (DERM 2009). For subsequent analyses I used four broad wetland types (Appendix A, Table S3.1) as well as sub-catchments where the wetlands occur to summarize adjacent disturbance pressures. I chose this broad classification of wetlands to allow for comparison of my results in other regions in Australia and the tropics. Using ArcGIS 9.3, I determined: 1) the total stream reach length (km) and adjacent sub-catchment area (km^2) for each stream order; 2) the total area (km^2) of the four wetland types; and 3) the total number of occurrences for each of the four wetland types in sub-catchments of each stream order.

Freshwater fish diversity

I used the Northern Australia Freshwater Fish Atlas database (http://www.jcu.edu.au/vhosts/actfr/Projects/FishAtlas/Index.htm), which is based on fish species presence/absence data collected between 1990 and 2009. Sampled stream reaches were well distributed across the Wet Tropics and representative of major catchments, instream habitats (runs, riffles, and pools), and length and width of reaches. From this database I selected species with strong association with fresh waters, including species also found in estuarine and marine systems. I eliminated duplicate records from sub-catchments to model only geographically unique occurrences. I also eliminated records older than 15 years and species with fewer than ten occurrences in the database to ensure adequate prevalence for modelling. The cleaned database contained records for 45 species from 445 of the7210 stream reaches in the nine selected catchments.

I modelled current distributions of the 45 fish species using 17 predictor variables that were available for all 7210 stream reaches (Table 3.1), including nine physical variables, four land-use variables and presence/absence of three invasive aquatic plants. The variables were attributed to stream reaches, adjacent sub-catchments, or upstream sub-catchments flowing into stream reaches using ArcGIS 9.3 and ArcHydro 1.1. I considered these models to be representative of the 45 species' current distributions as I accounted for potential responses to disturbance as well as to natural gradients (Hermoso et al. 2011a). Therefore, species should only be predicted with high probabilities of occurrence in stream reaches that were in good condition or where the disturbances included in the models did not exceed the species' tolerance levels (Hermoso et al. 2011a).

I determined modelled fish distributions using MARS (multivariate adaptive regression splines). I built a single multi-response MARS model for all 45 species. The model was fitted using code provided by (Elith & Leathwick 2007) for the mixture and flexible discriminant analysis (MDA) library in the R statistical software package, Version 2.10.1 (R Development Core Team 2009). MARS is a method for non-parametric regression modelling, useful for addressing complex non-linear relationships between response and explanatory variables. MARS enables exploration of interactions between predictors and can fit a multi-response model which simultaneously relates variation in the occurrence of all species to the environmental predictors (Elith et al. 2006). Multi-response species models have been shown to best recover overall variation in species composition compared to single-species models (Leathwick et al. 2006), because species that have been better sampled and represented in the dataset can help inform poorly sampled species (Leathwick et al. 2005; Elith & Leathwick 2007). Several researchers have demonstrated the utility of multi-response MARS models for freshwater conservation planning (e.g. Leathwick et al. 2005; Hermoso et al. 2011b)

To validate the predictive model I used the area under the receiver operating characteristic (ROC) curve (AUC) (Fielding & Bell 1997). The ROC addresses false-negative and false-positive predictions, and is quantified by the AUC. An AUC score of 0.5 indicates a model with no discriminatory ability while a score of 1 indicates that presences and absences are perfectly discriminated. A score of 0.60 or greater is generally considered an acceptable threshold for model performance (Fielding & Bell 1997). I used a k-fold cross-validation procedure (Fielding & Bell 1997) to determine the AUC. The cross-validation divided the presence/absence data into 10 random subsets, successively removing a single data point from each subset and refitting the model with the remaining data, before predicting the omitted data and calculating the average AUC across all subsets.

Table 3.1 Environmental variables, human-induced disturbances and their attributed features used for species distribution modelling.

Environmental variable	**Attributed feature**
Stream length (km)	Stream reach
Stream order	Stream reach
Minimum elevation (m)	Stream reach
Maximum elevation (m)	Stream reach
Minimum slope (degrees)	Stream reach
Maximum slope (degrees)	Stream reach
Alluvium cover (%)	Adjacent sub-catchment
Annual rainfall average (mm)	Adjacent sub-catchment, Upstream catchment
Woody foliage cover	Adjacent sub-catchment
Land use and invasive species	
Remnant vegetation cover (km^2)	Adjacent sub-catchment
Urban/residential cover (km^2)	Adjacent sub-catchment
Grazing cover (km^2)	Adjacent sub-catchment
Intensive agriculture/horticulture cover (km^2)	Adjacent sub-catchment
Olive hymenachne (*Hymenachne amplexicaulis*) presence	Adjacent sub-catchment
Pond apple (*Annona glabra*) presence	Adjacent sub-catchment
Salvinia (*Salvinia molesta)* presence	Adjacent sub-catchment

Protected area network

To determine the effectiveness of terrestrial protected areas for representing freshwater ecosystems and fish I used spatial data on the Wet Tropics World Heritage Area and the protected areas of Queensland Estate provided by the Queensland Department of Environment and Resource Management (DERM) (Figure 3.1c). The Queensland government has defined four types of protected areas in the Wet Tropics: National Park, State Forest, Timber Reserve and Forest Reserve, each of which has a separate IUCN protected area management category (DERM 2008). IUCN protected area management categories were developed to provide a basis for international comparison and are assigned according to the primary management objective in the legal definition of each protected area. In the Wet Tropics the IUCN management categories present are: category II, which includes areas managed primarily for ecosystem protection and recreation; category III, which includes areas managed primarily for conservation of specific natural features (both categories II and III are National Parks in the Wet Tropics); and category VI, which is managed primarily for the sustainable use of natural ecosystems (e.g. State Forest, Timber Reserves and Forest Reserves). I used the Queensland Government's protected area listing and the IUCN management categories for subsequent analyses, allowing us to provide informative results for both regional and national decision makers, as well as a means for international comparisons on levels of fresh water protection.

Land use and human-induced disturbances

I represented extant human-induced disturbances using spatial data on land use in 1999, provided by DERM (Witte et al. 2006) and aquatic invasive plants provided by Far North Queensland Regional Organization of Councils (Sydes 2009). All land-use data were mapped at nominal scales of 1:50 000 and 1:100 000 and aquatic invasive plants were mapped at a scale of 1km x 1km. While there have been some changes in land use in the Wet Tropics Region since 1999, they have not been substantial.

I designated seven land-use categories: 1) protected areas (as defined above), 2) remnant native vegetation that is not protected, 3) low disturbance uses (energy, power lines), 4) localized disturbances (mining, wastewater treatment, industry) which occupy < 1% of the landscape, 5) urban/residential, 6) grazing, and 7) intensive agriculture or horticulture. I excluded waterways as a land use for the assessment, so all area-based calculations of land use were based on a total area of 11 618 km^2. For subsequent analyses I considered urban/residential, grazing and intensive agriculture or horticulture land uses as human-induced disturbances as these land uses dominate the Wet Tropics landscape (Figure 3.1d). Because of the very small area occupied by the low and localized disturbances land-use types I omitted them from subsequent analyses.

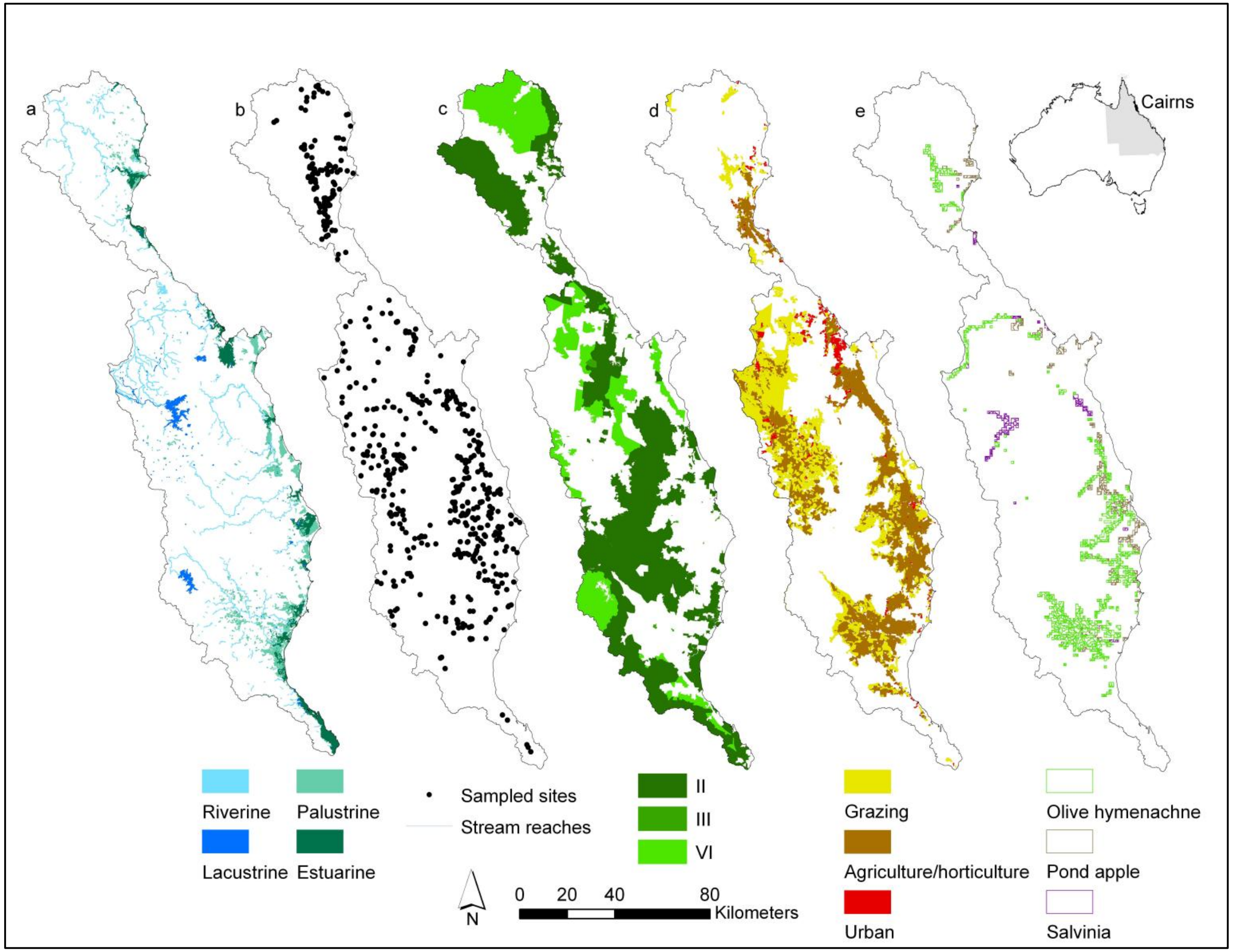


Figure 3.1 The Wet Tropics study area in north Queensland, Australia, showing the spatial distribution of: a) wetland types; b) stream reaches sampled for fish; c) IUCN protected area categories; d) land uses and e) aquatic invasive species.

Spatial data were available for three invasive macrophyte species that are known to have severe impacts on freshwater ecosystems across northern Australia: olive hymenachne (*Hymenachne amplexicaulis*), pond apple (*Annona glabra*) and salvinia (*Salvinia molesta*) (Figure 3.1e). I used existing mapped 1km x 1km grids of olive hymenachne, pond apple and salvinia presence based on existing data and information from an expert workshop held by Far North Queensland Regional Organization of Councils (Sydes 2009). I then attributed presence/absence of olive hymenachne, pond apple and salvinia to each of the adjacent sub-catchments for analyses.

Protection

I quantified the total stream length of each stream order and the area of the four wetland types protected in each of the IUCN categories II, III, and VI. I was particularly interested in determining the degree to which adjacent sub-catchments, wetland types and fish species were represented under IUCN category II, as this is the highest level of protection afforded to any terrestrial area in the Wet Tropics. I determined the percent of total adjacent sub-catchment and wetland area fully within an IUCN category II protected area (i.e., the entire sub-catchment and wetland area were protected). I then determined the percent of the distribution of the 45 fish species in the Wet Tropics that is represented in IUCN category II protected areas. As a benchmark, I evaluated how many ecosystems and fish species had at least 20% of their total area, length or distribution within the Wet Tropics represented within a protected area. While useful for comparisons, it is important to note that the use of a uniform percentage target gives equal importance to all ecosystems and species.

Quantifying human-induced disturbances

For each stream order I determined the percent of total adjacent sub-catchment area occupied by the seven land uses. To quantify the number of human-induced disturbances influencing freshwater ecosystems and species, I determined: 1) the percent of total adjacent sub-catchments (n= 7210) where olive hymenachne, pond apple and salvinia infestations are present; 2) the percent of total adjacent sub-catchments with 0, 1, 2, 3, 4, 5 or 6 of the human-induced disturbances present (urban/residential areas, grazing, intensive agriculture or horticulture, presence of olive hymenachne, pond apple or salvinia); and 3) the percent of adjacent sub-catchments, where the four wetland types occur, with 0, 1, 2, 3, 4, 5 or 6 of the prominent disturbances. Finally, I established the total stream reach length, adjacent sub-catchment area and number of stream reaches upstream of any protected area, irrespective of the protection level, with each level (0-6) of the human-induced disturbances present.

Results

The stream network derived from the 30 m x 30 m digital elevation model resulted in six stream orders (Appendix A, Figure S3.1). Palustrine and estuarine wetlands are distributed within the floodplains and coastal areas, while the lacustrine wetlands are distributed in the uplands (Figure 3.1a). Sub-catchments adjacent to streams in order 1 occupy the greatest area (7498 km^2), while those adjacent to stream order 6 occupy the least area (40 km^2) (Figure 3.2a). Estuarine wetlands occupy the greatest total wetland area (263 km^2); lacustrine wetlands, the least (2 km^2) (Figure 3.2b). Sub-catchments adjacent to order 1 streams support the greatest area of estuarine, lacustrine and palustrine wetlands (Figure 3.2c). The greatest area of riverine wetlands occurs in sub-catchments adjacent to stream order 5 (35 km^2) and 4 (28 km^2).

The average AUC (the area under the receiver operating characteristic (ROC) curve) value across all fish species predictions was 0.84. More than 85% of the 45 fish species had AUC > 0.75 (Appendix A, Table S3.2), indicating that the MARS model had strong discriminatory power. The maximum number of fish species predicted to occur in any one stream reach was 21; the minimum was 2. Areas of high fish species richness occur in stream orders 5 and 6 on the coastal plains (Appendix A, Figure S3.1).

The greatest stream reach length and wetland area is protected under IUCN category II, National Parks (Table 3.2). Streams in order 1 have the greatest length protected (2537 km = 25%), while streams in order 6 have less than 1% of the total reach length protected (Figure 3.2d). All four wetland types have the greatest area within IUCN category II (223km^2 = 36%) (Figure 3.2e). Palustrine wetlands have the greatest area within IUCN category II protected areas (104 km^2 = 91%). Less than 1 km^2 of estuarine and lacustrine wetlands is protected in categories III or VI, and less than 1 km^2 of riverine wetlands is within IUCN category III (Figure 3.2e).

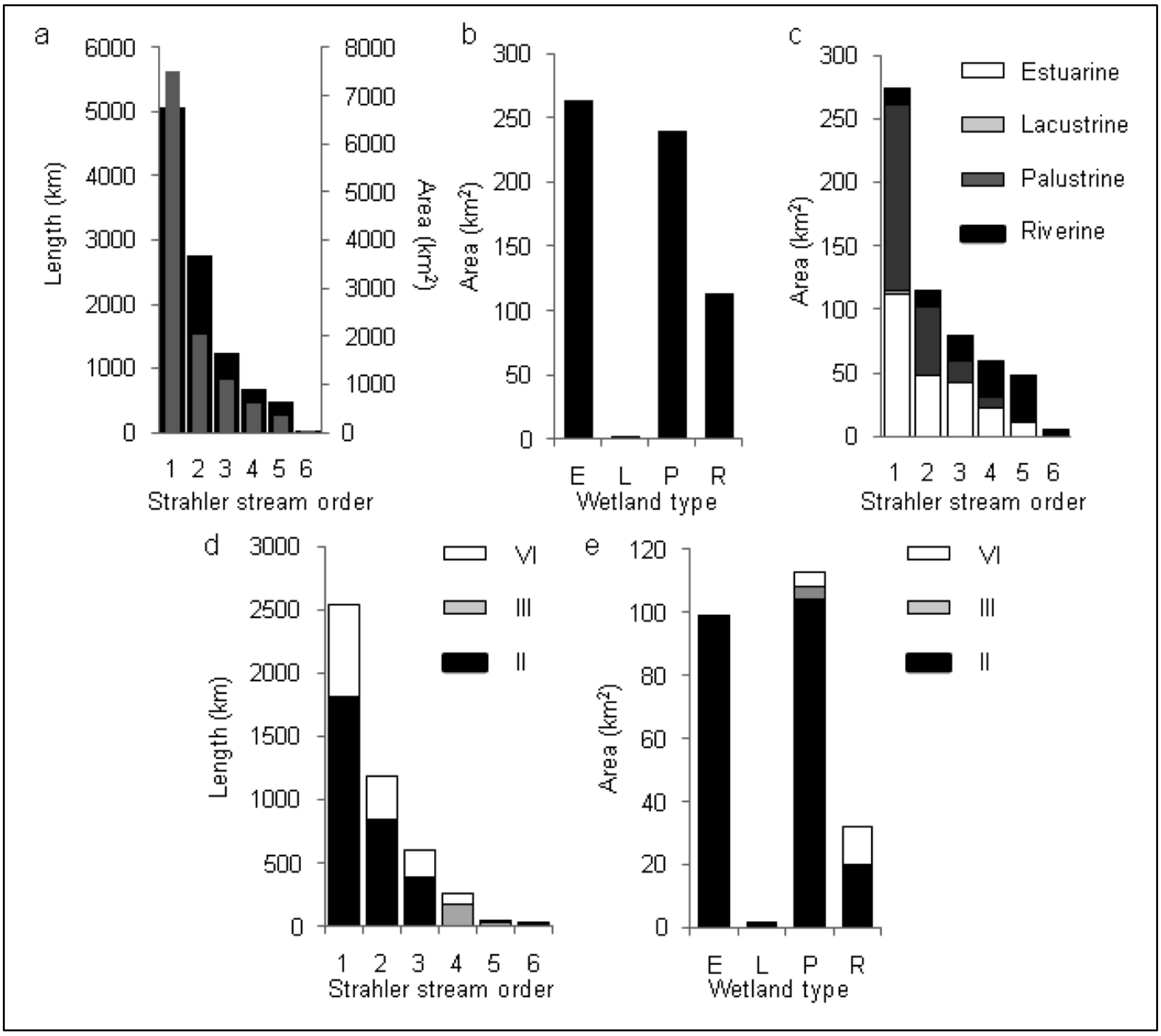


Figure 3.2 Statistics for stream reaches, sub-catchments and wetlands in the Wet Tropics. a) Length (grey bars) and area (black bars) of each Strahler stream order and adjacent sub-catchment; b) area of each wetland type; c) area of the four wetland types in adjacent sub-catchments for each Strahler stream order; d) length of each Strahler stream order, with IUCN categories indicated; and e) area of each wetland type represented within IUCN categories II, III and VI.

Only streams in order 2 achieved the minimum target of 20% representation in the IUCN category II protected areas (23%) (Figure 3.3a). Approximately two percent of sub-catchments adjacent to streams in order 6 are fully within an IUCN category II protected area (Figure 3.3a). Only lacustrine wetlands have greater than 20% of the total wetland area fully within an IUCN category II protected area (Figure 3.3b). Five of the 45 modelled fish species have at least 20% of their distribution represented within IUCN category II protected areas (Figure 3.3a). Twenty species have less than 10% of their distribution represented, while the remaining 20 have between 10 and 19% of their distribution represented in IUCN category II protected areas. None of the endemic fish species included in our analysis have better than 15% of their Wet Tropics distribution in IUCN category II protected areas (Figure 3.3a).

Table 3.2 The total stream reach length (km) and wetland area (km^2) protected in IUCN protected area management categories (IUCN category) and the State of Queensland's protected area classification in the Wet Tropics.

IUCN category	Queensland protected area	Length	Area
II	National Park	3250	223
III	National Park	19	4
VI	Forest Reserve	366	4
	State Forest	440	7
	Timber Reserve	562	6

More than 50% of sub-catchments adjacent to streams in orders 1-3 are protected. Adjacent sub-catchments of order 5stream reaches have the lowest percent area (27%) protected (Figure 3.4a). Sub-catchments adjacent to streams in order 5 have the highest percent area (48%) that is grazing or intensive agriculture or horticulture, while sub-catchments adjacent to streams in order 6 have the highest percent area that is urban/residential (10%) (Figure 4a). The highest percent of adjacent sub-catchments with weed infestations (olive hymenachne, pond apple, or salvinia) are of stream reaches in order 6 (Figure 3.4b).

There is a maximum of four human-induced disturbances found in any single sub-catchment. Stream order 5 has the highest percent (4%) of sub-catchments with four human-induced disturbances. Stream order 6 has the highest percent (38%) of adjacent sub-catchments with three human-induced disturbances (Figure 3.5a). Only sub-catchments supporting palustrine wetlands have four human-induced disturbances; these sub-catchments also have the highest percent (46%) occupied by one or more disturbances (Figure 3.5b).

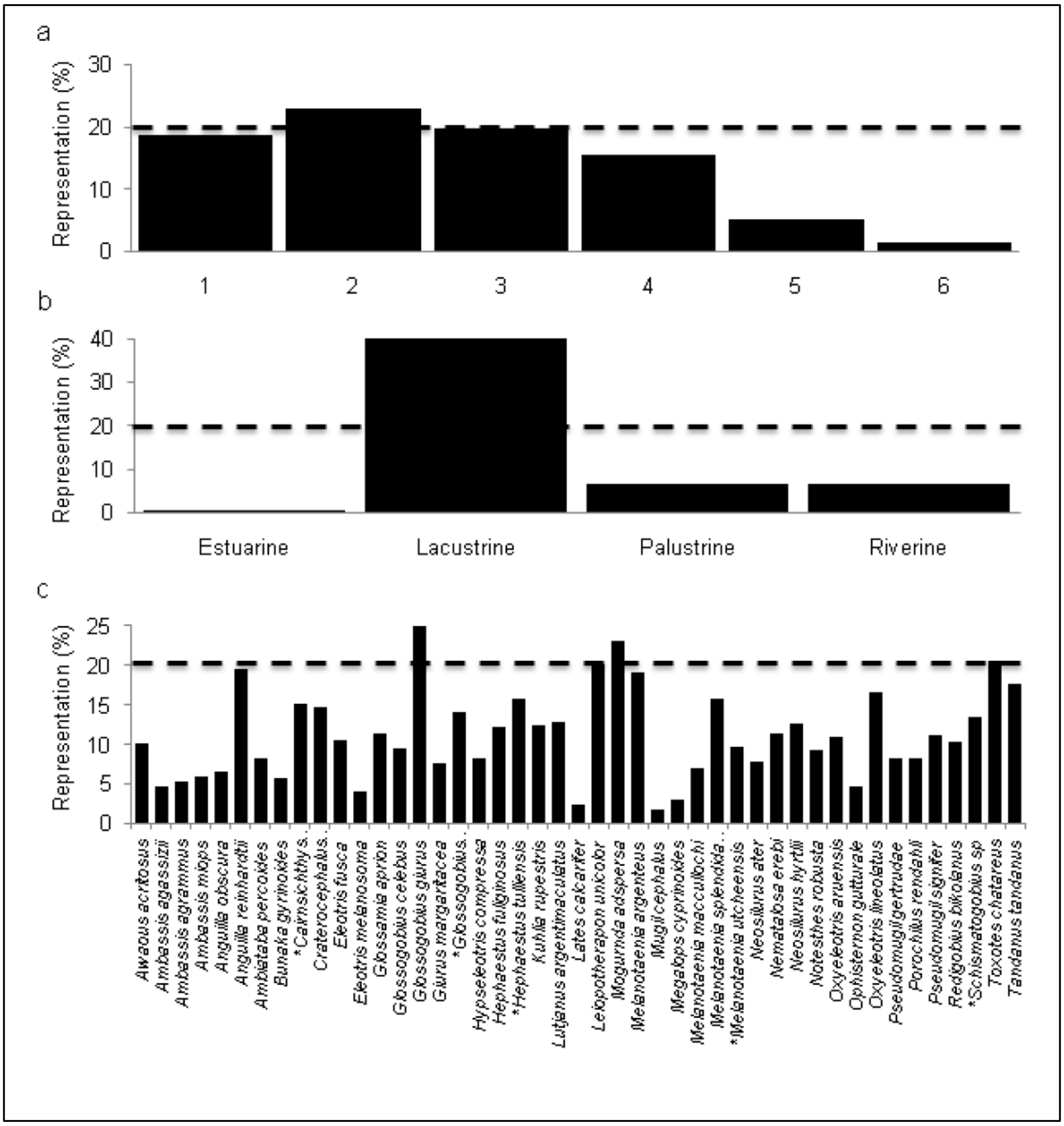


Figure 3.3 The percent representation of: a) sub-catchment area adjacent to streams in Strahler stream orders 1-6; b) wetland types; and c) each fish species distribution occurring completely within an IUCN category II protected area. * = species that are endemic to the Wet Tropics. The dashed lines indicate 20% representation.

Twelve percent of all stream reaches were modelled as having at least 10 fish species present. Sub-catchments adjacent to streams in order 1 that have at least 10 fish species present also have the highest percent of sub-catchments with no human-induced disturbances (Figure 5c). Nevertheless, those sub-catchments also have the highest percent with four human-induced disturbances (5%). Stream reaches in order 5 that support at least 10 fish species have the highest percent (90%) of sub-catchments occupied by one or more human-induced disturbance.

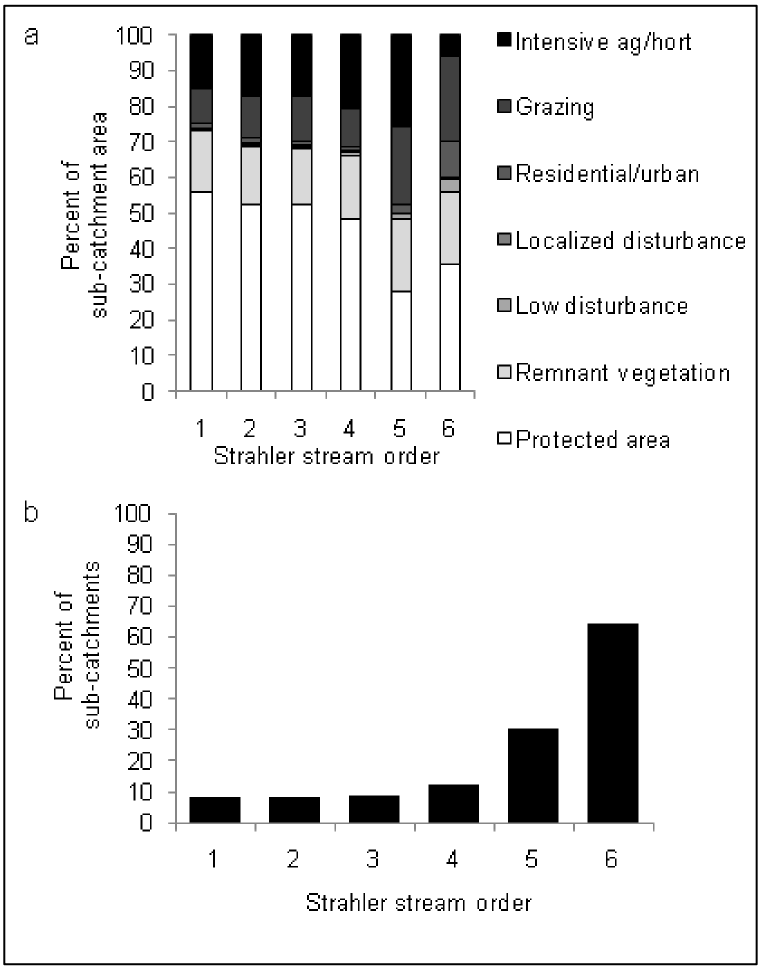


Figure 3.4 The percent of sub-catchment area adjacent to each Strahler stream order 1-6 (listed from bottom to top bars) that is: (a) protected area; unprotected remnant native vegetation; low disturbance; localized disturbances (mining, industry) which occupy a small proportion of the landscape (< 1%); urban/residential; grazing; intensive agriculture/ horticulture; or b) covered with an invasive macrophyte: olive hymenachne (*Hymenachne amplexicaulis*), pond apple (*Annona glabra*) and/or salvinia (*Salvinia molesta*).

Sub-catchments upstream of protected areas have a variable number of human-induced disturbances present (Figure 3.6a). The greatest stream reach length (1518 km), sub-catchment area (1600 km^2) and number of sub-catchments (919) upstream of a protected area have two human-induced disturbances present, while the least length (26 km), area (28 km^2) or number of sub-catchments (11) have four disturbances present (Figure 3.6b,c).

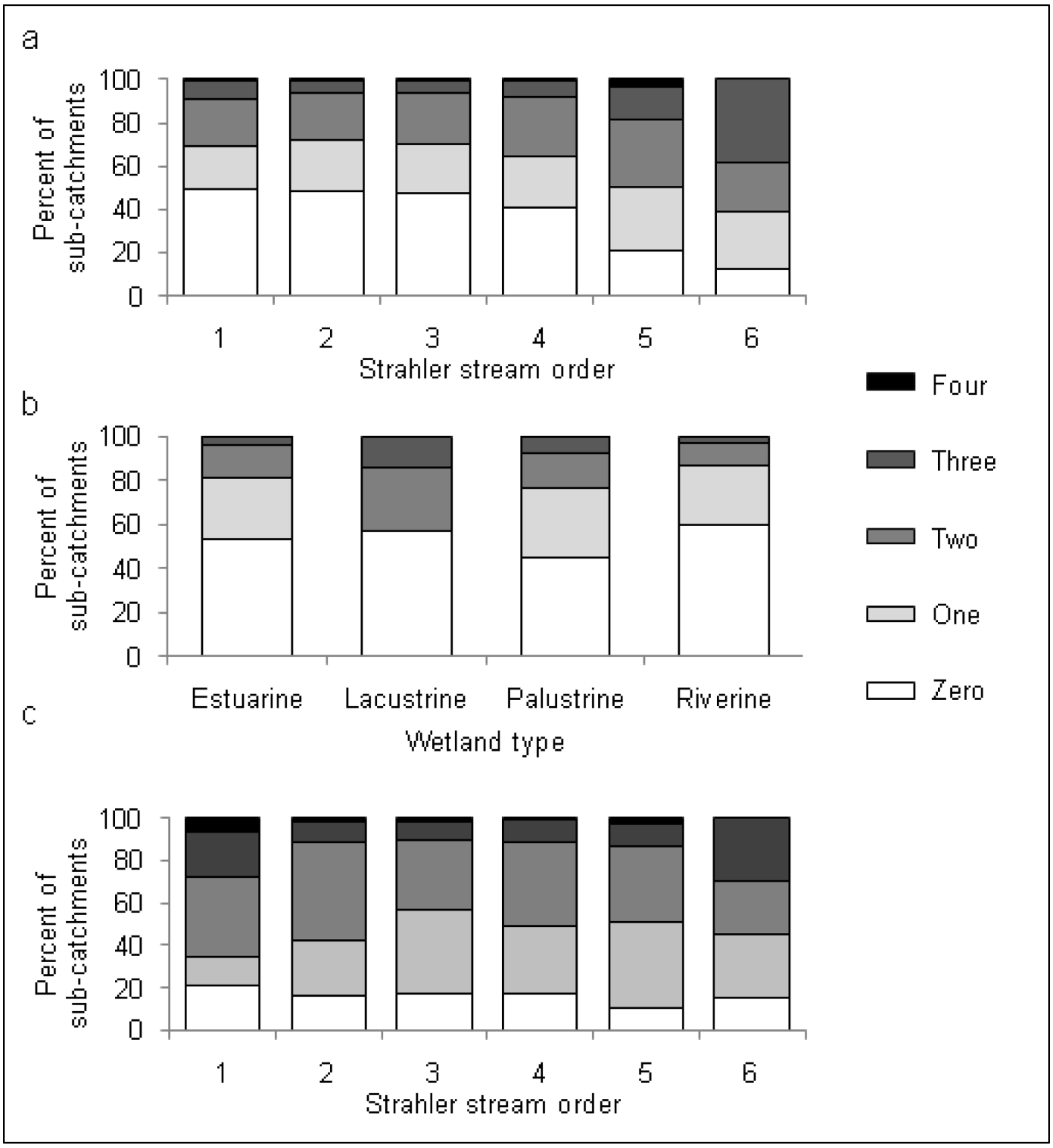


Figure 3.5 The percent of a) sub-catchments adjacent to Strahler stream orders 1-6; b) of sub-catchments supporting each of the four wetland types; and c) sub-catchments adjacent to each Strahler stream order 1-6 that support at least 10 fish species and that have 0, 1, 2, 3 or 4 human-induced disturbances present.

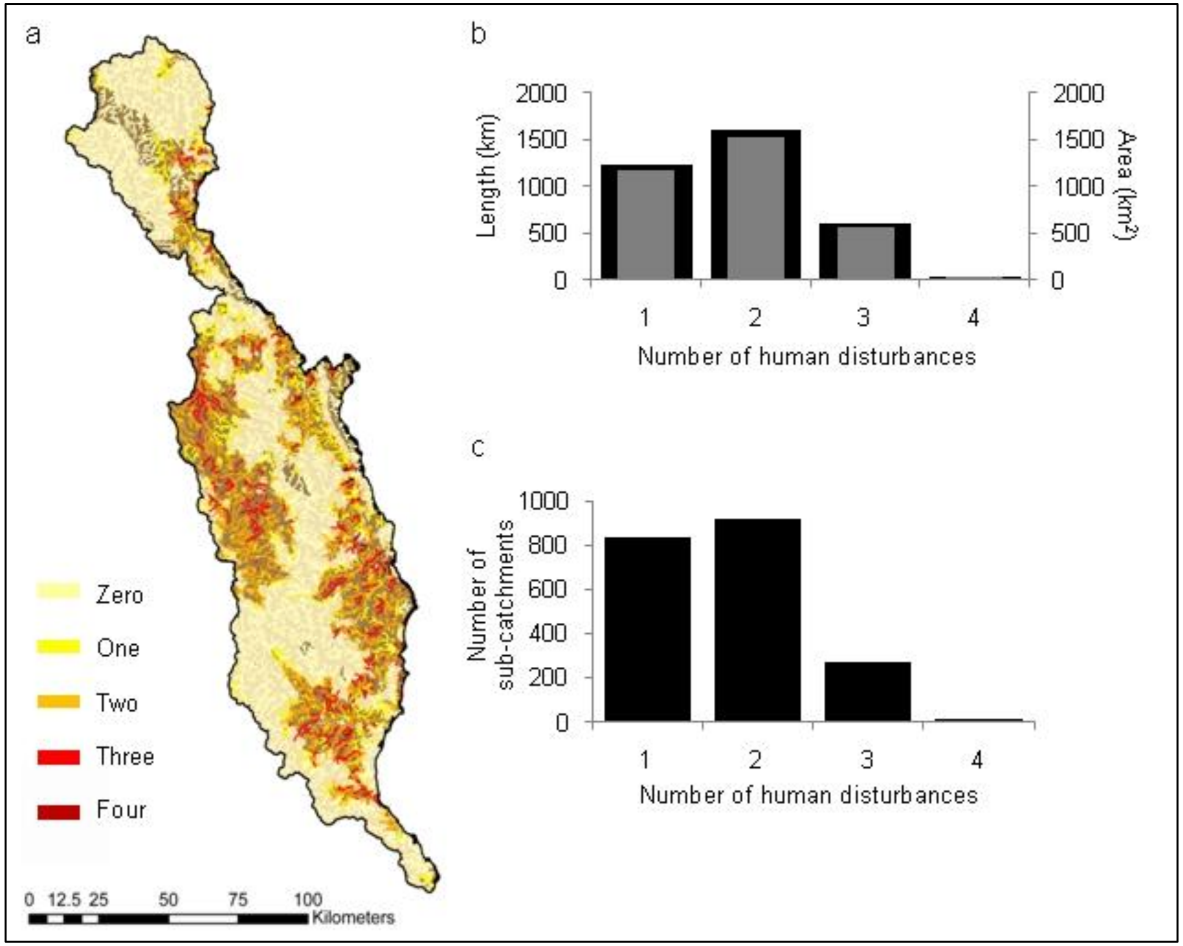


Figure 3.6 The distribution and prevalence of human-induced disturbances upstream of protected areas by: a) the number of stream reaches with 0, 1, 2, 3 or 4 human-induced disturbances; b) the total stream length (grey bars) and sub-catchment area (black bars) with one or more human-induced disturbance; and c) the number of sub-catchments with one or more human-induced disturbance.

Discussion

My evaluation of freshwater ecosystem and biodiversity representation in terrestrial protected areas, and of the number of human-induced disturbances occurring adjacent to and upstream of fresh waters and protected areas demonstrates that: 1) terrestrial protected areas do not afford effective protection to freshwater ecosystems and fish species; 2) higher-order streams and their associated wetlands are influenced by the greatest number of human-induced disturbances and are also the least protected; and 3) terrestrial protected areas are subjected to a variable number of human-induced disturbances from upstream sub-catchments.

My results reflect global trends of the state of freshwater ecosystems and biodiversity (e.g. Dudgeon et al. 2006; Vörösmarty et al. 2010), despite the high proportion of protected land area in the Wet Tropics. The poor protection of freshwater ecosystems in the Wet Tropics warrants attention with regard to policy, biodiversity planning and implementation of conservation actions.

Planning for the conservation of fresh waters and their dependent species requires whole-of-catchment (or sub-catchment) consideration of connectivity and disturbances and simple place-based protection is inadequate. This approach is a first step for identifying streams and wetlands that lie entirely within a protected area and that may act as a starting point for further protection or restoration.

Globally, there has been very little emphasis on proclaiming protected areas for the primary purpose of conserving freshwater ecosystems (Abell et al. 2007; Nel et al. 2007). It is therefore not surprising that my results demonstrate the inadequate representation of sub-catchments, wetlands and fish species. As in temperate regions of Australia (Turak et al. 2011a) the majority of protection afforded to stream reaches and wetlands in the Wet Tropics is restricted to upland, mountainous areas. For example, lacustrine wetlands are the only wetland type with greater than 20% of its total area in the Wet Tropics represented completely in IUCN category II protected areas, but are likely to have been protected by default given their iconic nature (they comprise mainly isolated crater lakes).

Furthermore, inclusion in protected areas does not guarantee conservation. While almost all of the palustrine wetlands listed under IUCN category II protection in the Wet Tropics are listed as endangered, their protection is highly fragmented. Only 7% of the total area of these wetlands lies completely within an IUCN category II protected area. In addition, palustrine wetlands lying in the floodplains of most catchments of the Wet Tropics have historically been filled or have had riparian vegetation heavily cleared for agriculture (e.g. sugar cane).

Many of the palustrine wetlands are or were endemic to the region, and, those remaining in the landscape are highly endangered, and as I have demonstrated, susceptible to landscape alterations and weed infestations (DERM 2009). Specifically, palustrine and estuarine wetlands are of particular interest to the international conservation community as they are important for freshwater biodiversity and ecosystem services, and are the types of aquatic ecosystems highlighted as priorities for protection as a result of the Convention on Biodiversity 10th Conference of the Parties in 2010 (CBD 2011). Given that IUCN category II protected areas afford the greatest level and area of protection to wetlands in the Wet Tropics there is clearly a need for greater conservation action to protect, restore and maintain ecosystem functioning of these wetlands in the region. This would not only meet international conservation targets, but also ensure conservation of critical habitats that support a number of endemic and range-restricted species in the Wet Tropics itself.

Fish species are poorly represented in the Wet Tropics protected area network as has been noted in previous assessments of protection gaps for freshwater fish (see Keith 2000; Herbert et al. 2010). Protected areas primarily occur in areas of higher elevation, while most freshwater fish species occur only in the lowlands. None of the endemic fish species I modelled have 20% of their Wet Tropics distribution within an IUCN category II protected areas. This is a major concern not only for the endemic and rare species that I was able to model, but especially for those species that I could not model, because of their rarity or restricted distribution in the Wet Tropics. The rarity and endemicity of many fish species in the Wet Tropics may warrant greater conservation action than at present. Many fish species could be at high risk because their prime habitat is in the poorly protected floodplain and coastal waterways.

My results concur with others (Nel et al. 2007; Turak et al. 2011a) in demonstrating that the six human-induced disturbances I evaluated increase the vulnerability of freshwater ecosystems and fish species both within and outside of protected areas in the Wet Tropics. I demonstrate that fresh waters within protected areas of the Wet Tropics are especially vulnerable to exogenous disturbances. For example, my results show that 3 288 km (32%) of stream reach length upstream of protected areas have at least one human-induced disturbance present. The continuous nature of freshwater ecosystems makes them particularly susceptible to external disturbances even if portions of a stream reach or wetland are protected (Nel et al. 2007; Linke et al. 2011). Therefore, while some stream orders have more protection than others, the distribution of protection does not necessarily reduce threats to these ecosystems, or to the species they support.

Management implications

The inadequacy of the Wet Tropics protected-area network in representing important freshwater ecosystems and species underscores the need for freshwater-specific conservation. The terrestrial protected area includes a large proportion of the Wet Tropics (approximately 60%), yet its spatial distribution is far from optimal in providing adequate coverage of freshwater ecosystems and species, especially endemics.

A major challenge to quantifying the effectiveness of protected areas for representing species is the lack of data available. Not unlike other tropical regions that support most of the world's species (Dudgeon et al. 2006; Boyero et al. 2009), the information on freshwater biodiversity is incomplete in the Wet Tropics. I was able to account for the effectiveness of terrestrial protected areas for representing many freshwater fish species as data were available; however, data are inadequate for other taxa, such as many invertebrate groups, frogs, reptiles and birds that are also reliant on these ecosystems but whose distributions across catchments differ markedly from those of most fishes. Thus it is likely that the protected area network is effective at protecting species of invertebrates that are reliant on the headwater streams, which are better protected than most other freshwater ecosystems. Given the differences in distribution and habitat dependence of different taxa, regional assessments of the effectiveness of protected areas for the full complement of taxa would be beneficial as it is unlikely that any one taxon can act as a surrogate for the whole biota.

Although the existing protected area network in the Wet Tropics does not include broad representation of freshwater ecosystems, the current network can provide starting points to establish further protection or to link existing undisturbed areas with other critical areas through restoration. Protection of an entire catchment may be preferred from a conservation standpoint, but this is rarely feasible given the multiple demands on resources that catchments and freshwater ecosystems experience (Saunders et al. 2002; Abell et al. 2007). Consequently, there is a need for off-reserve management of fresh waters on both public and private lands. Given that resources for management are typically limited, an important first step is to identify freshwater ecosystems and species that are particularly vulnerable to local and upstream/downstream disturbances (Linke et al. 2007; Nel et al. 2007).

Following the terminology and approaches proposed by Abell et al. (2007) I suggest the need for a combination of place-based and whole-of-catchment management strategies to ensure functional aquatic ecosystems in the Wet Tropics and comparable regions. Firstly, systematic approaches would be used to identify place-based focal areas that complement existing protected areas, but that could be set aside for specific freshwater ecosystems or species that require protection. Secondly, I suggest identifying critical management zones that complement and assist in maintaining functionality of identified focal areas, such as riparian zones where restoration of riparian vegetation and control of invasive species are being undertaken. Finally, I suggest the need to adopt catchment management zones for entire catchments upstream of critical management areas. Catchment management zones would also be a positive alternative to 'locking up' additional areas in formal protection, and would allow for productive lands to be utilized under best-management principles allowing for multiple uses and maintenance of ecosystem services.

There is a pressing need to consider the threat of global changes that are hard to plan for or manage. For example, in the Wet Tropics, rising sea levels are likely to reduce the extent of higher-order streams, which support the greatest diversity of fish. Changes in rainfall and cloud interception are likely to lead to increased variability of discharge, and reduced dry-season discharge, particularly in upland streams (McJannet et al. 2007) and resultant changes in habitat are likely to negatively affect many endemic species, particularly riffle specialists among the invertebrates (Pearson 2005), fish (Pusey et al. 2008) and frogs (Rowley & Alford 2007). Holistic approaches to conservation that consider both place-based protection and whole-of-catchment management would provide a better buffer than place-based protection alone, encouraging ecosystem and species persistence under current pressures and anticipated global change.

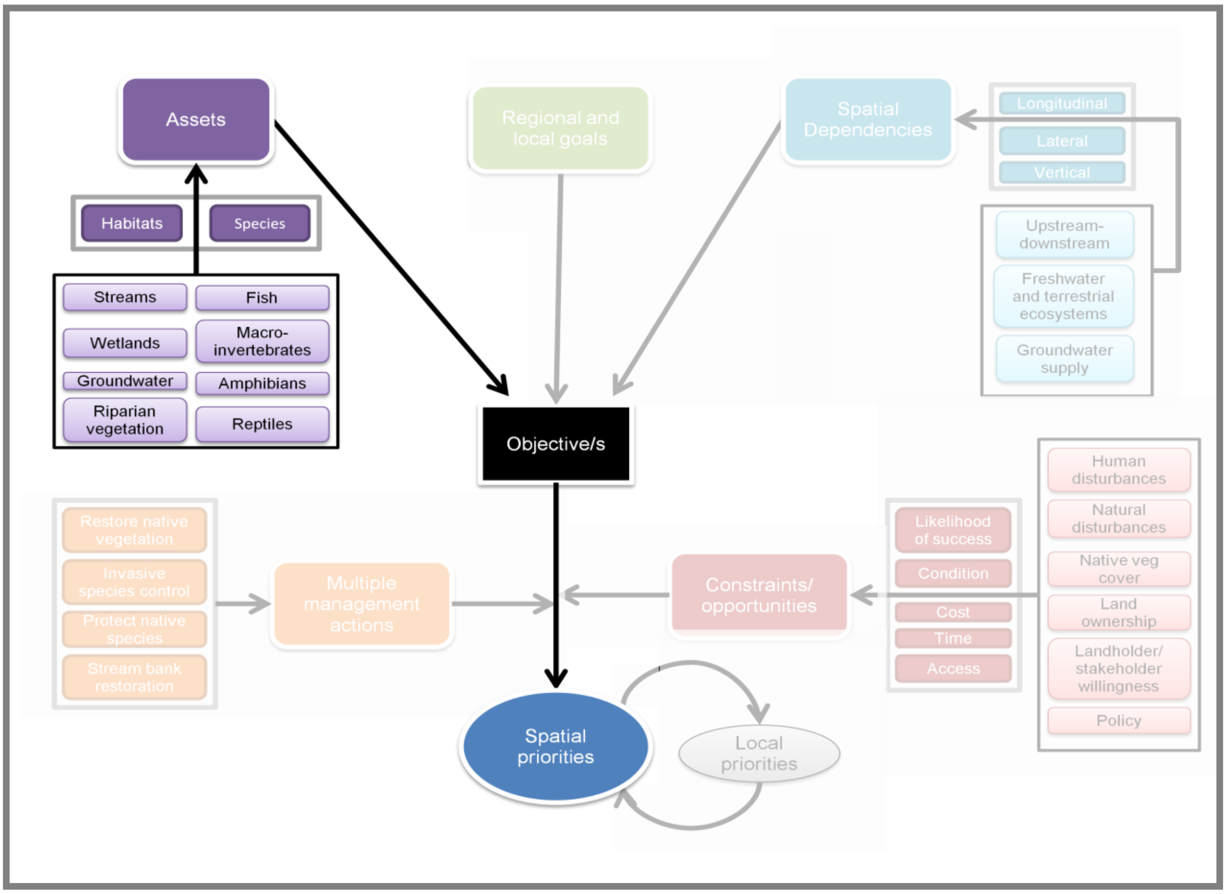
Given the high proportion of the Wet Tropics landscape that is protected, it might be expected that the protection of fresh waters in this region would be much higher than in other regions, especially in the tropics. However, I have demonstrated both the limitation of terrestrial protected areas for effectively protecting freshwater ecosystems and biodiversity and the failure of these protected areas in abating threats to these systems. Existing freshwater protected areas (e.g. Ramsar wetlands) often do not afford effective protection as protected areas lie downstream of disturbances, and little consideration is given to upstream protection or management to mitigate disturbance. Moreover, wetland protection tends to focus on specific sites (especially lentic systems) and ignores the interconnected network across catchments. I have demonstrated that protected areas cannot act as the only strategy for achieving freshwater conservation challenges. There is a need to build on existing protected areas networks to provide protection to focal freshwater ecosystems, and connect this with whole-of-catchment management.

Chapter summary

- I found that in the Wet Tropics 5 of the 6 stream orders and 3 of the 4 wetland types did not have at least 20% of their distribution represented within the terrestrial protected area network. Similarly, 40 of the 45 fish species I evaluated did not have at least 20% of their Wet Tropics distribution within the protected area network.
- I found that higher order stream orders have the highest number of human-induced disturbances present, and that the greatest stream reach length (1518 km), sub-catchment area (1600 km^2) and number of sub-catchments (919) upstream of a protected area have two human-induced disturbances present.
- The existing terrestrial protected area is not effective in protecting the ecological integrity of freshwater ecosystems. Not only is the protection of fresh waters and their dependent species poor, but also there are many of sub-catchments occurring upstream of protected areas that have multiple human-induced disturbances that influence the protected area.

Chapter 4

Coarse-filter surrogates do not represent freshwater fish diversity at a regional scale in Queensland, Australia[1]



[1]**Januchowski-Hartley, S. R**., Hermoso, V., Pressey, R. L., Linke, S., Kool, J., Pearson, R. G., Pusey, B. J. and VanDerWal, J. Coarse-filter surrogates do not represent freshwater fish diversity at a regional scale in Queensland, Australia. *Biological Conservation* 144: 2499-2511.

Introduction

A fundamental role of systematic conservation planning is to identify representative and complementary areas for protection or restoration ("conservation areas") that efficiently meet quantitative targets. Ideally, the distribution of all species across a study region would be known and adequately sampled in conservation areas. In reality, most described species are inadequately sampled and have distributions that are poorly understood (Rondinini & Boitani 2006), and most species observations are biased spatially (e.g. along roadsides) or toward particular taxa (Polasky et al. 2000; Funk & Richardson 2002). Improvements in field records are limited by lack of resources for surveys and taxonomy. Improvements in models of species' distributions are limited by their data requirements. Delays in conservation planning and action to wait for better data come at the cost of biodiversity loss (Grantham et al. 2008). A consequence of these constraints is that conservation planners require effective surrogates for biodiversity (Lombard et al. 2003; Wilson et al. 2005).

Two broad categories of surrogates have been identified (Margules & Pressey 2000; Wiens et al. 2008): 1) surrogate species, which most commonly include umbrella species, flagship species, indicator species, focal species, and species groups chosen on the basis of taxonomy, life-history, or ecological functions, and 2) coarse filters, which commonly include vegetation types, ecological communities, or ecosystems acting as surrogates for the species occurring in those areas. There are two broad approaches to defining coarse-filter surrogates (Figure 4.1). The first is based on discrete classes. Discrete classes can be defined qualitatively by identifying perceived discontinuities between broad habitat types (e.g. Ban 2009; Dalleau et al. 2010) or quantitatively with numerical classification. Of the quantitative methods, divisive approaches start from large, ecologically heterogeneous areas and divide these progressively into finer, more homogeneous parts (Figure 4.1). Agglomerative approaches begin with the smallest recognized areas (often individual sampling sites) and progressively merge them according to shared characteristics of interest (e.g. Rashleigh et al. 2009). The second broad type of coarse-filter surrogate (Figure 4.1) avoids allocation of areas to discrete classes by recognizing continuous environmental or biological variation between areas, albeit with gradients of varying steepness (e.g. Arponen et al. 2008).

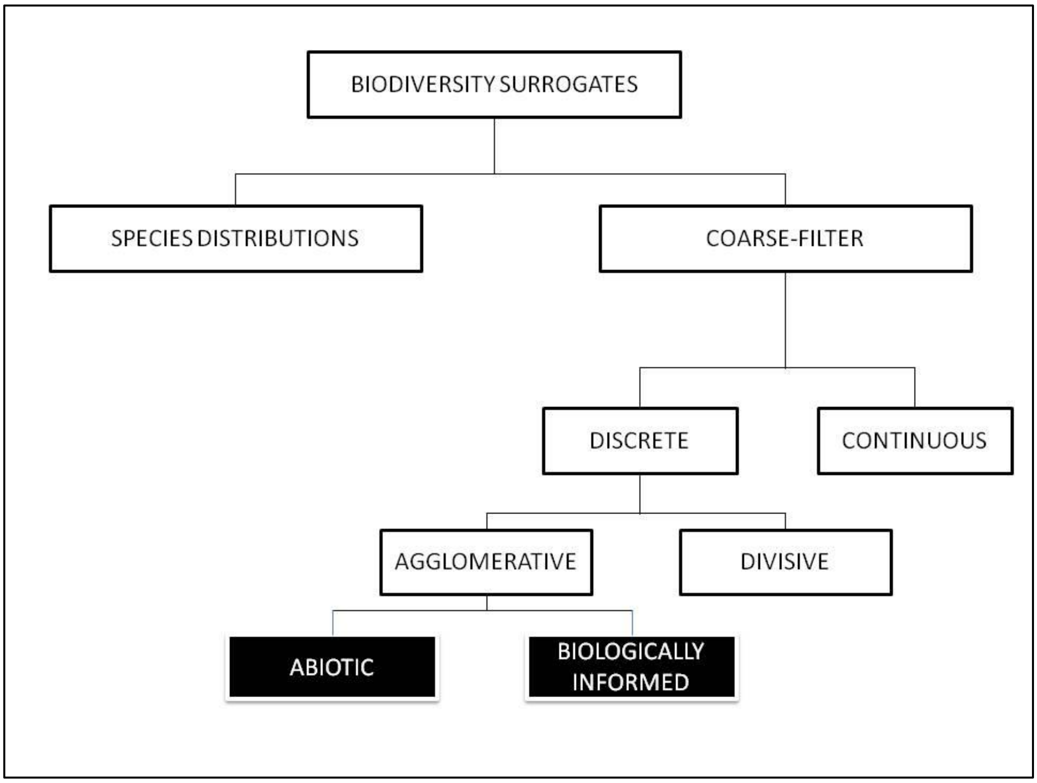


Figure 4.1 Classification of coarse-filter surrogates used in this study (no attempt has been made to subdivide species surrogates). Shaded boxes indicate the two types of coarse-filter surrogates compared here.

Testing the effectiveness of surrogates can inform planners about their unavoidable limitations. The term effectiveness refers to how well a surrogate explains the distribution of a species it is intended to represent. To date, considering surrogate effectiveness has not been common practice in systematic conservation planning. However, if effectiveness of coarse-filter surrogates is not accounted for, planners risk poorly representing species. There are several reasons why coarse-filter surrogates might not be effective (Pressey 1992), including: 1) the relationship between surrogates and variation in the distribution of species is unclear and difficult to quantify, 2) species could be patchily distributed within surrogates, 3) some species that are threatened or endemic to a region may require conservation actions additional to representation of surrogates, 4) surrogates might not identify critical areas for population persistence, and 5) many species require combinations of habitats that are unlikely to be identified by surrogates. Therefore, knowing how well coarse-filter surrogates lead to protection of species is critical to understanding the data requirements for effective biodiversity conservation (Lombard et al. 2003; Grantham et al. 2010).

Two general testing methods – selection-based and pattern-based – are commonly used to quantify the effectiveness of coarse-filter surrogates (Grantham et al. 2010). Selection-based methods select conservation areas using the surrogate and then measure how well those selected areas represent the test features (Kirkpatrick & Brown 1994). Pattern-based methods measure the spatial relationship between the surrogate and the test features. Both methods have their shortfalls. Selection-based methods address conservation decisions, but require the assumption that particular configurations of selected areas will match conservation action on the ground or in the water. Pattern-based methods address inherent aspects of species distributions relative to surrogates. While their lack of assumptions about conservation actions avoids the reliance of effectiveness on particular spatial configurations of conservation areas, it also leaves unresolved their relevance to conservation decisions. Therefore, testing of surrogate effectiveness is likely to require complementary assessments, using both pattern- and selection-based methods (Grantham et al. 2010).

Among the few studies on freshwater conservation planning, a number of these have depended on coarse-filter surrogates (e.g. Noss et al. 2002; Thieme et al. 2007; Rashleigh et al. 2009). However, I know of no evaluations of surrogate effectiveness for conservation planning in fresh waters. The purpose of this study was to determine how well fish species were represented by conservation areas selected using coarse-filter surrogates. I chose a data-rich study region in north Queensland, Australia to test three methods for deriving discrete coarse-filter surrogates from environmental data. I used three agglomerative classification methods, Unweighted Pair Group Method with Arithmetic Mean (UPGMA) based on abiotic data alone, and Discriminant Function Analysis (DFA) and naïve Bayesian classification to produce biologically informed classes based on the relationship between the biological data for some stream reaches and abiotic data available for all streams. My test features were the modelled occurrences of 28 freshwater fish species. I used selection-based methods to test the effectiveness of the surrogates. I identified priority areas for conservation based on the surrogates, then measured how well these areas represented the species and, finally, how well they matched the areas selected independently to represent the species.

Methods

Planning units

Planning units are the spatial units of assessment and comparison in most exercises in systematic conservation planning. Studies for terrestrial environments have frequently used equal-sized grid cells as planning units (Moore et al. 2003; Sarkar et al. 2002). However, such cells are not appropriate for conservation planning in fluvial systems as they neither define streams accurately nor account for hydrological connectivity between stream reaches and within catchments. More hydrologically relevant fluvial planning units are stream reaches and related sub-catchment boundaries (Hermoso et al. 2011b; Klein et al. 2009a).

I identified 7210 planning units. Each planning unit was a stream reach, defined as a portion of river length between two consecutive nodes of river connections (Figure 4.2). I also used the adjacent sub-catchment area (Figure 4.2) and upstream aggregated sub-catchment areas of each stream reach to attribute environmental characteristics to planning units. Stream reaches and associated sub-catchments were derived from a 30 m-resolution digital elevation model (Appendix C). Analysis was carried out using ArcHydro 1.3 in ArcGIS 9.3. Average stream reach length was 1.42 km, average adjacent sub-catchment area 160 ha, and average upstream catchment area 11 012 ha.

Species data

My biological data consisted initially of presence/absence records for 78 freshwater fish species in 445 planning units and across all nine river catchments (Northern Australian Freshwater Fish Atlas, http://www.jcu.edu.au/vhosts/actfr/Projects/FishAtlas/Index.htm). The data were compiled from sampling between 1990 and 2009. All fish were identified to species level. Sampled stream reaches were representative of the study region in terms of major catchments, length and width of reaches, and instream habitats (runs, riffles, and pools). Fish presence/absence in wadeable streams was determined using single and multiple pass backpack electrofishing and, in non-wadeable sections, boat electrofishing methods and dip-, gill-, and seine netting. The sampling methods used in both wadeable and non-wadeable streams are effective for characterising species' presence/absence in a variety of habitats and for determining patterns of species composition over large areas (Pusey & Kennard 1996).

I selected a subset of all sampling records (excluding fish species that were highly or exclusively dependent on estuarine environments), modelling the distributions of 28 freshwater species that occurred in at least 5% of the 445 sampled planning units (planning unit n = 443). This set of species included 15 widespread species, 12 of which have both freshwater and estuarine dependence, and 13 freshwater-dependent species with more restricted ranges in the study region (e.g. *Cairnsichthys rhombosomoides, Tandanus tandanus*).

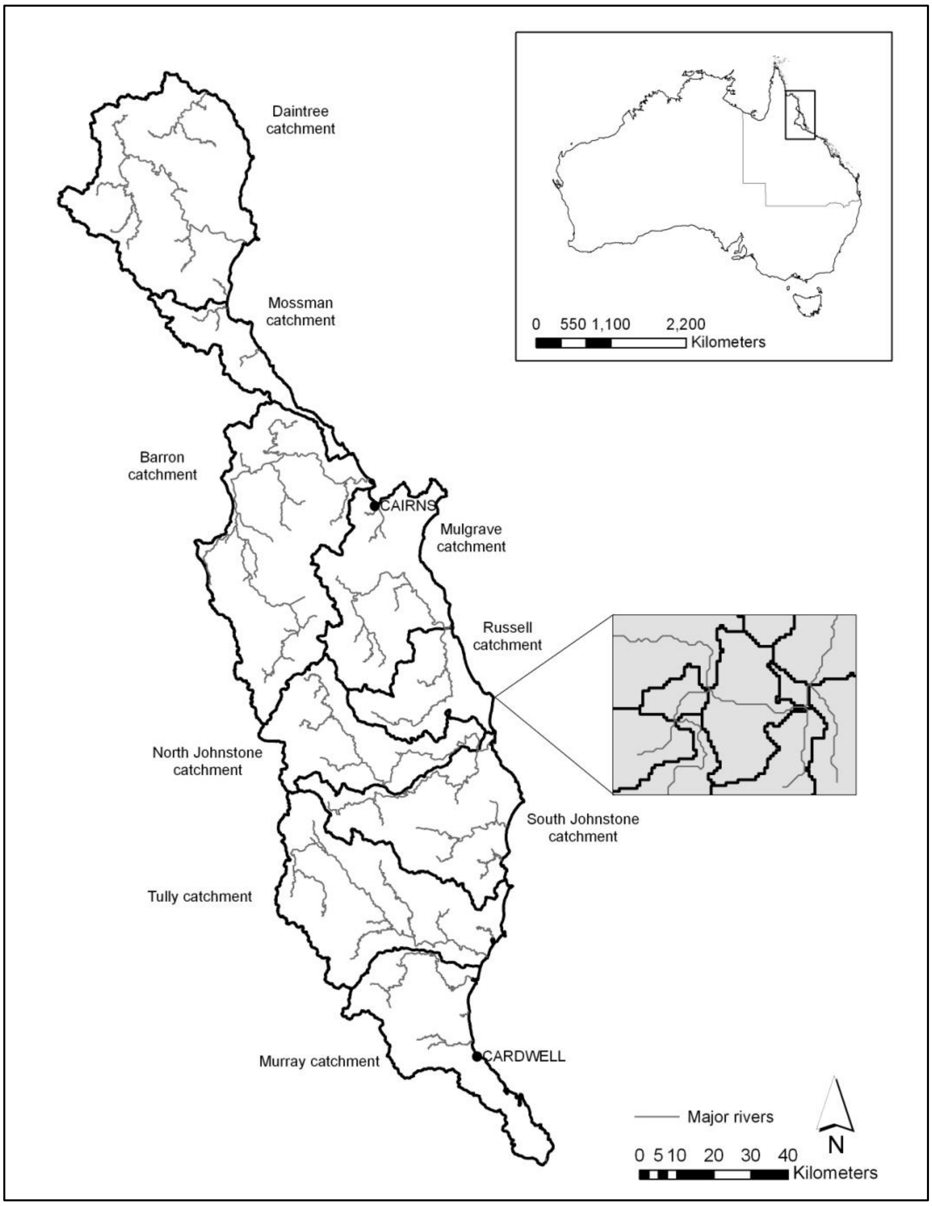


Figure 4.2 The Wet Tropics study area. The inset shows an expanded view of part of the Russell catchment, stream reaches (planning units) are light grey and stream reach sub-catchments are darker grey.

Environmental variables

I assembled data on ten environmental variables to model fish species distributions and derive coarse-filter surrogates (see below). I was specifically interested in environmental data that were available for all 7210 planning units to enable complete predictive coverage. Therefore, I focused on landscape scale environmental variables that have previously been shown to be the most ecologically relevant environmental predictor variables for fish in my study area (see Pusey et al. 2000; Pusey et al. 2004). The ten variables were attributed to stream reaches, adjacent sub-catchments, or aggregated upstream sub-catchments flowing into stream reaches (Table 4.1). Stream length and order were attributed using ArcGIS 9.3. Minimum and maximum elevation and slope were attributed using Hawth's Tools 3.27 (http://www.spatialecology.com/htools/versionhist.php). For adjacent and upstream sub-catchments, I analysed data with Zonal Statistics in ArcGIS 9.3.

Table 4.1 Environmental variables considered for species distribution modelling and derivation of coarse-filter surrogates. Also shown are attributed stream or catchment features.

Environmental variable	Attributed stream feature
Stream reach length (km)	Stream reach
Stream order	Stream reach
Minimum elevation (m)	Stream reach
Maximum elevation (m)	Stream reach
Minimum slope (degrees)	Stream reach
Maximum slope (degrees)	Stream reach
Alluvium cover (%)	Adjacent sub-catchment
Annual rainfall average (mm)	Upstream sub-catchments, Adjacent sub-catchment
Woody foliage cover	Adjacent sub-catchment

Distribution modelling of fish species

I predicted the distribution of the 28 fish species across all nine catchments using MARS (multivariate adaptive regression splines) (Elith & Leathwick 2007). For testing of surrogates I assumed that the MARS model predictions for the 28 species represented their "true" distributions. I based this assumption on the strong performance of my MARS model, and the previously strong performance of MARS for describing freshwater fish distributions in other regions (Leathwick et al. 2005).

MARS is a method for non-parametric regression modelling, useful for addressing complex non-linear relationships between response and explanatory variables. MARS enables exploration of interactions between predictors (Leathwick et al. 2006), and can fit a multi-response model which simultaneously relates variation in the occurrence of all species to the environmental predictors (Olden 2003). Multi-response species models have been shown to best recover overall variation in species composition compared to single-species models (e.g. Generalized Additive Models) because models of species that have been better sampled and represented in the dataset can help inform models of poorly sampled species (Leathwick et al. 2005; Elith & Leathwick 2007). Leathwick et al. (2006) observed higher AUC scores for low prevalence species from a MARS multi-response model compared to equivalent scores for those species using individual MARS models. Several researchers have demonstrated the utility of multi-response MARS models for freshwater conservation planning (Leathwick et al. 2005; Hermoso et al. 2011b).

I built a single multi-response MARS model for the 28 fish species and the 7210 planning units. The model was fit using the presence/absence data for the 28 fish species (planning unit n = 443) and all nine environmental variables. I used the MDA (Mixture and Flexible Discriminant Analysis) library (Elith & Leathwick 2007) in the R statistical software package, Version 2.10.1 (R Development Core Team, 2009). Model performance was evaluated using the area under the ROC curve (AUC) with a *k*-fold cross-validation procedure (Fielding & Bell 1997). The cross-validation divided the presence/absence data into 10 random subsets, successively removing a single data point from each subset and refitting the model with the remaining data, then predicting the omitted data and calculating the average AUC across all subsets. An AUC score of 0.5 indicates a model with no discriminatory ability. A score of 1 indicates that presences and absences are perfectly discriminated. An AUC > 0.60 is generally considered an acceptable threshold for model performance (Fielding & Bell 1997).

I used histograms to depict the frequency distribution, across all 7210 planning units, of predicted probability of occurrence for each of the 28 species. I also summed the predicted probability of occurrence across all 28 species in each planning unit, with a maximum possible value of 28 in any unit.

Derivation of biodiversity surrogates

For each of the 7 210 planning units I defined four levels of classification (2, 4, 6, 8 classes) with three classification methods previously used in freshwater research. This gave me twelve coarse-filter surrogates. I used UPGMA to define classes based on abiotic data alone. The DFA and naïve Bayesian classes were defined based on presence/absence data for the 28 fish species from the 443 planning units. These methods then used the relationship between the biological classes and environmental data to allocate all reaches to classes. Classes from DFA and naïve Bayesian could be expected to better reflect fish distributions than classes from abiotic methods but are less widely applied because of the reliance on field sampling.

UPGMA is an agglomerative method commonly used to cluster naturally occurring groups based on biological, physical or hydrological characteristics of freshwater ecosystems (e.g. Kennard et al. 2006; Sanchez-Montoya et al. 2007). UPGMA cannot, however, be used to predict clusters defined with one dataset onto new data. DFA identifies the set of continuous predictor variables that best discriminate between two or more naturally occurring groups, allowing stream reaches or other features not involved in the original classification to be allocated predictively to classes (e.g. Frappier & Eckert 2007; Doledec & Statzner 2008). The naïve Bayesian method is a probabilistic classifier based on Bayes' theorem with strong (naïve) independence assumptions (Berger 1985). Naïve Bayesian classification is less common in freshwater ecology, although (Webb et al. 2007) recently used it (implemented with Autoclass – Hanson et al. 1991; Cheeseman & Stutz 1996) to link stream ecological condition to catchment-scale factors such as land use.

I used all 10 environmental variables to apply UPGMA to the 7210 planning units, implemented with the AGNES package, R statistical software. For the DFA and naïve Bayesian methods, I defined classes initially based on the presence/absence data for the 28 fish species from the 443 planning units. For the naïve Bayesian and DFA, I used, respectively, the package e1071 in R and PROC Stepdics in SAS (SAS System 2005). For the naïve Bayesian, a nearest shrunken centroid method (Tibshirani et al. 2002) was used to partition fish observations into *k* classes, using the PAM package in R. I used forward and backward stepwise removal of the independent abiotic variables to select those variables with greatest discriminatory power for both the DFA and naïve Bayesian classification (Table 4.2).

Table 4.2 Environmental variables used to define classes of planning units with Discriminant Function Analysis and naïve Bayesian classification.

Classification method	2 classes	4 classes	6 classes	8 classes
Discriminant Function Analysis	Minimum elevation, Alluvium cover	Minimum elevation, Maximum slope, Minimum slope, Stream order, Annual rainfall average (upstream sub-catchments), Alluvium cover	Minimum elevation, Maximum slope, Minimum slope, Stream order, Annual rainfall average (upstream sub-catchments), Alluvium cover, Woody foliage cover	Minimum elevation, Maximum slope, Minimum slope, Stream order, Annual rainfall average (upstream sub-catchments), Alluvium cover, Woody foliage cover
naïve Bayesian	Minimum elevation, Stream order, Annual rainfall average (adjacent sub-catchment), Annual rainfall average (upstream sub-catchments), Alluvium cover, Woody foliage cover	Minimum elevation, Stream order, Annual rainfall average (adjacent sub-catchment), Annual rainfall average (upstream sub-catchments), Alluvium cover, Wood foliage cover, Stream length	Minimum elevation, Stream order, Annual rainfall average catchment, Annual rainfall average upstream, Alluvium cover, Wood foliage cover, Stream length	Minimum elevation, Stream order, Annual rainfall average (adjacent sub-catchment), Annual rainfall average (upstream sub-catchment), Alluvium cover, Wood foliage cover, Stream length

The selected abiotic variables were then used to allocate planning units without fish records to classes defined by the occurrence of fish species in sampled reaches.

I used classification strength to measure the informativeness of the 12 surrogates about spatial variation in fish species composition. Classification strength (CS) is calculated as ($D_{between}$ – D_{within}), where $D_{between}$ is the mean of all between-class site similarities and D_{within} is the mean site dissimilarity within classes (Van Sickle 1997). I used the Bray-Curtis distance for the DFA and naïve Bayesian classifications, and I used Euclidean distance for the UPGMA classifications. CS approaches 0 with 'poor class structure', and increases toward 1 with a perfect classification (Van Sickle 1997). To calculate CS I used the Multi Response Permutation Procedure (mrpp) in the vegan package, R statistical software. I also used the package's permutation test to determine if the surrogates explained variation in species composition significantly better than random.

Selection of planning units for conservation

I used Marxan conservation planning software (Ball et al. 2009) to select sets of stream reaches to achieve quantitative targets for each surrogate. This involved 12 different selection analyses to test the combinations of surrogates. I tested the effectiveness of the surrogates by measuring the incidental representation of the 28 modelled fish species in the selected stream reaches.

For each of the 12 surrogates, I set Marxan to restart 100 times with 1 million iterations per restart to ensure that the decision-space was sampled adequately. I adopted the minimum-set framework to achieve targets for all features at the lowest cost (Kirkpatrick 1983; Margules & Nicholls 1987; Possingham et al. 1993) and selected the best solution from the 100 restarts. I gave each stream reach an equal unit of cost (value of 1) and set the connectivity constraint (boundary length modifier, Game & Grantham 2008) to zero. I did this because my aim was to examine how well conservation planning solutions, determined from the 12 surrogates, represent individual species. Including cost and connectivity could have confounding effects on the overall solutions and not tell the true abilities of the surrogate methods alone for representing individual species. I used two percentage targets – 10% and 30% of total stream reach length occupied by each class – and ensured that all targets were fully achieved. While these targets are not sufficient to prevent further loss of biodiversity in many areas, the 10%

target has a foundation in policy, with global and national aspirations to conserve 10% of a country's natural assets (Pressey et al. 2003), even if increasingly criticized (e.g. Svancara et al. 2005), and the 30% target is the lower bound of what is more generally accepted by science (Pressey et al. 2003).

Tests of effectiveness of the surrogates

To test the effectiveness of the 12 surrogates, I measured the percentage of each of the 28 predicted species distributions (summed probabilities of occurrence of each species across all planning units) selected in sets of stream reaches that achieved targets for the surrogates (Grantham et al. 2008). The distribution of representation values was normally distributed ($p < 0.005$) so I used one-way Analysis of Variance (ANOVA) (stats package in R) to test for significant differences in representation between classification methods and numbers of classes. To do this I used the average representation across the 28 species and analysed results for the 10% and 30% surrogate targets. For each of the 12 surrogates and two target levels, I also compared the observed average species representation across the 28 species to the average species representation from 4999 randomly selected sets of planning units. I determined if observed representation was significantly different from random based on 95% confidence intervals. For each comparison, each of the 4999 random sets contained the same number of planning units as the actual solution to which it was being compared. I generated random planning solutions using the nboot application in Matlab 7.10 (The Mathworks, http://www.mathworks.com/products/matlab/). I also used Pearson's correlation (stats package in R) to determine if there was a relationship between classification strength and average species representation values.

As a second test of effectiveness, I derived selection frequencies of planning units for each surrogate and target level (24 comparisons) and used Pearson's correlation to determine if there was a relationship among the 12 surrogates as well as between the 12 surrogates and selection frequencies derived from achieving the corresponding target levels for all 28 modelled species distributions (MARS). Marxan's selection frequency measures how many times out of the total restarts (100 used here) each planning unit was selected. It is analogous to irreplaceability, and is often interpreted as a measure of importance (Ball et al. 2009).

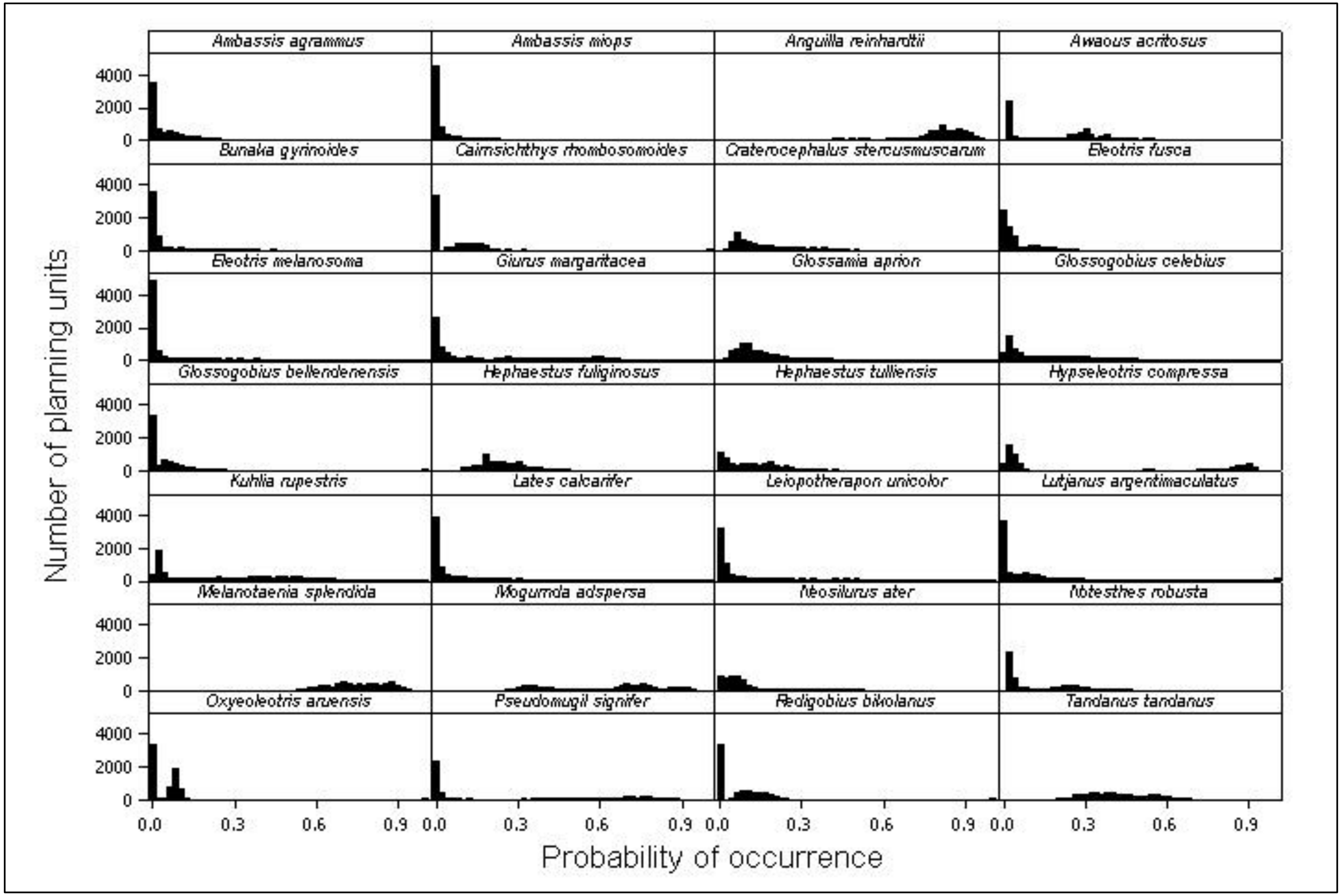


Figure 4.3 Frequency distributions of predicted probabilities of occurrence for the 28 fish species.

Results

Models for all 28 fish species had AUC > 0.60 (Appendix B, Table S4.1). The overall mean AUC across all 28 predictions was 0.79, and more than 60% of the 28 species had AUC > 0.75, indicating that the MARS model produced strong predictions.

Most of the 28 fish species had modelled distributions that were right-skewed, dominated by planning units with low probabilities of occurrence (Figure 4.3). Exceptions were *Anguilla reinhardtii*, *Hypseleotris compressa*, *Melanotaenia splendida splendida*, *Mogurnda adspersa*, *Pseudomugil signifier* and *Tandanus tandanus*. These six species had more evenly distributed predicted probabilities across planning units, agreeing with previous reports that these species are widespread in the study region (Pusey et al. 2004). The highest summed probability of occurrence was in lowland stream reaches close to the coast and along the lower reaches of the main rivers (Figure 4.4).

All 12 surrogates performed poorly in explaining spatial variation in fish species composition. Although all surrogates were significantly better than random ($p \leq 0.001$), the classification strength (CS) did not exceed 0.08 for any method regardless of the number of classes. The worst CS values (≤ 0.01) were for UPGMA, regardless of the number of classes. The naïve Bayesian and DFA methods had the same CS values for two to eight classes (0.06, 0.06, 0.07, and 0.08, respectively). Classification strength improved with increasing numbers of classes for all methods.

Overall, the 28 freshwater fish species were poorly represented by the 12 surrogates (Figure 5). None of the surrogates led to any of the 28 species being represented close to the 10% or 30% surrogate targets (Figure 4.5). None of the surrogates led to average species representation significantly better than the average representation from 4999 random selections. Both the maximum and minimum values of species representation resulted from the naïve Bayesian classification for both the 10% and 30% surrogate targets (Figure 4.5). The maximum representation for any species with the 10% surrogate target was just over 6% while the minimum was just under 3%. With the 30% target, maximum representation for any species was 18% and the minimum was 11% (Figure 4.5). On average, across all 12 surrogates, only 4% and 14% of the 28 predicted species distributions were represented with surrogate targets of 10% and 30%, respectively.

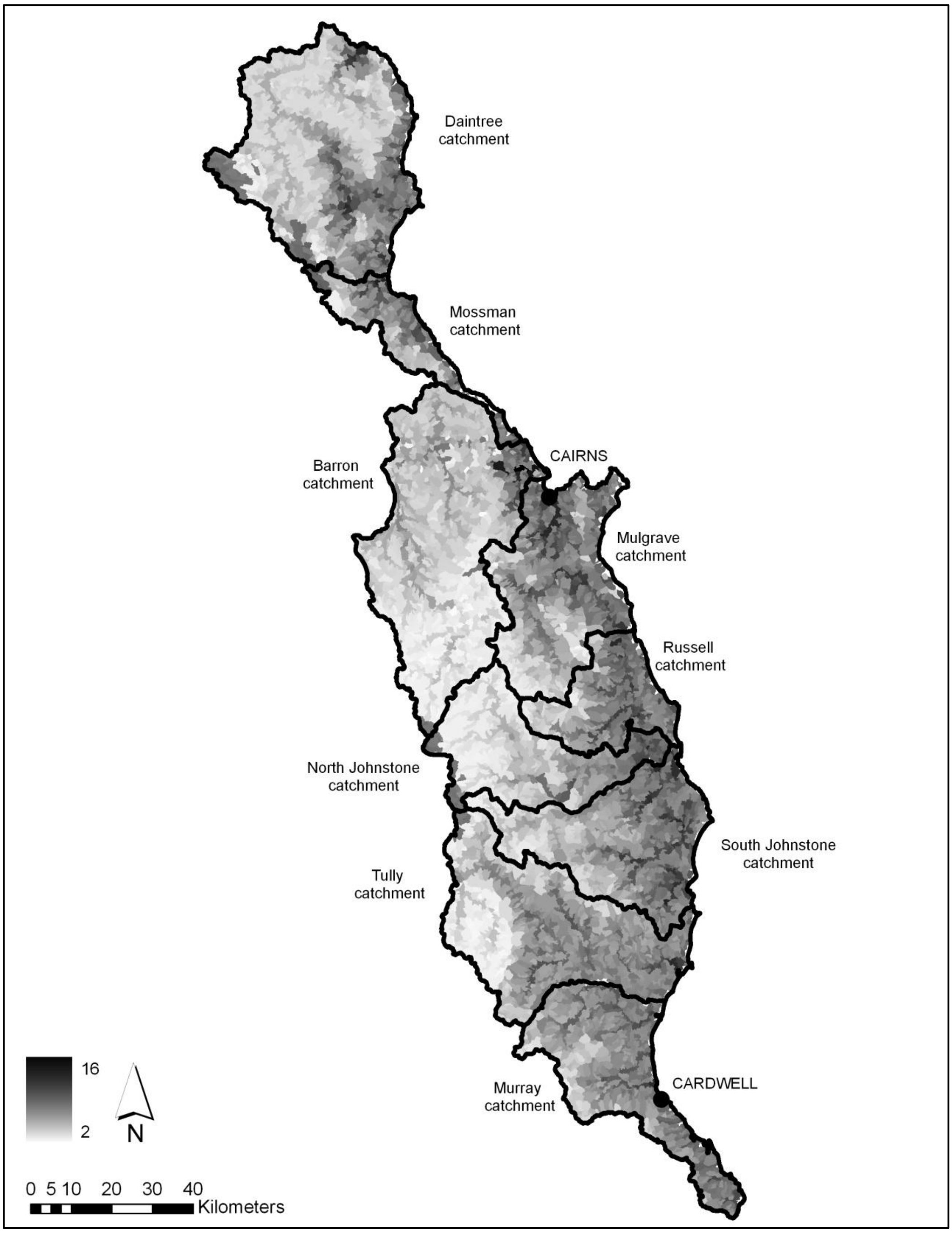


Figure 4.4 Summed probabilities of predicted occurrence for the 28 fish species in the Wet Tropics study area. For clarity, values are mapped for sub-catchments adjacent to each of the 7 210 stream reaches. The maximum summed probability was 16 (shaded black).

For both the 10% and 30% targets, with few classes (2 or 4), ANOVA showed no significant difference in species representation between the three classification methods. However, for both target levels with 6-8 classes, ANOVA showed that species representation from the naïve Bayesian method was significantly better than either DFA or UPGMA ($p \leq 0.05$). There was no significant difference in species representation between numbers of classes for the 10% target. For the 30% target, there was a significant increase ($p \leq 0.05$) in species representation with increasing number of classes, but only for the naïve Bayesian method.

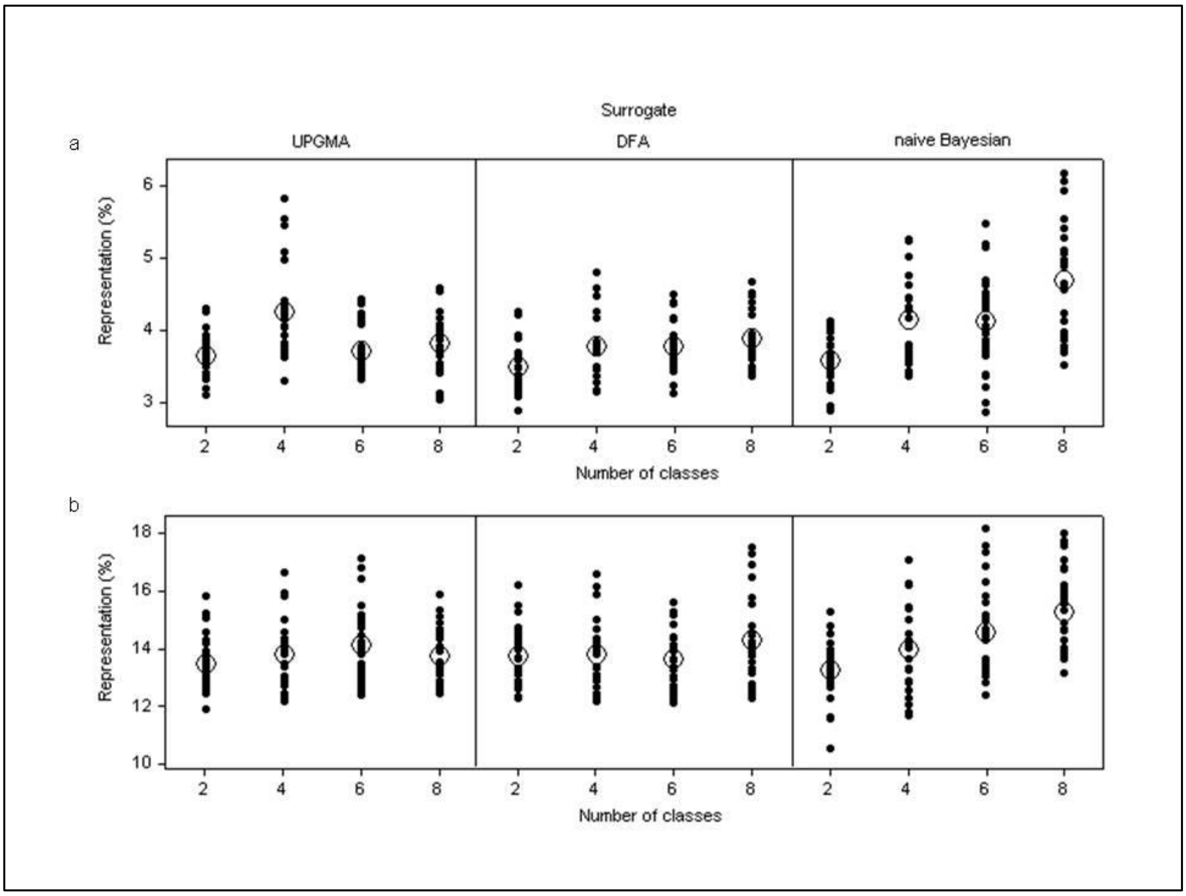


Figure 4.5 Plots of representation of the 28 fish species as percentages of total predicted occurrences for each of the 12 surrogates and two target levels: a) 10% and b) 30%. Each of the species is represented by a black dot. Average representations across species are shown with open circles. None of the average representations were significantly higher than the corresponding value from 4999 randomly generated solutions, based on the 95% confidence interval.

Species representation was related to classification strength (CS). Across all 12 surrogates, CS was positively related to average species representation. Across numbers of classes, the relationship was strongest for naïve Bayesian with a 30% target and DFA with a 10% target ($r = 0.97$, $p \leq 0.05$ for both) but also strong for UPGMA for both target levels ($r = 0.84$ and 0.82, both $p \leq 0.05$). For naive Bayesian with a 10% target and DFA with a 30% target, there was no significant relationship between CS and average species representation across numbers of classes.

Selection frequencies were correlated between the 12 surrogates ($r \geq 0.88$, all $p \leq 0.001$) for the 10% surrogate target (Table 4.3a). The correlations were less strong but still significant for the 30% surrogate target ($r \geq 0.79$, all $p \leq 0.001$) (Table 4.3b). Correlations between selection frequencies from the surrogates and those from the species distributions were only moderately high for the 10% and 30% targets ($r \geq 0.59$ and $r \geq 0.67$ respectively, all $p \leq 0.001$) (Table 4.3).

There was no clear spatial pattern of differences between selection frequencies for surrogates and those for species distributions, exemplified with a comparison between the naïve Bayesian method (8 classes) and species models for the 30% target (Figure 4.6). With 10% targets, the maximum absolute difference between selection frequencies from any surrogate and the species models was 98 (out of a possible 100) and the minimum was zero. With 30% targets, the maximum difference was 92 and the minimum zero

There were differences between surrogates and species models in the distributions of selection frequencies. For example, the distribution for the naïve Bayesian method (8 classes) and 30% target (Figure 4.7a) was more strongly right-skewed than the distribution for the species models with a 30% target (Figure 4.7b). The naïve Bayesian distribution had almost double the number of planning units (4966 vs. 2876) selected less than 10 times. The distribution from the species models had many more planning units with selection frequencies higher than 50 (664 vs. 79).

Table 4.3 Pearson's correlation coefficients of selection frequencies based on selection of surrogates and species models, a) using a 10% surrogate target and b) using a 30% surrogate target. Numbers after classification and MARS methods indicate numbers of classes. MARS refers to species distribution models.

a)	UPGMA 2	UPGMA 4	UPGMA 6	UPGMA 8	DFA 2	DFA 4	DFA 6	DFA 8	naïve Bayesian 2	naïve Bayesian 4	naïve Bayesian 6	naïve Bayesian 8
UPGMA 4	0.98											
UPGMA 6	0.98	0.98										
UPGMA 8	0.98	0.98	0.98									
DFA 2	0.98	0.98	0.98	0.98								
DFA 4	0.97	0.97	0.97	0.97	0.97							
DFA 6	0.95	0.95	0.96	0.95	0.96	0.96						
DFA 8	0.95	0.95	0.95	0.95	0.95	0.96	0.96					
naïve Bayesian 2	0.98	0.98	0.98	0.98	0.98	0.96	0.97	0.95				
naïve Bayesian 4	0.98	0.98	0.98	0.97	0.97	0.96	0.96	0.95	0.97			
naïve Bayesian 6	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.93	0.95	0.95		
naïve Bayesian 8	0.91	0.91	0.90	0.91	0.90	0.90	0.90	0.88	0.95	0.95	0.93	
MARS	0.64	0.64	0.64	0.64	0.63	0.62	0.63	0.63	0.64	0.64	0.63	0.59

b)	UPGMA 2	UPGMA 4	UPGMA 6	UPGMA 8	DFA 2	DFA 4	DFA 6	DFA 8	naïve Bayesian 2	naïve Bayesian 4	naïve Bayesian 6	naïve Bayesian 8
UPGMA 4	1.00											
UPGMA 6	0.95	0.95										
UPGMA 8	0.94	0.94	0.94									
DFA 2	0.95	0.95	0.95	0.95								
DFA 4	0.93	0.93	0.94	0.93	0.94							
DFA 6	0.92	0.92	0.92	0.91	0.92	0.92						
DFA 8	0.91	0.91	0.91	0.90	0.91	0.92	0.94					
naïve Bayesian 2	0.95	0.95	0.95	0.94	0.95	0.93	0.92	0.91				
naïve Bayesian 4	0.94	0.94	0.94	0.93	0.93	0.92	0.91	0.90	0.93			
naïve Bayesian 6	0.90	0.90	0.90	0.90	0.90	0.90	0.88	0.88	0.89	0.90		
naïve Bayesian 8	0.83	0.83	0.82	0.82	0.81	0.81	0.80	0.79	0.81	0.83	0.84	
MARS	0.70	0.70	0.70	0.70	0.70	0.69	0.69	0.69	0.71	0.70	0.69	0.67

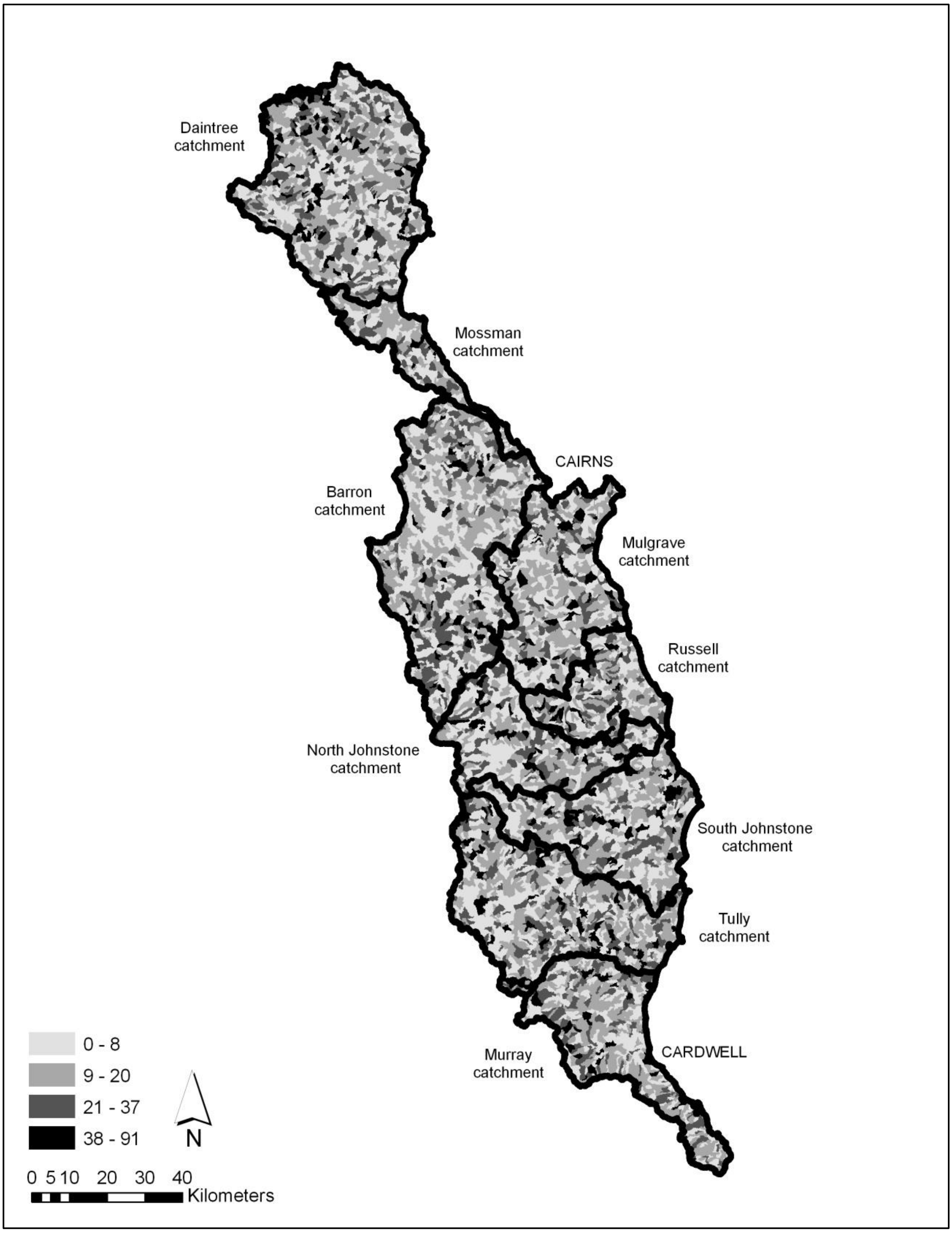


Figure 4.6 Spatial distribution of absolute differences in planning unit selection frequency for 30% targets applied to the naïve Bayesian classification (8 classes) and 30% targets applied to the 28 modelled species distributions. For clarity, values are mapped for sub-catchments adjacent to each of the 7 210 stream reaches.

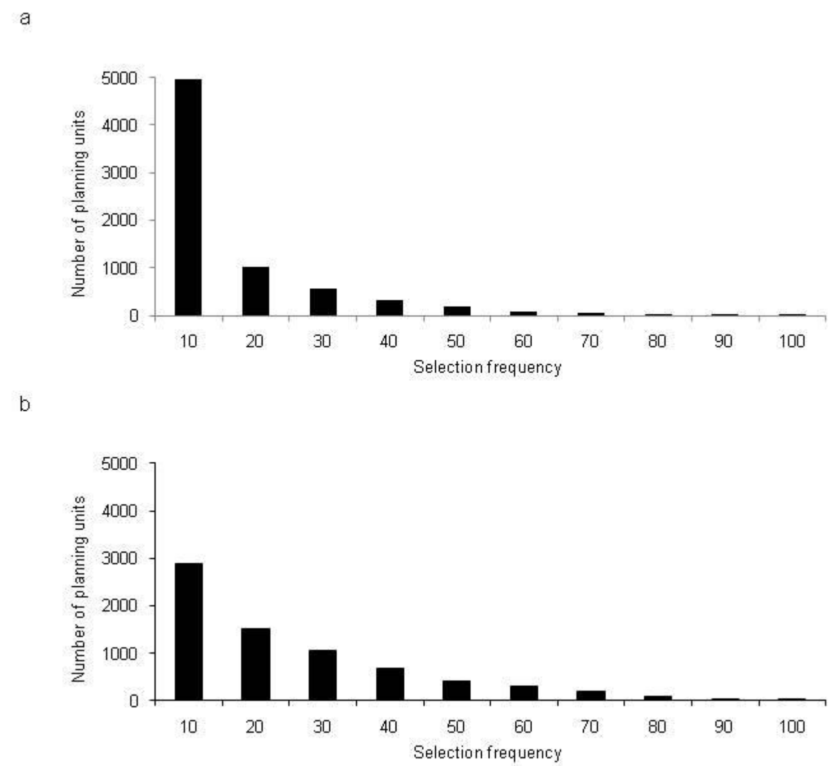


Figure 4.7 Histograms of planning unit selection frequencies based on: a) naïve Bayesian classification (8 classes) and b) MARS predicted species distributions. Targets were 30% for both. Labels for bars are upper values of the categories and represent the number of times (out of 100 restarts) that planning units were selected.

Discussion

I aimed to determine how well conservation areas, selected using coarse-filter surrogates for streams, represented fish species. I did not set out to develop a comprehensive conservation plan for freshwater fish species as a comprehensive plan would have used the records of the many rare and endemic species that could not be modelled, and considered habitat requirements in relation to different life-history stages.

In the following sections, I comment on the relative performance of abiotic and biologically informed surrogates in my study, discuss the ability of my classification methods to derive classes that were informative about the distribution of fish species, consider the reasons why my surrogates did not perform well in terms of incidental representation, and identify areas for further research.

Abiotic vs. biologically informed classifications

Coarse-filter surrogates are commonly used in systematic conservation planning in terrestrial, marine, and freshwater realms (e.g. Lombard et al. 2003; Thieme et al. 2007; Ban 2009). In freshwater bioassessment and conservation planning, it is commonly assumed that biologically informed classifications make better surrogates than purely abiotic ones because they more accurately reflect the responses of organisms to environmental heterogeneity (Wiens 2000; Paavola et al. 2003; Fieseler & Wolter 2006, but see Grantham et al. 2010). Based on this assumption, I anticipated that surrogates derived from my biologically informed methods (DFA and naïve Bayesian) would represent species better than those based on environment alone. This proved not to be the case. The biologically informed surrogates did not significantly improve the average representation of fish species over purely abiotic ones.

While this study demonstrates the limitations of coarse-filter surrogates for representing freshwater fish, these limitations are more pervasive (see for example Lombard et al. 2003; Beger et al. 2007; Ban 2009). Generalizations about the most effective surrogate are difficult, and the optimal surrogate is likely to depend on a number of factors (Margules & Pressey 2000; Wiens 2000; Grantham et al. 2010), including: 1) the study region, 2) the realm (terrestrial, marine, freshwater), 3) the spatial extent of the planning region, 4) the spatial resolution of areas being assessed for conservation action, 5) the choice of surrogate, 6) the choice of test features (e.g. species, communities, habitat types) used to measure effectiveness, and 7) the analytical method for testing surrogate effectiveness. Studies of coarse-filter surrogates vary in all these ways, so it is difficult to extrapolate results from one study region or taxon, or to establish a rules-of-thumb for the effectiveness of surrogates. The lack of reliable generalizations helps to explain the unresolved debate in scientific literature (e.g. Brooks et al. 2004; Pressey 2004).

Ability of classifications to account for spatial variations in composition of fish species

Both biologically informed and abiotic classifications had low values for classification strength. I can identify three reasons for this result. First, freshwater fish species in the Wet Tropics, like those in other regions, appear to respond to changes in environment in a species-specific manner, not as components of strongly aligned assemblages (Grossman & Ratajczak 1998; Pusey et al. 2000). This is demonstrated by the strong performance of the MARS models for all 28 species, with species having different relationships with the various environmental variables.

Second, and related to the first reason, the classification methods did a poor job of discriminating important environmental gradients that influence the distribution of fish species. For example, the majority of freshwater fish species in the Wet Tropics had highest predicted probabilities of occurrence ($P > 0.50$) in lower stream reaches and main river channels of the Daintree, Mulgrave, Russell, North and South Johnstone, and Tully catchments. One reason for the skewed distribution of species is a major escarpment blocking passage to the west for most of the region's fish species (Pusey & Kennard 1996). Upstream of the escarpment, only 4 of the 28 species had predicted probabilities of occurrence greater than 0.50. The remaining 24 species are less capable of traversing the escarpment and had highest probabilities of occurrence (> 0.50) in the lower stream reaches and main river channels of the Daintree, Mulgrave, Russell, North and South Johnstone, and Tully catchments. However, none of the classification methods distinguished this difference in species composition above and below the escarpment. This might have been expected for the abiotic method but was surprising for the biologically informed methods. The biologically informed methods defined their classes based on species data below the escarpment where variation in species composition between stream reaches was greatest, then allocated reaches above the escarpment to one or more of these classes based on environmental similarity.

A third reason for poor classification strength was the inability of discrete classes to detect gradual downstream transitions in fish assemblages (see for example, Rahel & Hubert 1991; Van Sickle & Hughes 2000; Snelder et al. 2004; McGarvey & Hughes 2008), making them relatively uninformative. In contrast to the distinct subset of species above the escarpment, there is a gradual transition in species composition from the base of the escarpment towards the coast. This reflects the increased availability of habitat arising from more stable flows and increasing structural complexity such as riffles and deep pools (Pusey & Kennard 1996).

Why did the coarse-filter surrogates represent freshwater fish species poorly?

My main findings about the ability of surrogates to represent fish species were that: 1) all 12 surrogates resulted in species being represented at levels well below the surrogate targets; 2) none of the surrogates gave average representation of fish species significantly better than random; and 3) differences in selection frequencies between surrogates were smaller than between any of the surrogates and those from the fish species models.

There are at least two reasons for the first two findings. First, the surrogates had low classification strengths (CS), so poorly explained the spatial variation in fish species composition. The significant relationships between CS and average representation of fish species suggest that higher CS values would have given better representation. Importantly, however, even these significant correlations concerned values of average representation that was no better than from random selections. Second, as a consequence of the first reason, when based on surrogates, selections of planning units by Marxan were effectively random within classes with respect to probabilities of occurrence of fish species. Consequently, given the right-skewed distributions of probabilities of occurrence for most fish species, planning units with low probabilities of occurrence would have been overwhelmingly selected, giving poor representation and similar results to overall random selections.

The mismatch in selection frequency distributions between surrogates and species models also demonstrates Marxan's constrained ability to select planning units important for species when focused on coarse-filter surrogates. Selection based on species models discriminated between planning units with high and low probabilities of occurrence. This led to a distribution of selection frequencies with fewer very low values and more high values than the distributions for surrogates, because planning units with high probabilities of species occurrence were specifically selected and limited the spatial flexibility of selections. In turn, this difference led to spatial patterns of selection frequency being more similar between surrogates than between surrogates and species models.

Future directions

Given the complexity of natural gradients influencing fish species occurrence, and the apparent absence of discrete fish assemblages in the Wet Tropics region, coarse-filter surrogates are not useful as a basis for representing freshwater fish diversity in the region. This conclusion might also apply to other regions, but there are few other studies from which to draw generalizations. For the Wet Tropics, any planning for fish species would clearly proceed with modelled distribution data rather than surrogates. However, I also recognize the limitations of planning with distribution models, including uncertainties around the predicted probabilities and the difficulty of modelling the rare species that make up the majority of the region's fish fauna. Identifying priorities for conservation of fish in the Wet Tropics would benefit from expert advice on locality records and habitat associations of rare species, and from exploration of uncertainties in predictions, for example with confidence limits. Decisions that explicitly considered uncertainty would allow planners, for example, to identify reaches with little uncertainty around the predicted values (e.g. Burgman et al. 2001) or to use lower bounds of predicted probabilities to minimize the risk of failing to reach targets in selected areas (Kerley et al. 2003).

I cannot, however, discount the potential for coarse-filter surrogates to represent other taxonomic groups in the region. Coarse-filter surrogates might be useful for representing taxa such as macroinvertebrates, whose species composition changes over different spatial scales from those of fish, and which are closely associated with specific habitats. Given the sparse data on macroinvertebrates and other taxonomic groups in the region's streams, it is precautionary to base conservation planning on composite data sets of coarse-filter surrogates, species models, and species locality records (Pressey 2004).

In regions where species data are largely unavailable (e.g. Thieme et al. 2007) it is understandable that assessments of surrogate effectiveness cannot be undertaken.

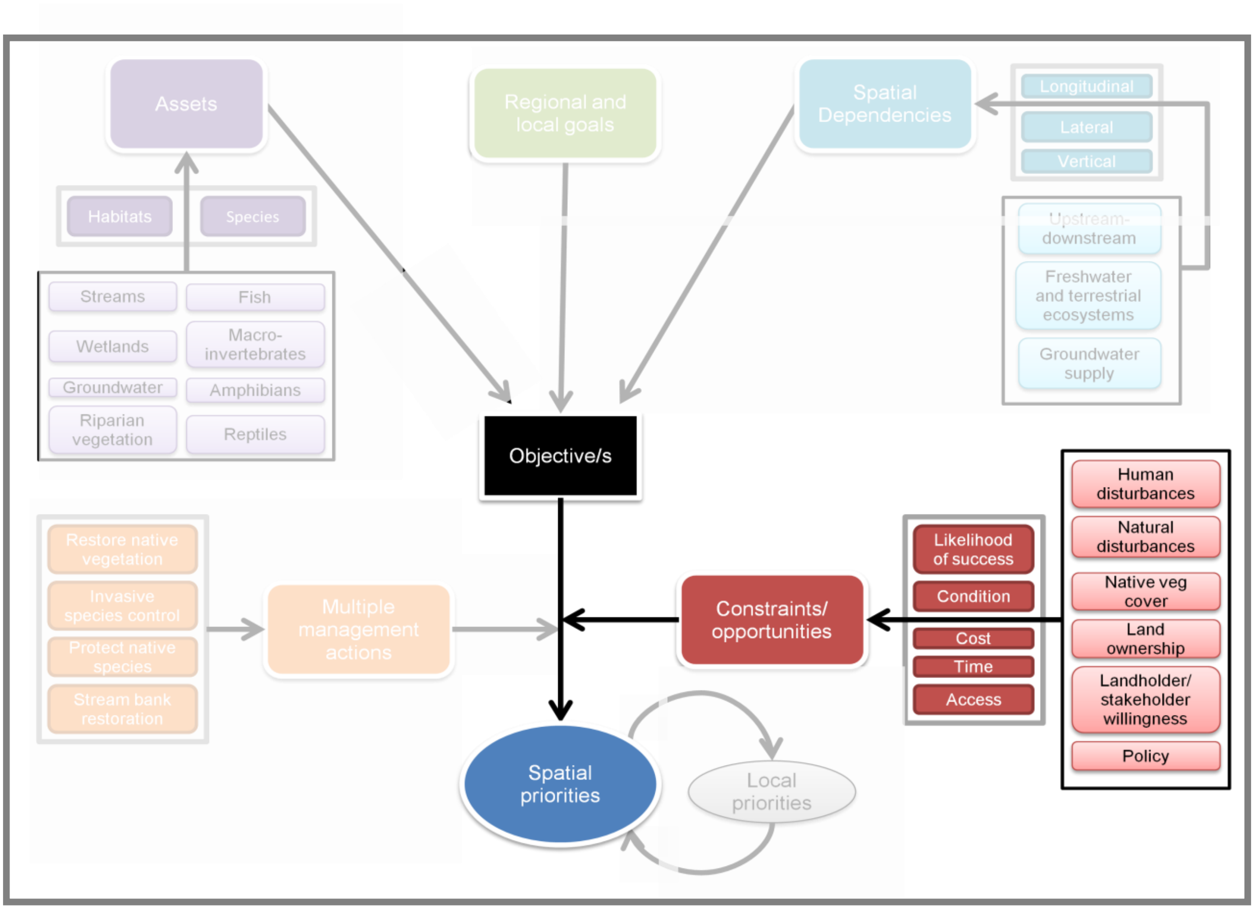
Nevertheless, as I demonstrated here, an assumption that coarse-filter surrogates effectively represent areas of importance for freshwater fish can be wrong. Evidence from this and previous studies (e.g. Grantham et al. 2010) indicates there is no single optimal surrogate and that rules of thumb about the relative effectiveness of surrogates are difficult to formulate. There remains a need for further studies in regions with rich biological data sets to test the effectiveness of different coarse-filter surrogates. This is essential for effective and transparent decisions by conservation planners and to advance our understanding of how to use imperfect data on biodiversity to maximize the chances of favourable conservation outcomes for as many species as possible.

Chapter summary

- Although the classification strength of coarse-filter surrogates based on both abiotic (environmental attributes) and biotic (freshwater fish) classifications were significantly better than random, the classification strength of each was low.
- There was a relationship found between classification strength and surrogate effectiveness.
- No single coarse-filter classification method (UPGMA, naïve Bayesian or DFA) was consistently more effective than the other methods for representing freshwater fish.
- Regardless of the target or number of classes, the three coarse-filter surrogate methods were not effective at representing freshwater fish species. In addition, there was no significant difference in the effectiveness of abiotic and biotic classifications for representing freshwater fish species.
- There is a need for further assessments aimed at quantifying the effectiveness of surrogates for representing freshwater species.

Chapter 5

Effective control of aquatic invasive species in tropical Australia[1]



[1]Januchowski-Hartley, S. R., VanDerWal, J. and Sydes, D. 2011. Effective control of aquatic invasive species in tropical Australia. *Environmental Management* 48: 568-576.

Introduction

Effective management of aquatic invasive species will contribute to the overall global effort to reduce freshwater biodiversity decline (Simberloff 2009). Most freshwater ecosystems are subject to multiple pressures, such as invasive species, agriculture intensification and urbanization (Didham et al. 2005). Complexities of achieving effective control or eradication of aquatic invasive species are further challenged by the technical solutions needed and by the budget constraints imposed on managers (e.g. Epanchin-Niell & Hastings 2010). Even when aquatic invasive species management strategies are applied, the effectiveness of the strategy is rarely monitored or quantified (Simberloff 2009; Stewart et al. 2007). This has been limited by accessibility to straightforward and robust methods (Palmer et al. 2005; Roni et al. 2008b). Yet, such quantification is valuable in addressing adaptive management practices (e.g. Downs & Kondolf 2002; Christian-Smith & Merenlender 2010), and if conducted at various stages of management could document temporal changes in prevalence and abundance (Blossey 1999; Stewart et al. 2007).

Novel approaches have been applied to determine the factors influencing the distribution of species (native and introduced). One such approach is the application of ecological niche modelling (Peterson 2003; Elith et al. 2006; Peterson & Vieglais 2008; Steiner et al. 2008; Dullinger et al. 2009). The application of ecological niche models to forecast the spread of invasive species has shown to be an effective tool for proactive management (Clark et al. 2001). These models can be used to estimate the suitability of particular habitats to support invasive species, associating where a species occurs with a suite of environmental descriptors as well as other indicators, such as propagule pressure, expected to influence species' persistence (e.g. Dullinger et al. 2009).

VanDerWal et al. (2009) extended this further, suggesting that if such factors also influence the abundance of the species it may follow that those habitats with high environmental suitability will support higher species abundance. Not only would the application of ecological niche models provide managers with a better understanding of those factors driving potential species distributions but could also estimate the level of invasion (referred to here as local abundance) (Chytrý et al. 2008). The coupling of ecological niche modelling with invasive species abundance data, in 'managed' and 'non-managed' stream reaches and wetlands, could be used to evaluate the effectiveness of on-ground management for reducing and containing invasive species. Benefits gained from continued management investment could then be assessed by comparing the difference in species abundance between non-managed and managed areas over different time periods.

Here I demonstrate the application of ecological niche modelling and linear quantile regression to assess the effectiveness of management actions targeting the invasive macrophyte, olive hymenachne in the Wet Tropics of northern Australia. In Australia bioregions are large, geographically distinct areas of land with common characteristics such as geology, landform patterns, climate, ecological features and plant and animal communities (DSEWPC 2011). To date, there has been no quantitative assessment of the habitat properties or of other factors such as propagule pressure (as defined by Williamson & Fitter 1996; Lockwood et al. 2005; Colautti et al. 2006) that act as determinants of invasive macrophyte occurrence or infestation level in the Wet Tropics. Managers also require straightforward and repeatable methods that can be used to quantify management effectiveness. Often such approaches are not readily accessible, but would provide managers with a better understanding of factors influencing invasion and enable them to quantify effectiveness of their management programs. To begin addressing this, I asked three questions: 1) where do potentially suitable environments to support the invasive macrophyte olive hymenachne (*Hymenachne amplexicaulis*) occur in my study area; 2) can environmental suitability predicted by ecological niche models predict the upper limits of olive hymenachne abundance; and 3) can the relationship between environmental suitability and abundance be used to quantify the effectiveness of management (reduction in local abundance) under different management investments?

Methods

This study focused on the Tully-Murray and Herbert River catchments in the southern part of the Wet Tropics (Figure 5.1). I used existing spatial data on wetlands, which were mapped at a scale of 1: 100 000 by the Queensland Department of Environment and Resource Management (DERM) (DERM 2009).

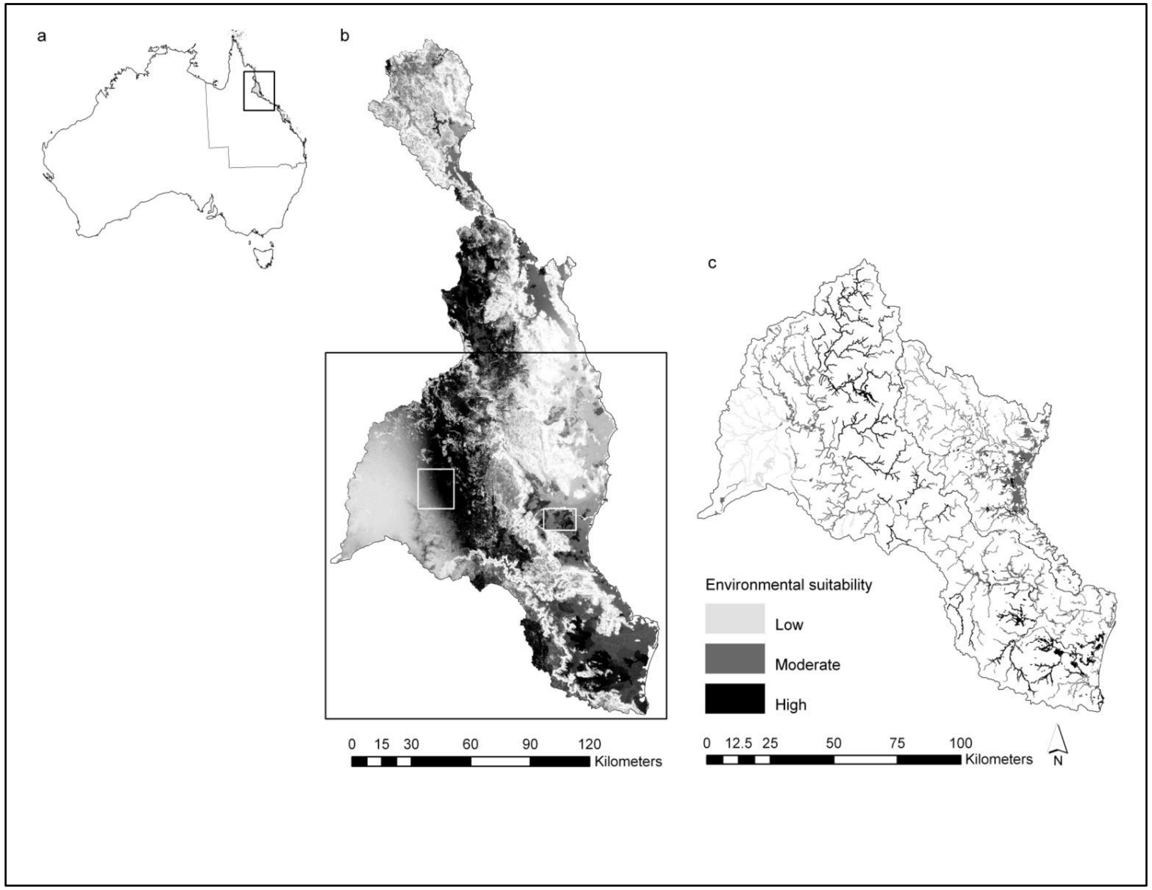


Figure 5.1 a) Location of the study area; b) Wet Tropics showing the distribution of environmental suitability, as determined by Maxent (Phillips et al. 2006), for olive hymenachne (*Hymenachne amplexicaulis*). The white boxes highlight areas of interest where environmental suitability for olive hymenachne is variable; and c) Tully-Murray (upper) and Herbert (lower) catchments with thresholds of environmental suitability, represented within individual stream reaches and wetlands: low (0 – 0.07), moderate (0.10 – 0.44) and high (0.44– 0.76), for olive hymenachne (*Hymenachne amplexicaulis*).

Stream reaches were delineated from a 30-m-resolution digital elevation model (see Appendix C) with an added 10-m buffer around the extent of each stream reach. The delineated reaches represented six stream orders from the headwaters (order 1) to the main river channels (orders 5 and 6). I considered 1353 mapped wetlands and stream reaches in the Tully-Murray and 2736 in the Herbert catchment.

Study species

Olive hymenachne is a robust rhizomatous perennial grass native to seasonally flooded environments along river banks and wetlands in South America and the West Indies (Gordon & Yasmira 2007). It was introduced as a commercial cultivar to Queensland, Australia in the early 1970's. Subsequently the plant has rapidly invaded freshwater ecosystems across northern Australia, proving particularly successful in the Wet Tropics. In the Wet Tropics olive hymenachne has a competitive advantage over native plants due to its rapid adaptation to changes in water level and nutrient uptake. This competitive advantage has resulted in olive hymenachne causing major socio-economic and environmental impacts in wetland and stream ecosystems (Sydes 2009). Degradation caused by extensive olive hymenachne infestations such as reduction in water quality, flow alterations, and blocked fish passage (Pusey et al. 2004) pose threats to the unique fauna that characterize the rivers of the Wet Tropics (Houston & Duivenvoorden 2002; Pusey et al. 2004; Sydes 2009).

Ecological niche modelling

I used the ecological niche model Maxent (Phillips et al. 2006; Phillips & Dudik 2008) to estimate the environmental suitability of olive hymenachne. Maxent is a deterministic model that has been shown to outperform other algorithms and techniques traditionally used to predict environmental suitability (Elith et al. 2006). Maxent can be used to address a number of questions related to invasive species, including modelling the increased risk of invasions under changing climate scenarios (e.g. Bradley et al. 2010), determining the relationship between past and current land use to predict future spread scenarios (e.g. Ficetola et al. 2010), predicting establishment success (e.g. Strubbe & Matthysen 2009) and identifying source populations (e.g. Steiner et al. 2008). This modelling method does make assumptions (e.g. equilibrium and environmental information limits the species distribution) and suffers from issues common to such algorithms (e.g. uncertainty when projecting onto novel environments (Peterson et al. 2007; but see Phillips 2008) and sample selection bias in training data

(Phillips 2008). However, these concerns are not applicable to this study because here I extend the current distribution (not projecting onto novel environments) of olive hymenachne for which the distribution is aggressively monitored such that any observed aggregation of occurrences should not be misinterpreted as sampling bias. Although there may be minor differences in the current prediction due to different algorithms, the pattern of distribution (including the predicted environmental suitability) would likely be consistent across most model algorithms, as demonstrated by Elith et al. (2006).

The Maxent model runs used the optimized settings outlined in Phillips & Dudik (2008). Average model performance was assessed using the area under the receiver operating characteristic curve (AUC) (Fielding & Bell 1997), using a leave-one-out cross-validation procedure.

I used only geographically unique occurrences (i.e., redundant records were removed by Maxent before commencing analysis) so that predicted environmental suitability was not biased toward areas with a higher number of records. Maxent models were trained using 385 unique occurrence records and 500 ‘background’ records, which were regarded as a random sample from the potential sampling distribution in the Wet Tropics. Both training and background records represented habitats beyond the two catchments defining my study area, in an effort to represent the range of environments where olive hymenachne occurs and could occur across the entire Wet Tropics. Background records were generated using Hawth’s Tools in ArcGIS 9.3. Each of the 885 training and background records was identified to a mapped stream sub-catchment area. These areas were used to attribute specific environmental descriptors and proxy values for propagule pressure to the training and background points that were measured as percentages of total sub-catchment area

Environmental descriptors and proxies of propagule pressure were prepared for the entire Wet Tropics (Table 5.1). All variables were represented as 30-m-resolution raster data. Where applicable I converted vector mapping to 30-m-resolution raster grids using ArcGIS 9.3. Slope was selected as a topographic descriptor of olive hymenachne as the species tends to occur in areas with minimal slope, where slower flowing water is common, and is unlikely to occur in the fast flowing steep environments along the escarpment that traverses the region. Average annual rainfall and topographic wetness index were used to indicate the balance between water accumulation and drainage conditions at the local scale, as olive hymenachne has been shown to prefer, in both its native and naturalized range, deeper and slower flowing areas of wetlands and streams where standing water is present all year (Gordon & Yasmira 2007; Sydes 2009). Alluvium was selected as it is commonly reported as a soil feature associated with habitats that support olive hymenachne (Sydes 2009). My proxies for propagule pressure were the percentage of sub-catchment area occupied by intense and low-intensity agriculture. Use of variables accounting for human activity in the landscape has previously been shown to act as an effective proxy for propagule pressure (e.g. Pyšek & Prach 1993; Chytrý et al. 2008). These proxies improve model performance when data from the species native range are not available, and the species may not have yet reached a state of equilibrium (Chytrý et al. 2008; Dullinger et al. 2009).

Table 5.1 Environmental descriptors and proxies of propagule pressure used to predict environmental suitability for olive hymenachne using Maxent (Phillips et al. 2006). Also shown are the spatial data sources from which the environmental descriptors and proxies for propagule pressure were derived.

Environmental descriptors	Sources
Slope (percent)	30-m-resolution digital elevation model (Appendix C)
Average annual rainfall (mm)	30-m-resolution digital elevation model (Appendix C) and ANUCLIM 5.1 (Houlder et al. 1999)
Topographic wetness index	30-m-resolution digital elevation model (Appendix C)
Alluvium soil (presence/absence)	1: 100 000 geological and soil mapping (DERM 2004)
Proxies of propagule pressure	
Percent of sub-catchment dominated by intensive agriculture (e.g. irrigated sugar cane, banana farming)	1: 50 000 land use mapping (DERM, see Witte et al. 2006)
Percent of sub-catchment dominated by low intensity agriculture (e.g. cattle grazing)	1: 50 000 land use mapping (DERM, see Witte et al. 2006)

Environmental suitability as part of the species' potential distribution was estimated as a function of the above variables for each 30m x 30m raster grid. The output from the Maxent was represented as a continuous logistic output ranging from 0 to 1, with higher values indicating higher environmental suitability for olive hymenachne. I used Zonal Statistics in

ArcGIS 9.3 to summarize the average environmental suitability for the mapped stream reaches and wetlands in the Tully-Murray and Herbert catchments.

To demonstrate the spatial variability of environmental suitability across the study area I applied the ‘balance training omission, predicted area, and threshold value’ to define a threshold of low environmental suitability for olive hymenachne (0.07) (Phillips & Dudik 2008). I selected the ‘balance’ threshold to define low environmental suitability as it was one of the lowest threshold values reported by Maxent, and had the lowest commission errors. I applied the maximum training sensitivity plus specificity threshold to define the upper limit of moderate suitability (0.44), that meant that areas considered as highly suitable would have to have a predicted environmental suitability value greater than 0.44. I selected the maximum training sensitivity plus specificity threshold to define the lower limit of areas considered as highly suitable because this approach has previously been shown to have one of the lowest false positive and negative rates (e.g. Liu et al. 2005). In fact, it had the lowest reported omission and commission rate over any other threshold reported in my Maxent output. In addition, my selected combination of thresholds to define low, moderate and high environmental suitability were identified as the best depiction of stream and wetland environmental suitability for olive hymenachne based on expert opinion. I used the expert opinion of the Cassowary Coast Regional Council’s (CCRC) strategic coordinator, who had been working on olive hymenachne control in the Wet Tropics for seven years (Damon Sydes, CCRC, personal communication).

Quantifying management effectiveness

I sought to quantify the limiting effect of management actions on olive hymenachne local abundance. While it was beyond the scope of the work presented here to evaluate the influence of multiple limiting factors, I recognize the need to identify how multiple factors may or may not interact to influence deviation from upper limits.

Given the history of olive hymenachne presence in the Tully-Murray and Herbert River catchments (approximately 25 years) and that intensive monitoring and management was only established 7 years ago it is difficult to estimate exactly when infestations began in each stream reach and wetland. The data used for the two and five year management areas used in this study are based on well established infestations that existed at least seven years ago when

CCRC began to implement the current long-term management strategy. The aim of the intensive control strategy used for well established infestations of olive hymenachne is to make an impact on the overall abundance in the catchment. The *ad hoc* managed areas are a combination of well established and more recently observed infestations, however, CCRC did not have an estimate of the time such establishment for these infestations either. I do recognize the value of obtaining this information for newly observed infestations and for future studies.

The records of olive hymenachne abundance in managed (spray control areas) and non-managed wetlands and streams were obtained from two sources: CCRC for the Tully-Murray and through remote sensing for the Herbert catchment. The Tully-Murray records (n = 46) were collected by CCRC management crews while carrying out management actions and field surveys. Local abundance was estimated (by CCRC management crews) as the proportion of total stream reach or wetland area infested (ha) with olive hymenachne. The Herbert catchment estimates (n = 29) were derived from high resolution aerial photography (25 cm) (L. Wearne et al. unpublished data) as the size of the area and general difficulty of accessing sites (e.g. crocodiles) ruled out the effective use of ground surveys. Remote sensing can readily detect changes in vegetation type and has proven to be an effective method for identifying aquatic invasive species infestations among native vegetation (Lass et al. 1996; Wang et al. 2008). Infestations of olive hymenachne were interpreted from aerial photographs using a supervised classification in ECHO spectral classifier (http://cobwebecnpurdueedu/~biehl/MultiSpec/). I then used Zonal Statistics in ArcGIS 9.3 to determine the local abundance.

I assessed the ability of predicted environmental suitability to estimate the upper limit of olive hymenachne abundance using linear quantile regression (e.g. VanDerWal et al. 2009). Linear quantile regressions are robust regression analysis techniques that permit the assessment of limiting relationships (Scharf et al. 1998; Cade et al. 1999). To demonstrate how the upper limit of abundance relates to a more commonly applied regression method, I also evaluated the ability of ordinary least squared (OLS) regression to explain the mean relationship between environmental suitability and abundance.

The differences of management investment times were assessed by quantifying the deviation from the upper limit of abundance (residuals as a proportion of the upper limit). Management investment, as examined here, represented varying lengths of time over which spray control was repeated. I identified four management investment times: no management (n=29); *ad hoc* (n = 5); two years (n = 23); and five years (n = 18). *Ad hoc* management represented areas where management occurred infrequently and opportunistically; the two and five year management times were used to represent consistent management investment by CCRC on a bi-annual basis for at least the defined time period. All analyses were performed using R, version 2.5.1 (http://wwwR-projectorg) and the quantreg library.

Results

The average Maxent model was accurate (AUC = 0.98). The maximum predicted environmental suitability was 0.78. While much of the upland and lowland areas with low slope (indicated by the white boxes in Figure 5.1) in the Tully-Murray and Herbert River catchments were predicted to have at least moderately suitable environments for olive hymenachne, environmental suitability of these areas was variable (Figure 5.1b). Based on my selected thresholds the majority of the Wet Tropics stream reaches and wetlands had moderately (58%) or highly (32%) suitable environments for olive hymenachne. Only 10% of the 4089 mapped stream reaches and wetlands in the study area were of low environmental suitability (Figure 5.1c). The low suitability areas occurred in steep terrain and along the immediate coastline, where salinity levels are unsuitable for olive hymenachne.

For stream reaches and wetlands I used to demonstrate the relationship between environmental suitability and abundance those with no management had the highest average abundance (0.33 of the total stream reach or wetland area). Streams and wetlands under *ad hoc* management had slightly less average abundance, with olive hymenachne occupying 0.26 of the total stream reach or wetland area. In stream reaches and wetlands managed for two years, olive hymenachne occupied, on average, 0.07 of the total area, while those managed for five years had the lowest average abundance (0.05 of total stream reach or wetland area).

The upper limit of abundance was defined by the 95th percentile of the quantile regression. There was a significant positive relationship between mean and upper limit of the relationship between environmental suitability and abundance as shown by the OLS (slope = 0.42, $p \leq 0.001$) and the 95th percentile of the quantile regression (slope = 0.69, $p \leq 0.001$). Although both relationships were significant, the amount of variance explained was low for the OLS regression (R^2= 0.16).

All managed stream reaches and wetlands (*ad hoc*, 2 and 5 years) showed environmental suitability below 0.65, while those that were not managed ranged between 0.15 and 0.75, the majority around 0.70 (Figure 5.2a). The majority of stream reaches and wetlands managed for two or five years had abundance values distributed below the OLS regression; however, with two exceptions the first lying just above the OLS regression was managed for five years, while the other above the 95th percentile was managed for two years (Figure 5.2a). Abundance of olive hymenachne in non-managed streams and wetlands was variable, ranging from 0 to 0.60 of the total stream or wetland area.

Ad hoc management was the least effective management investment strategy, with less reduction in local abundance (-0.40, SE = +/- 0.08) than in those streams and wetlands that had at least two (-0.85, SE = +/- 0.05) or five (-0.92, SE = +/- 0.04) years of management invested (Figure 5.2b). There was no significant difference in the reduction of olive hymenachne abundance in streams and wetlands with *ad hoc* management compared to non-managed streams or wetlands (Figure 5.2b). However, there was a significant difference in the reduction of olive hymenachne abundance between those streams and wetlands that had not been managed, and those that had had at least 2 years of management invested.

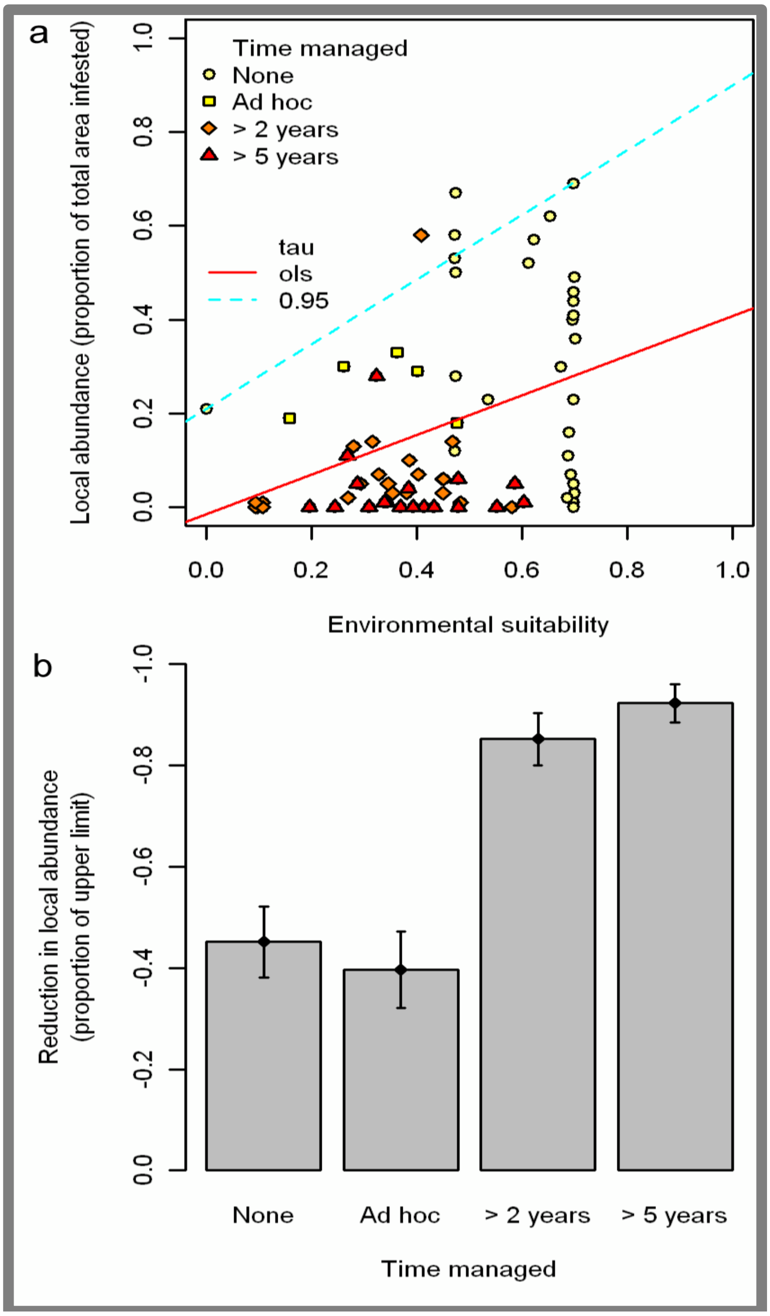


Figure 5.2 a) Relationship between predicted environmental suitability (X-axis) and olive hymenachne (*Hymenachne amplexicaulis*) local abundance (Y-axis) as a proportion of total stream or wetland area (ha) depicted for two percentiles ('tau'), ordinary least squares (OLS – solid line) regression and the 95th percentile (dashed line) based on linear quantile regression, which represents the upper limit of local abundance; symbols represent amount of time managed; and b) relationship between management investment (X-axis) and the reduction in local olive hymenachne abundance as a proportion of the upper limit of abundance (±standard error), represented here by the 95th percentile (Y-axis).

Discussion

Using Maxent I predicted suitable environments for olive hymenachne in the Wet Tropics, and demonstrated the utility of using both environmental descriptors and proxies of propagule pressure to determine environmental suitability for an invasive species. I have shown a strong, consistent relationship between predicted environmental suitability from ecological niche models and spatial variation in the abundance of this species. There was a significant positive relationship between local abundance and environmental suitability. However, little of the variance in abundance could be explained by OLS regression. This was a novel application, demonstrating the relationship between environmental suitability and abundance to quantify the effectiveness of management (reduction in local abundance) under different management investments.

The relationship between management investment and olive hymenachne abundance showed a diminishing return after two years (Figure 5.2b). This threshold reflects the nature of the olive hymenachne management problem, related to the prolonged seed bank, and management strategy employed by CCRC in several sub-catchments. Over the past seven years, CCRC have adopted an intensive control strategy to reduce the total abundance of olive hymenachne in highly infested stream reaches and wetlands. Once abundance was reduced CCRC then shifted their effort from high volume spray control to more directed spraying of subsequent emergent vegetation. This approach, as I demonstrate, appears to be effective in reducing high abundances, and maintaining that reduction. It would be beneficial for CCRC to continue reporting on management investment up to the expected ten-year seed-bank viability (Sydes 2009) as the additional information could assist in confirming if the threshold I determined is an accurate depiction of the relationship between management investment and reduction in abundance of olive hymenachne.

More broadly, longer-term reporting and reassessment of management effectiveness after ten years of investment could also provide the evidence necessary to endorse a manager’s decision to discontinue management and move on to other areas. Longer-term reporting and reassessment of management effectiveness by CCRC up to the ten-year seed-bank expectancy could provide considerable benefit to managers in other tropical regions, providing information about the effort needed for containment or eradication in particular wetland and stream types.

While my results indicate CCRC management has a positive influence on reducing olive hymenachne abundance, the geographic location of particular stream reaches and wetlands should be given further consideration when allocating management actions across the landscape. Two of the CCRC managed wetlands allowed me to identify external factors that were not accounted for in the predicted environmental suitability and that could hamper management effectiveness. The two wetlands had high environmental suitability and abundances comparable with most non-managed areas (Figure 5.2a). One had been managed for two years the other for five years. The geographic location of the wetlands in the landscape was the factor that limited management success. Both wetlands are situated at the bottom of the catchment, with a number of infested stream reaches and wetlands upstream flowing to them. Consequently, they are likely exposed to re-infestation annually. CCRC may not wish to write-off the investment in these sites, despite continual reinvasion, and give further consideration and management priority to upstream infested areas to restrain further reinfestation.

To date, one of the major inefficiencies of invasive species management has been the general lack of reporting on management intervention and successful examples of sustained management (Simberloff 2009; Yokomizo et al. 2009). Having the ability to determine and monitor the effectiveness of management investments, as shown here, can lead to more informed and adaptive management strategies (Johnson 1999; Park 2004; Stewart et al. 2007). I identified several limitations associated with the availability of data on management investment in the study region. For example, CCRC is the only local government agency that had available data on management investment over time, with four other local government agencies lacking any clear evidence on which to assess management effectiveness. Further, while the data provided by CCRC were useful for us to demonstrate my proof-of -concept, these data had clear limitations in allowing me to further explore questions about the effectiveness of different types, or combinations of, management actions (e.g. revegetation, fire). This was mainly due to the poor sampling representation of other management strategies. With additional data on spray control and other types of management actions, the evidence needed to inform other managers targeting olive hymenachne in this and other tropical regions (e.g. south Florida) could be assembled.

There are several advantages that these methods can offer to managers and researchers. First, these methods can be used to address similar questions in other regions and across freshwater, terrestrial or marine realms to evaluate management and report on limitations and successes. Second, using a measure of best-fit, the percentile that best represents the modelled relationship between environmental suitability and abundance as determined by the linear quantile regression can be extrapolated to other stream reaches and wetlands. Predicted abundance could also be used in relation to time spent carrying out management actions to determine management costs (see for example Chapter 5). This type of information can be used in spatial prioritization models to identify stream reaches and wetlands that are of highest priority if managers wish to effectively minimize spread and re-infestation whilst minimizing their management costs.

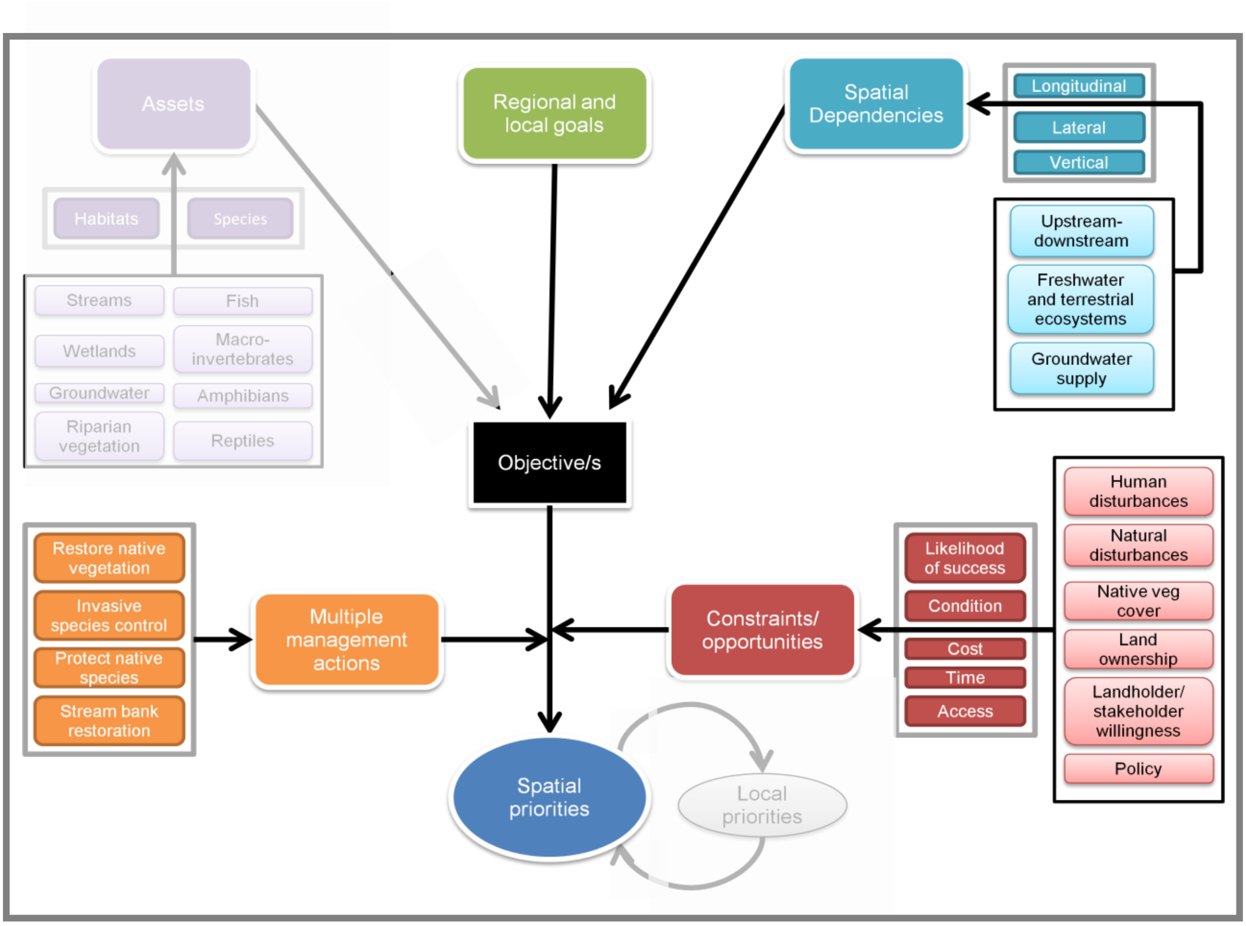
Chapter summary

- There is a consistent relationship between environmental suitability derived from ecological niche models and spatial variation in the abundance of aquatic invasive species. Further, the relationship between environmental suitability and abundance can be used to quantify the effectiveness of management (reduction in local abundance) under different investments.
- Maxent produces robust predictions of suitable environments for olive hymenachne when using environmental descriptors and proxies of propagule pressure. Habitat suitability and olive hymenachne local abundance varied across the Tully-Murray and Herbert River catchment. Highly suitable environments were predicted to occur across a broad area of the Herbert River catchment.
- The relationship between management investment and olive hymenachne abundance showed a diminishing return after two years.
- Management by Cassowary Coast Regional Council is having a positive influence on reducing olive hymenachne abundance. However, the geographic location of

particular stream reaches and wetlands should be given further consideration when allocating management actions across the landscape.

Chapter 6

A systematic approach for prioritizing multiple management actions for invasive species[1]



[1]**Januchowski-Hartley, S. R.**, Visconti, P. and Pressey, R. L. 2011. A systematic approach for prioritizing multiple management actions for invasive species. *Biological Invasions* 13:1241-1253.

Introduction

There are high economic costs associated with managing invasive species infestations to eradicate them or reduce the probability of their reinvasion. However, the costs of managing the spread of and damage resulting from invasive species are rarely accounted for when making management decisions or when allocating funding to management programs (Simberloff 2009). Costs vary depending on the species concerned, the ecosystem it has invaded, and the methods used to manage it. Management costs of a single well-established species can reach millions of dollars. For example, in South Africa, the total cost of clearing 15 invasive tree species that occupied almost 17 million hectares of forestry lands was estimated at $60 million USD/year over 20 years (van Wilgen et al. 2001). However, this estimate was reduced by $30 million USD/year by recognizing that several of the species did not affect natural systems and by considering multiple management actions. This study demonstrated the financial benefits that can be gained from 1) using spatially explicit planning strategies, 2) considering multiple management actions, and 3) accounting for the costs associated with different actions.

Methods used by managers to identify management priorities for invasive species typically consider the values of biodiversity and ecosystems affected, but few methods account for the costs associated with management actions (e.g. Gosper & Vivian-Smith 2006). By costs I mean the financial requirements of applying management actions, including salaries, travel costs, and purchase or lease of materials and capital equipment. Prioritisation methods commonly used by pest managers range from “best guesses” to more explicit methods such as: 1) the use of geographic information systems to overlay different natural values (e.g. Roura-Pascual et al. 2009a) and 2) decision-support methods that use scoring approaches to combine a range of criteria (e.g. Ratcliffe et al. 2009; Roura-Pascual et al. 2009b). I refer hereafter to these methods as non-systematic because they do not account for one or both of two key characteristics: 1) explicit, quantitative objectives for control of invasive species; and 2) the contribution each action or set of actions makes towards achieving an objective.

The large and expanding literature on systematic conservation planning describes methods that have two characteristics in common (Margules & Pressey 2000): 1) explicit and usually quantitative objectives and 2) assessment of areas or area-specific actions according to their relationship with other areas and actions. Explicit, quantitative objectives inform managers about the local, regional or national significance of their investments, make available a powerful array of decision-theory methods for solving spatial problems, and allow managers to measure progress through time (e.g. Carwardine et al. 2008; Segan et al. 2010). Two typical aspects of context-dependent assessment are complementarity and connectivity, so that the contribution of actions and areas depends on the features shared between areas and the spatial relationships between areas (Vane-Wright et al. 1991; Nicholls & Margules 1993; Margules & Pressey 2000; Magurran 2004; Sarkar et al. 2006). The use of complementarity is considered the main common denominator of systematic methods, reducing unwanted redundancy of conservation actions and improving the cost-effectiveness of solutions to conservation problems (Margules &Pressey 2000; Justus & Sarkar 2002b). Connectivity, which influences the likelihood of invasion and reinvasion from source populations, is a particularly important consideration for riverine and wetland ecosystems. Without spatial considerations regarding complementarity and connectivity it is difficult to identify the best configurations of areas to achieve a set of objectives (e.g. Beger et al. 2010; Hermoso et al. 2011b).

To address the limitations of non-systematic methods for prioritizing management of invasives, I propose a method that can be used to identify spatially explicit configurations of areas to implement management actions. I aim to minimize management costs and the likelihood of reinvasion. I demonstrate the application of this method to identifying management priorities for an invasive aquatic macrophyte, olive hymenachne (*Hymenachne amplexicaulis*), which has spread across tropical northern Australia. This work was developed and carried out in collaboration with the manager responsible for reducing the spread of olive hymenachne in the Tully-Murray catchment in the Wet Tropics of north-eastern Queensland, Australia (see Chapter 2, Figure 2.1). I present the results of five management prioritisation scenarios. Each scenario has unique parameters and objectives aimed at reducing the area infested with olive hymenachne. Using the modelled solutions for each of the five scenarios, I illustrate: 1) the higher cost-effectiveness of systematic planning, relative to non-systematic methods, to prioritize management actions for invasive species, 2) the higher cost-effectiveness and reduced likelihood of reinvasion when accounting for connectivity between areas in the decision method, and 3) the reduction in total cost when setting objectives across all planning units in the study area rather than setting objectives only for certain ecosystem types within the study area.

Methods

Study species

Olive hymenachne is a robust rhizomatous perennial grass native to seasonally flooded environments along river banks in tropical and subtropical wetlands of America (Gordon & Yasmira 2007). Olive hymenachne was introduced as a commercial cultivar to Queensland, Australia in the early 1970s. It was first reported invading agricultural drains and natural waterways in northern Queensland in the late 1980s. Subsequently, the plant has invaded freshwater ecosystems across northern Australia causing major environmental impacts in wetlands and streams in much of eastern Queensland and parts of the Northern Territory and northern New South Wales. Olive hymenachne commonly grows from 1- 2.5 m tall, with leaves 10-45 cm long and up to 3 cm wide. It can be distinguished from Australia's native *Hymenachne* species by the characteristic stem-clasping leaf bases (Sydes 2009). Olive hymenachne produces large numbers of viable seeds that germinate readily on waterlogged soil. In northern Australia, flowering occurs between September and May, with most flowering occurring between mid-April and May. However, in the Wet Tropics, olive hymenachne is reported to flower up to three times a year, outside of the typical flowering seasons (Damon Sydes, Cassowary Coast Regional Council, personal communication).

Olive hymenachne develops roots at each node along the stolon when contact is made with moist soil. Secondary dispersal, or floating, of olive hymenachne stolons in flood waters is one of the major factors causing the spread of the plant during annual flooding events typical of northern Australia. The seed bank remains viable for up to 10 years (Sydes 2009). To ensure complete removal of olive hymenachne and its seed bank, infested areas in the Wet Tropics region are managed for up to 15 years. Dense stands of olive hymenachne can modify water flow and watercourses. Floating mats become dislodged in floods and are easily transported downstream. Weed mats can damage infrastructure, clog small streams, and block fish passage (Houston & Duivenvoorden 2002). The establishment of olive hymenachne can fundamentally change vegetation structure by displacing emergent and submergent native species. Invasions of the species dramatically reduce diversity of native aquatic plant, invertebrate and fish assemblages, and support increased abundances of introduced fish species (Houston & Duivenvoorden 2002).

Planning units

I identified 1353 wetlands and stream reaches across the Tully-Murray study region, and defined these reaches as my planning units. Wetlands were mapped at a scale of 1:100 000 and classified by the Queensland Department of Environment and Resource Management (DERM 2009). Discrete wetlands were identified as single planning units regardless of their size. Stream reaches (sections of streams between confluences) were delineated from a digital elevation model with a spatial resolution of 30 m (see Appendix C) using ArcHydro 1.3. I applied a 5 m buffer to each side of the defined stream reaches using ArcGIS 9.2.

Species distribution modelling

I used Maxent (Phillips et al. 2006) for all distribution modelling. Maxent is based on a maximum entropy algorithm for the prediction of species' potential geographical distributions. It has been shown to be generally better than other modelling methods for predicting species occurrences, and deals well with the small sample sizes commonly available for species distribution modelling (Elith et al. 2006; Hernandez et al. 2006).

I collated presence/absence data (47 total observations) for olive hymenachne from local managers and researchers in the Tully-Murray catchment. Presence/absence data were collected from sites with a range of environmental conditions. Olive hymenachne has been present in the landscape for over 15 years, and has likely reached the potential range of environmental characteristics present in the catchment (D. Sydes, Cassowary Coast Regional Council, personal communication). Therefore, even if the distribution of olive hymenachne is still expanding, it is not likely to encounter different environmental conditions from those behind the expansion front.

Presence was determined in planning units where: 1) managers are currently managing infestations or 2) infestations are known but there is no active management. The training dataset consisted of 36 presence points from the 47. The remaining 11 points were known absences. I used the 11 known absences from the field surveys and generated an additional 100 background points, which were regarded as a random sample from the sampling distribution. I located the background points with Hawth's Tools in ArcGIS® 9.2 (Environmental Systems Research Institute 2006) and decided on 100 as sufficient to represent the distribution of environmental conditions in the study area (Phillips & Dudik

2008). As potential predictors, I used a combination of landscape-scale environmental variables that, based on advice from managers, have the most influence on the probability of olive hymenachne infestation: 1) presence of intensive agriculture (as a surrogate for areas of high nutrient input), 2) presence of low-intensity grazing, 3) wetland type, 4) elevation, and 5) average foliage projective cover of woody vegetation. All environmental data were analysed in 30-m resolution spatial layers.

Maxent produces spatial predictions of probability of presence (hereafter referred to as probability of infestation) as logistic output values ranging from 0 (not suitable) to 1 (most suitable) (Phillips et al. 2006). Probability of infestation was determined, as a function of the environmental variables, for each 30m x 30m cell within the study area. I used Zonal Statistics in ArcGIS 9.2 to determine the average environmental suitability of each of the planning units, based on the 30m x 30m cells falling within planning units. I converted the logistic output value estimated by Maxent to a binary estimate of infested or non-infested planning units using the 'equal training sensitivity and specificity threshold' which is automatically reported by Maxent. This threshold has been used in other studies (e.g. Cantor et al. 1999), and has been shown to produce low false positives and negatives (< 20%) (Liu et al. 2005). Based on this threshold, I considered only planning units with $P \geq 0.30$ (where P is the probability of infestation) as either currently supporting or having the potential to support olive hymenachne (Figure 6.1). I also assumed that planning units potentially supporting olive hymenachne could act as sources of infestation as did planning units with known infestations. Based on the local manager's knowledge of the species, this was a reasonable assumption, given the species' rapid spread across the study area since it first established there (D. Sydes, Cassowary Coast Regional Council, personal communication).

I used the cross-validation setting in Maxent to validate my model. The cross-validation procedure divides the modelled data into replicate folds. I used a leave-one-out cross validation. For evaluation of model performances I used the threshold-independent receiver operating characteristic (ROC) which addresses false negative and false positive predictions. The ROC is quantified by the area under the curve (AUC), with values ranging from 0 to 1 and high values indicating good performance. An AUC > 0.60 is usually defined as acceptable model performance (Fielding & Bell 1997). The average modelling performance of the cross-validated Maxent models was 0.95.

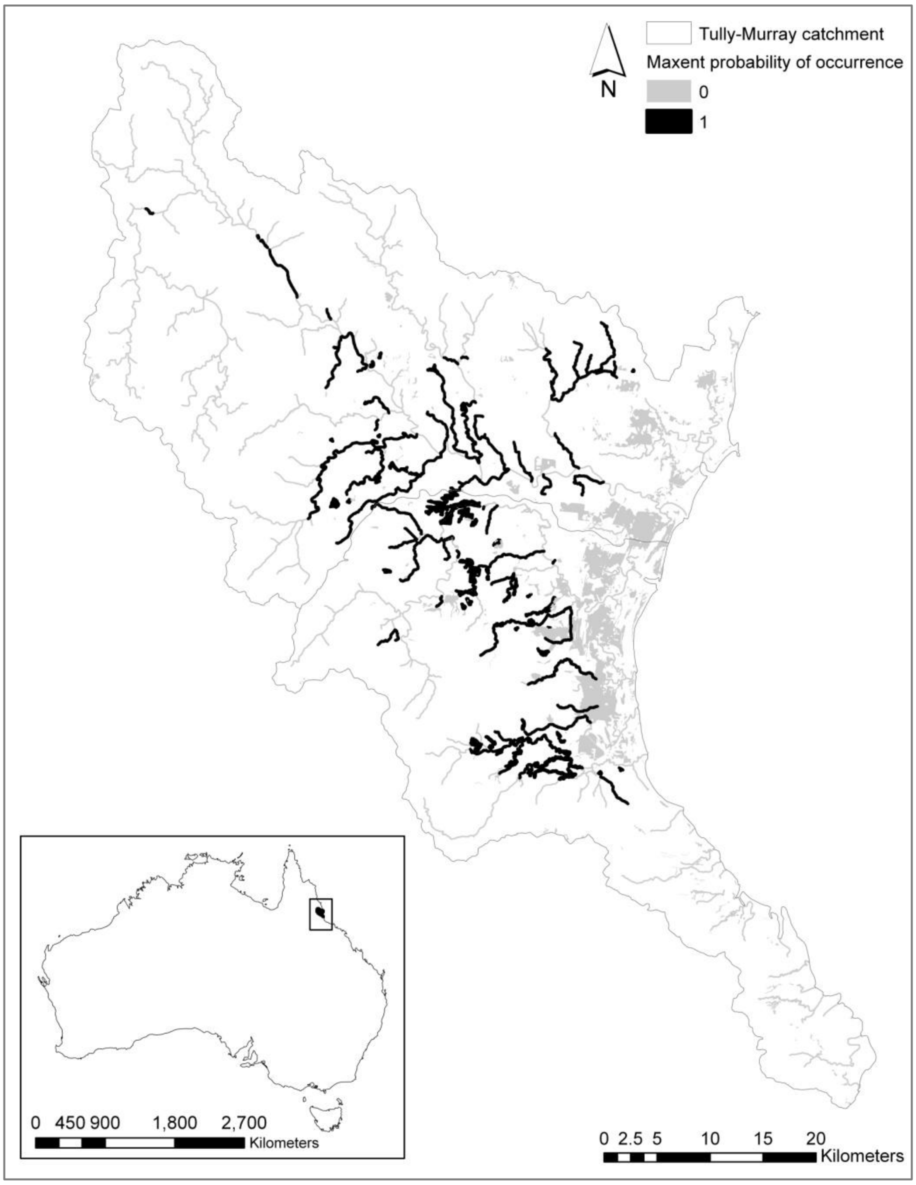


Figure 6.1 Probability of occurrence of olive hymenachne in the Tully-Murray study area in north-eastern Queensland, Australia. Across 1353 planning units, values of zero indicate that olive hymenachne is not predicted to be present; values of 1 are those where the species currently occurs or is predicted to occur by a Maxent model. Presence is defined by a threshold probability of occurrence, $P \geq 0.30$.

Estimating area infested

I did not have access to relative abundance estimates for all planning units. Therefore, I estimated the "potential" area infested (ha) by olive hymenachne in all planning units using data on the proportion of area infested by olive hymenachne in managed (n = 46) and non-managed (n = 29) planning units. I regressed values of proportion infested against the probability of olive hymenachne occurrence (as determined by Maxent) using quantile regression, because the variance of the proportion infested increased with increasing probability of occurrence. Quantile regression is robust to outlying data values and skewed data distributions (Cade et al. 1999). Most of my observations were from planning units with large proportions infested and both low and high probabilities of occurrence, with fewer observations from planning units with moderate to low proportions infested.

By fitting quantiles of y (proportion of area infested) as a function of x (probability of occurrence), quantile regression estimates the position of the edge of a triangular data scatter (e.g. Johnson & VanDerWal 2009). The magnitude of the slope of each regression line is a measure of the size of the relationship between probability of occurrence and proportion infested. I determined the quantile that best described this relationship using a goodness-of-fit measure for quantile regressions (e.g. VanDerWal et al. 2009). I then used this quantile to predict the proportions infested for all managed and non-managed planning units using the modelled probabilities of occurrence. I multiplied the proportions by the areas of planning units to derive areas infested.

Management costs

I identified three types of costs associated with management of olive hymenachne in the Tully-Murray catchment. These were based on advice from the strategic coordinator at Cassowary Coast Regional Council (CCRC) who is responsible for decisions on pest management across the study area. I identified the most appropriate management action for each planning unit depending on the wetland type, size of the stream reach, and soil type. I considered the following three actions: 1) high volume spraying (HV), 2) HV + Argo (amphibious machine), and 3) revegetation.

The total cost of taking action in planning unit u (d_u) was a function of the amount of time spent managing a planning unit h_u, the number of people managing m_u and the fuel cost incurred in travelling from CCRC's depot t_u. The equation defining the total management cost of a single planning unit u was:

$$d_u = w_u * m_u * (h_u + 2) + t_u \qquad \text{(Equation 1)}$$

All variables are described in Table 6.1.

I had information on the number of hours spent undertaking management actions (*h*) for only a sample of managed planning units. To extrapolate this information to all planning units, I estimated the relationship between area infested with olive hymenachne and the amount of time spent managing a planning unit (actual management times recorded by CCRC managers). I did this for the HV (Equation 2) and HV + Argo (Equation 3) actions by fitting a linear regression model. In both models, the r^2 value was 0.73. The best fitting models were as follows:

$$HVTime\ (h) = 0.45 * area\ infested + 11 \qquad \text{(Equation 2)}$$

$$HVArgoTime\ (h) = 0.66 * area\ infested + 2.9 \qquad \text{(Equation 3)}$$

The cost associated with revegetation was not dependent on time because of the involvement of volunteers in this work. Rather, the number of plants to be purchased was the major driver of cost associated with this action. I used the cost incurred by CCRC for purchasing plants ($4 000 AUD/ha).

Objective function

My objective was to reduce the area infested with olive hymenachne to a specified level, while minimizing management costs and the number of connections (my proxy for probability of reinfestation) for each selected planning unit. The objective function was minimized using the simulated annealing algorithm in Marxan conservation planning software (Ball et al. 2009). Simulated annealing can find many close-to-optimal solutions for a multi-criteria objective function and can solve large problems (involving up to hundreds of thousands of planning units and features[1]) in a reasonable time. The Marxan software has been used in diverse conservation planning studies worldwide, including marine (e.g. Ban 2009; Beger et al. 2010), terrestrial (e.g. Adams et al. 2010; Visconti et al. 2010) and freshwater (Hermoso et al. 2011b; Linke et al. 2008) applications that range in scale from

[1] A feature is any biodiversity element that is targeted in a conservation plan (e.g. a species, habitat type, or natural process). The conservation features of interest for this work are stream reaches and wetlands which coincide with the units of conservation assessment (i.e., planning units).

local (e.g. Huber et al. 2010; Payet et al. 2010) to global (e.g. Rondinini et al. 2005). As far as I know, this is the first application of Marxan, and more generally of systematic conservation planning methods, to address the spatial allocation of management actions and funds for invasive species management at a local scale.

I defined the problem using the following objective function (all symbols and notations are referenced in Table 6.1):

$$\min\left(\sum_{f}^{F} p_f r_f H(\Delta_f)\left(\frac{\Delta_f}{t_f}\right) + b\sum_{i}^{I}\sum_{j\neq i}^{J} c_{ij}(1-x_i)x_j + \sum_{u}^{U} d_u x_u\right) \qquad \text{(Equation 4)}$$

The objective function is a mathematical notation of the problem a manager would like to solve. In this case, the problem is to achieve reduction in the total area infested with olive hymenachne in streams and wetlands at the minimum monetary and opportunity cost. By opportunity cost I mean the cost of having to treat a site again due to reinfestation. The best solution to the problem is the one with the minimum value of equation 4. p_f is the feature penalty factor, and is used in Marxan to weight the penalty for not meeting the objective for a given conservation feature in respect to the other elements of the objective function. I used iterative tests to determine an adequate feature penalty factor *(p* of 25) to ensure that the objective for each feature was met and that each feature was weighted equally. When the objective was removal of hymenachne across the study area (not only in particular wetland types), there was a single objective and single penalty value. r_f is the cost of meeting the objective for feature *f* starting from no representation in the conservation area network (see details in Game & Grantham 2008).

Table 6.1 Variable descriptions for Equations 1 and 4.

Equation 1	
d_u	Cost of undertaking a management action in the planning unit *u*
w	Cost/hour of work per person
m	Number of people involved in the action
h	Number of hours spent managing
t	Fuel cost of travelling to the planning unit from the Cassowary Coast Regional Council's depot
2	A constant representing time worked but not spent actively managing
Equation 4	
d_u	Cost of undertaking a management action in the planning unit *u*
a_{uf}	Amount of hymenachne infestation in planning unit *u* with feature type *f*. For the scenarios focused on all wetland types there was just one objective and one associated penalty. For scenarios focused on the two specified wetland types, *f* indicated the wetland type.
c_{ij}	Presence of a connection between planning unit *i* and planning unit *j* where *i* is upstream of *j*
x	Decision binary variable taking the value of 1 for planning units that are currently managed or are selected for management in the prioritization process
p_f	Penalty factor for feature *f* applied to the objective function to ensure the objective is met regardless of the total cost of taking management action
r_f	The cost of meeting the objective for each feature *f*
T_f	Objective for feature *f*, established as a percentage reduction in area covered by feature *f* infested with olive hymenachne
b	Boundary length modifier. A weighting factor used in Marxan to give different weight to the connectivity component (c_{ij}) in the objective function

Δ_f is the shortfall of potential hymenachne infestation reduced by the set of existing and simulated conservation areas relative to the objective of reduction for feature *f* (wetland and stream type). $\Delta_f = t_f - \sum_u^U a_{uf} x_u$.

$H(\Delta_f)$ is the Heaviside function and takes the value of 1 when $\Delta_f > 0$ and 0 otherwise.

The first part of the objective function $\sum_{f}^{F} p_f r_f H(\Delta_f)\left(\frac{\Delta_f}{t_f}\right)$ is equal to the cost that a manager would incur for having to meet the objective given the shortfall $_f$ for all features. An accurate description of this penalty comes from Game & Grantham (2008): “[The shortfall penalty] is based on the principle that if a conservation feature is below its target representation level, then the penalty should be an approximation of the cost of raising the representation of that conservation feature up to achieve the target. Thus, if one conservation feature is completely unrepresented, then the penalty would be the same as the cost of adding the simple set of planning units to meet the target”. This is achieved internally by Marxan using a greedy algorithm. In my case, the first and the last components of the objective function are in the same units (Australian dollars). As I ensured, with the feature penalty factor, that each objective would be met, the first component of the objective function for all the solutions presented here is 0.

b is the boundary length modifier, a parameter set in Marxan that gives weighting to connectivity in the objective function (see details in Game & Grantham 2008). I accounted for connectivity by setting b to 1300. This value was calibrated as giving the best trade-off between the number of connections and cost. To determine this I plotted, for increasing values of b, the average number of connections across 100 Marxan solutions against the average cost of those solutions. The resulting plot was a concave curve. The inflection of the curve was the point where there was a significant reduction of connections but a modest increase in cost, and the corresponding b value was considered to represent the best trade-off. Scenarios that did not consider connectivity had this value set to 0. c_{ij} is the binary entry of the connectivity matrix for planning units i and j. x_u is a binary decision variable taking the value of 1 if planning unit u is currently managed or selected for management in the optimization process. d_u is the cost of taking action in planning unit u. It depends on the kind of action that is most effective in planning unit u (which I decided *a priori* – see Management costs, above) and the extent of potential olive hymenachne infestation in u.

The objective function represents a multi-criteria problem in which two different measures are minimized: overall cost and the number of connections (my proxy for probability of infestation). These terms are in different currencies because I had no way of converting number of connections to dollar values in this study. Clearly, though, minimizing connections and therefore probability of reinfestation will reduce long-term costs. If I minimize the probability of infestation or reinfestation to planning units where management was not previously necessary or is active, I also reduce the potential for additional costs to be incurred. In turn, this frees up funds for management of untreated planning units.

Management scenarios

I designed scenarios to test the influence of previous non-systematic management of olive hymenachne, the influence of incorporating connectivity *b* into the objective function, and the effects of constraining management to specific wetland types.

In scenario 1 (Table 6.2) I aimed to reduce the total area infested with olive hymenachne by 90% in two specific wetland types. These were selected because they have been identified as endangered and susceptible to weed invasion because of disturbance and location in the landscape. The two wetland types have each been mapped as regional ecosystems (DERM 2009): 1) "floodplain wetland with *Eucalyptus* vegetation in highly disturbed areas", and 2) "*Melaleuca* palustrine wetlands". These wetland types also have high biodiversity values because they support several endangered species endemic to the Wet Tropics region.

In scenarios 1-3 (Table 6.2), any infested planning units in the study area could be selected for management, but planning units only contributed to the final solution if they: 1) contained one or both of the two specified wetland types, or 2) contained other types of wetlands and streams but reduced the probability of reinfestation in planning units containing the specified wetland types. The initial set of managed planning units for scenario 1 was empty, meaning that I did not force the currently managed planning units into the final solution. I did, however, account for the current management influence in the landscape by adjusting management cost downward for those planning units with previous management investment. By comparing this scenario with scenario 2, I wanted to demonstrate the benefits associated with systematic planning from the outset of management actions.

Table 6.2 Descriptions of management scenarios and parameters.

Scenario	Objective	Managed PUs# locked into solution	Connectivity	Objective(s) met (Yes/No)	Solution area (ha)	Cost (AUD)	Connections*
1	Reduce total area infested by 90% in wetland types 1) "floodplain wetland with Eucalyptus vegetation in highly disturbed areas" and 2) "*Melaleuca* palustrine wetlands"	No	Yes	Yes	3325	$7,024,029	209
2	Reduce total area infested by 90% in wetland types 1) "floodplain wetland with Eucalyptus vegetation in highly disturbed areas" and 2) "*Melaleuca* palustrine wetlands"	Yes	Yes	Yes	3321	$7,016,943	226
3	Reduce total area infested by 90% in wetland types 1) "floodplain wetland with Eucalyptus vegetation in highly disturbed areas" and 2) "*Melaleuca* palustrine wetlands"	Yes	No	Yes	3320	$6,996,168	314
4	Reduce the total area infested by 70% in all infested planning units	Yes	Yes	Yes	4255	$2,275,182	172
5	Reduce the total area infested by 90% in all infested planning units	Yes	Yes	Yes	5470	$8,972,343	24

Planning units

* The higher the number of connections the higher the likelihood a managed planning unit will be reinfested with olive hymenachne from an upstream planning unit that is infested.

Scenario 2 (Table 6.2) had the same objective as scenario 1 but differed in having the subset of planning units that had been actively managed by CCRC for the previous five years forced into the final solution. Scenario 3 (Table 6.2) had the same objective as scenarios 1 and 2 and, like scenario 2, had managed planning units forced into the solution. Scenario 3 differed from the previous two by not accounting for the susceptibility of selected planning units to reinfestation from upstream. I set a *b* value of zero in this scenario to give no importance to connectivity. The key point I aimed to demonstrate with scenario 3 was that accounting for connectivity in the objective function reduces the likelihood of reinfestation in planning units selected for management. I used the number of connections between the set of managed planning units and the unmanaged and infested or potentially infested planning units as a surrogate for the likelihood of reinfestation. While the likelihood of reinfestation would not necessarily increase linearly with the number of connections, I do not have a model to relate them. In any case, the relationship is likely to be highly idiosyncratic, depending on the extent of upstream infestation and the strength of hydrological connections. Moreover, the aim of these analyses was to demonstrate the implication of considering connectivity rather than providing an exact estimate of the likelihood of reinfestation.

In scenarios 4 and 5 (Table 6.2), my objective was to reduce the total area infested with olive hymenachne by 70% and 90%, respectively, considering all infested or potentially infested planning units, regardless of the wetland or stream types they contained. I accounted for connectivity of planning units in these scenarios to mitigate reinfestation. Both scenarios had all actively managed planning units locked into the final solutions.

Results

The total cost of management was virtually identical for scenario 1, without managed planning units locked into the solution, and scenario 2, with managed planning units locked in. However, scenario 1 reduced the number of connections by 8% compared to scenario 2. The spatial implications of this difference (Figure 6.2a, b) were that scenario 1 produced a more compact configuration of planning units and selected fewer downstream planning units to meet the same objective.

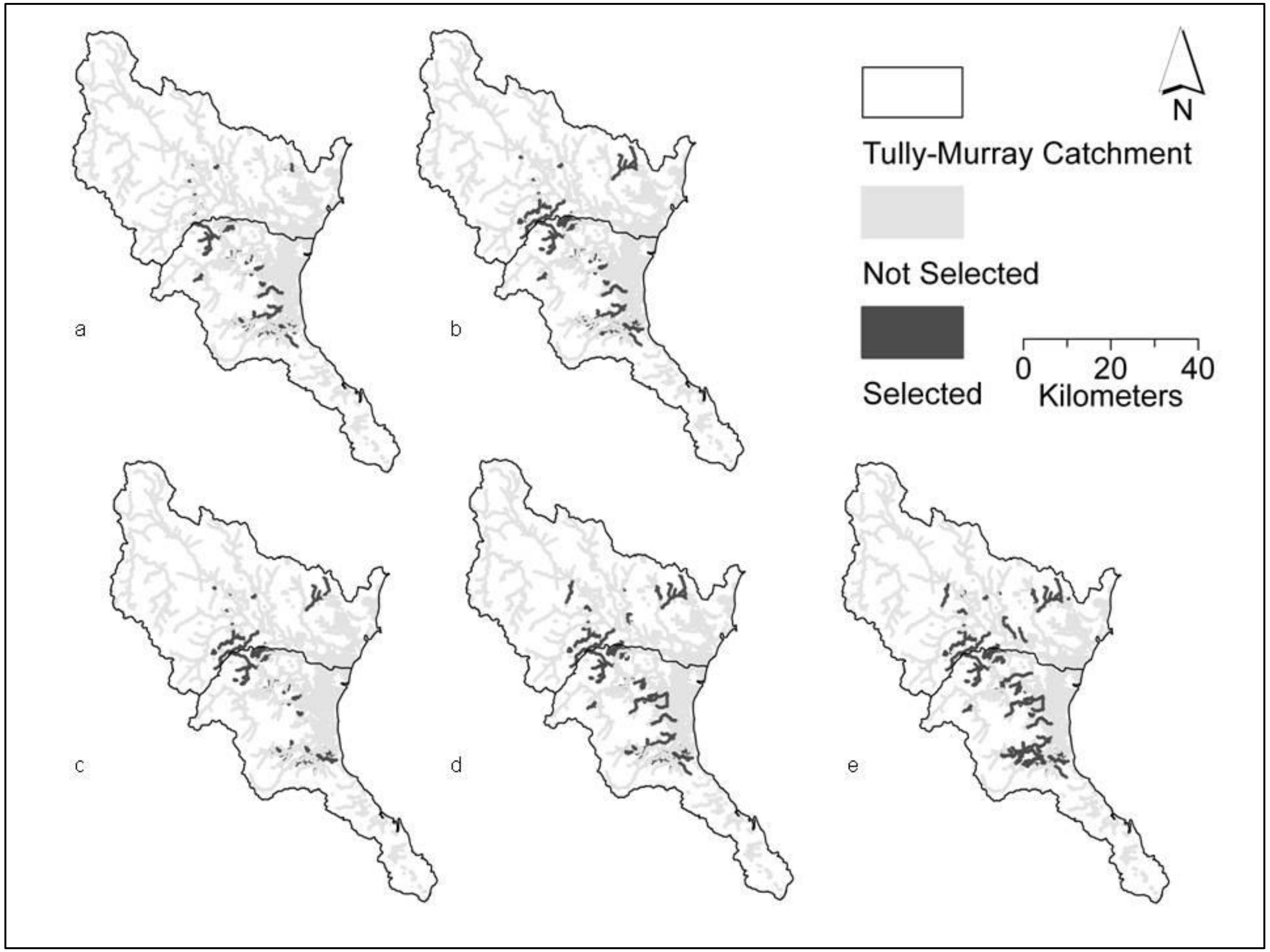


Figure 6.2 Solutions for five management scenarios established to prioritize management actions aimed at reducing olive hymenachne (*Hymenachne amplexicaulis*) in the Tully-Murray study area. Each scenario is presented sequentially from one a) to five e). Areas not selected were not part of the prioritization solution.

The solution for scenario 3, which ignored connectivity, resulted in a minimal cost difference with scenario 2, which considered connectivity, but a 50% greater number of connections than scenario 2 (Table 6.2). This also led to spatial differences between the solutions (Figure 6.2b, c).

Reducing the total area infested by 70% in all planning units (scenario 4) increased the total area selected for management by 78% relative to meeting the objectives for the two specified wetland types (scenarios 1-3). But this was done at one third of the cost (Table 6.2). Reducing the total area infested in all planning units by an extra 20% (scenario 5) required about $6.7 million AUD more than for scenario 4, but selected an additional 1216 ha of infested area and lowered the number of connections with infested areas by 13% (Table 6.2).

Notably, the spatially unconstrained scenarios 4 and 5 provided more effective reduction of connections and therefore less likelihood of reinfestation of selected planning units than solutions for scenarios 1-3. This presents managers with trade-offs between overall outcomes and outcomes for selected types of planning units. Areas of the two specified wetland types, selected for management in scenarios 1-3 because of their endangered and susceptible status, were, respectively, 3325, 3321 and 3320 ha. The solution for scenario 4, while selecting larger areas for management overall, also selected a smaller total area of the two endangered wetland types (2368 ha). The solution for scenario 5 selected a larger total area of these wetland types than scenarios 1-3 (3424 ha), but at greater cost.

Discussion

I have tested an approach for invasive species management that is based on the main characteristics of systematic conservation planning, namely: quantitative objectives, explicit rules for prioritisation, and algorithms that consider the spatial context of areas in terms of complementarity and connectivity.

The first finding supports my opening argument that the problem of prioritizing invasive species management is too complex to be solved only with non-systematic methods. The greater number of downstream planning units susceptible to reinfestation under scenario 2, compared with scenario 1, and that used a systematic approach from the start of planning, demonstrates the inefficiency associated with non-systematic methods. It also accords with previous work documenting the disadvantages of *ad hoc* management decisions (Pressey & Tully 1994).

Further, this finding supports the conclusions of a recent review on invasive species management that highlights a need for control strategies based on limited information and incorporating spatial aspects of invasion management (Epanchin-Niell & Hastings 2010). My approach adds to previous decision-theory approaches aimed at prioritizing resources for invasive species management (e.g. Odom et al. 2005; Firn et al. 2008) by explicitly accounting for connectivity between infestations and management costs, and exploring alternative scenarios defined by different objectives, constraints and opportunities. Importantly, this and previous tools do not replace the experience and judgment of managers. However, my approach offers a structured, explicit method that is open to scrutiny and can be constantly improved while involving managers and benefiting from their experience. Managers are able to refine objectives, inform decisions about input data, and guide the selection of areas for investment.

The second finding demonstrates the importance of accounting for connectivity when reinfestation is important and predictable. Ignoring connectivity comes with an additional cost associated with the higher likelihood of managed planning units being reinfested (Epanchin-Niell et al. 2010). The difference in dollar costs between scenario 2 (with connectivity) and scenario 3 (which ignores connectivity) is very slight (just over $20 000 AUD), with scenario 2 slightly more expensive. However, scenario 3 has 72% more connections, or a much larger number of infested or potentially infested upstream sources that are not being managed. The potential consequences of ignoring connectivity in planning for freshwater invasive species are 1) the need to reinvest in planning units where management has already been applied, and 2) the need to manage additional planning units (at additional cost) to those already selected to abate reinfestation from upstream. These consequences are minimized with a systematic approach that accounts for connectivity.

The third finding demonstrates that managers should carefully consider the objectives they set out to achieve and, where possible, use scenarios to assess the risk of unexpected consequences. The low cost of scenario 4 relative to scenarios 1-3 was due to selections being unconstrained by objectives related to specific wetland types. This provided greater spatial flexibility and allowed the optimization algorithm to explore the full set of planning units to find the most cost-effective solution. The lack of constraints in scenario 4 and 5 also meant that connectivity could be considered more effectively, reducing the overall risk of reinfestation. At the same time, scenarios 1-3 involved management of larger areas of the endangered wetland types than scenario 4, albeit with larger costs and greater likelihood of reinfestation. Scenario 5, although somewhat more expensive than scenarios 1-3, selected larger areas of the endangered wetland types and, because of the lack of spatial constraints, had a solution with many fewer connections. These results demonstrate the need for managers to trade off, in my example, management of valued wetland types against overall benefits of management and cost-effectiveness. My results also show that trade-offs cannot be evaluated a priori, but can only be elucidated with spatially explicit scenarios.

My method has several advantages: it encourages managers to identify explicit, quantitative objectives and to invest public funds more transparently and accountably to achieve these objectives; it can be used to evaluate the monetary costs associated with different objectives; and it allows managers to build upon their existing approaches to setting priorities. If they have already invested time and money into priorities identified with non-systematic methods they can capitalize on those investments by locking managed areas into any systematic solution to achieve the most cost-effective future management. Estimating the costs of alternative scenarios is particularly useful for local managers to explain to government and other funding bodies what factors limit their ability to manage for invasive species. My method could be extended, for example, to estimate the long-term outcomes and costs of successive pulses of funding, any one of which is insufficient to effectively manage invasive species and so allows the species to reinfest managed areas when funding stops.

One present limitation of my method is that I use two currencies in comparing scenarios: 1) monetary cost, which is a function of the area infested and the area selected for management; and 2) number of connections, as a measure of the likelihood of selected planning units being reinfested. If it were possible to convert connections to dollar values, the message to managers about the trade-offs associated with the different scenarios would be much clearer. This is a tractable area for improvement of the method described here. A second limitation of the method and scenarios is that they are static: they do not inform managers about the best sequence of actions over time. While the static scenarios are essential for identifying overall priorities in the landscape, elaboration of the method is needed to account for the risk of repeated reinfestation of planning units and to develop a schedule of annual actions. The results of a scheduling exercise could be used to illustrate the limitations of current budget allocations to achieve effective on-ground management in a reasonable time. I am currently developing a scheduling strategy based on one of the solutions presented here. A third limitation that can also be addressed in later work concerns the uncertainty inherent in my data. Inevitably, my method is based on models of occurrence, models of areas infested, models of the likelihood of reinfestation, and models of time required for application of management actions. All these models can be updated as managers provide more field data, but some uncertainty will always remain. The method will be more robust when I can identify solutions that take explicit account of uncertainties in the data and consider uncertainty in comparing scenarios.

Chapter summary

- Managing invasive species infestations to eradicate them or reduce the probability of their reinvasion management is a costly undertaking. However, methods exist that can be used to identify cost-effective solutions to invasive species management by prioritizing the allocation of resources.
- To inform the planning and management of olive hymenachne I developed a systematic approach to prioritize the allocation of management actions aimed at reducing the abundance and probability of olive hymenachne reinvasion in streams and wetlands in the Tully-Murray River catchments.
- I used Marxan to identify five solutions, based on scenarios aimed at demonstrating the benefit of using a systematic approach and the benefit of accounting for connectivity when prioritizing actions for aquatic invasive species management.
- I demonstrated that using a systematic approach from the start of planning results in a more cost-efficient solution than non-systematic methods. I also showed that ignoring connectivity when planning for invasive species management comes with an additional cost, which is associated with the higher likelihood of managed planning units being reinfested from infestations upstream of the managed areas.

- Finally, I found that managers should give careful consideration to their conservation objectives. I showed that there was greater spatial flexibility when Marxan was not constrained to select specific wetland types. This allowed the optimization algorithm to explore the full set of planning units to find the most cost-effective solution.

Chapter 7 General discussion

Thesis outcomes, scientific advancements and conservation implications

The aim of this thesis was to advance the scientific basis and application of systematic approaches for the conservation of fresh waters. To achieve this aim I addressed the following objectives: 1) to determine the occurrence of disturbances, and the incidental protection of fresh waters in terrestrial protected areas of the Wet Tropics; 2) to identify the effectiveness of using coarse-filter surrogates for representing freshwater fish diversity in systematic conservation planning; 3) to develop methods to evaluate the effectiveness of invasive species management; and 4) to integrate management costs into systematic conservation planning to identify invasive species management priorities, and inform the design of future conservation (protection and/or restoration) of fresh waters. I addressed these four issues using the Wet Tropics as a case study.

The data available for addressing conservation questions for streams, wetlands, freshwater fish and some invasive species (mostly those listed as Weeds of National Significance, WONS 2009) are readily available and robust in the Wet Tropics. Therefore, working in this bioregion has provided a unique opportunity to: 1) address questions regarding systematic conservation planning for fresh waters related to data and management effectiveness; and 2) demonstrate new applications of systematic conservation planning methods to address resource allocation for off-reserve management actions such as invasive species management. Here I evaluate how this thesis has advanced the theory and methods of systematic conservation planning for freshwater ecosystems. I discuss how each chapter can influence decision making for the conservation of freshwater ecosystems and biodiversity

Objective 1: Determine the occurrence of disturbances, and the incidental protection of fresh waters in terrestrial protected areas

The streams and wetlands of the Wet Tropics support some of the highest diversities of freshwater vertebrates and invertebrates in Australia as well as globally (Chapter 2). However, streams, wetlands and freshwater fish are poorly represented by the existing protected area network and are exposed to a variety of human-induced disturbances both within and outside of protected areas (Chapter 3).

Given that fresh waters typically are not specifically protected for their intrinsic values (exceptions include Ramsar sites) there is a need to evaluate their incidental protection, and that of the species they support, by terrestrial protected areas. While terrestrial protected areas are not likely to afford effective protection for fresh waters, they may be the most appropriate starting points for establishing additional protected areas for focal freshwater ecosystems, and for incorporation into whole-of-catchment management. In addition, identifying current human-induced disturbances to fresh waters can be important in selecting additional reserves or areas for off-reserve management actions such as restoration or invasive species management.

In Chapter 3, I showed that, while the protected area network of the Wet Tropics is extensive (> 60% of the total land area), it does not effectively represent freshwater ecosystems and fish species. There was only one stream order and one wetland type with at least 20% of their distributions in the Wet Tropics represented in IUCN category II protected areas. Similarly, only five of the 45 fish species in this study had at least 20% of their Wet Tropics distributions represented in these protected areas. In addition to their low levels of protection, high order streams (4-6) and palustrine and estuarine wetlands were found to be highly susceptible to more than one human-induced disturbance, with greater than 50% of all sub-catchments adjacent to these stream orders, or supporting these wetland types, having at least one disturbance present. I also found that protected areas are not only ineffective at representing freshwater ecosystems and biodiversity, but that all sub-catchments upstream of protected areas have at least one human-induced disturbance present. Nearly 60% of all sub-catchments upstream of protected areas have two or more human-induced disturbances present. These results demonstrate the need for whole of catchment conservation decision making that gives better consideration to the disturbances influencing freshwater ecosystem condition. In the Wet Tropics, where there is extensive protection of terrestrial ecosystems, it is unlikely that additional protected areas will be added for the sake of freshwater ecosystem protection. Therefore, if terrestrial protected areas are going to act as replacements for specifically designed freshwater protected areas in this region, greater consideration needs to be given to management actions that extend beyond protection, such as restoration, on-farm best management practices and invasive species control.

Even in regions with extensive terrestrial protected areas the area of terrestrial ecosystem protection does not translate to effective protection for fresh waters and dependent species (e.g. Herbert et al. 2010). As the Wet Tropics is likely to act as a best-case scenario for the level of protection afforded to terrestrial ecosystems in tropical regions (>60% of the total land area), my results strongly suggest that there is a need for better consideration to be given to the conservation of fresh waters in the Wet Tropics and in other tropical regions.

It would be informative to apply the approach I used in Chapter 3 to other tropical regions in Australia, and elsewhere, to quantify how effective terrestrial protected areas are for representing fresh waters and their dependent species. Knowledge gained from this approach could identify ongoing threats to the condition of these ecosystems and could provide conservation planners with an improved understanding of how to build on existing terrestrial protected area networks to enhance freshwater conservation. Even so, protected areas cannot act as the only strategy for achieving freshwater conservation challenges. To conserve freshwater ecosystems and biodiversity effectively, planners will need to apply a suite of conservation actions outside protected areas networks to protect focal freshwater ecosystems and connections across the landscape, and incorporate these into whole-of-catchment management (Abell et al. 2007).

Objective 2: Identify the effectiveness of using coarse-filter surrogates for representing freshwater fish diversity in systematic conservation planning.

Coarse-filter surrogates are commonly used in systematic conservation planning to represent biodiversity, particularly species, for which limited data are available. However, the effectiveness of those surrogates is rarely evaluated because of a lack of species data. Prior to this study (Chapter 4), the effectiveness of coarse-filter surrogates for representing freshwater biodiversity had not been evaluated. The availability of species data in the Wet Tropics provided the opportunity to use this region as a case study to evaluate the effectiveness of three classification methods commonly used to define coarse-filter surrogates for freshwater biodiversity. I used a single abiotic and two biologically informed classifications to serve as the coarse-filter surrogates for fish biodiversity patterns in the Wet Tropics. I derived four classes for each classification method, resulting in 12 coarse-filter surrogates. I used stream reaches as planning units, attributing predicted fish occurrences to each planning unit. As conservation objectives, I used two percentages – 10% and 30% – of the total stream reach length occupied by each class. I then used the conservation planning software Marxan to select sets of stream reaches to achieve the two targets for each of the 12 surrogates. I used the best minimum set solution from 100 Marxan restarts to test the effectiveness of the surrogates by calculating the percentage of 28 predicted freshwater fish species distributions selected in sets of stream reaches that achieved targets for each of the surrogates.

While coarse-filter surrogates are commonly used in systematic conservation planning in all realms, my results showed that they perform poorly for representing freshwater fish species. All 12 surrogates performed poorly and all 28 fish species were poorly represented by the 12 surrogates (Figure 4.5). In fact, none of the fish species were represented close to the 10% or 30% surrogate targets for each surrogate method respectively. My results suggest that coarse-filter surrogates should not be used to represent freshwater fish biodiversity in the Wet Tropics and that future conservation decision making should continue with modelled distributions of individual species. While my results are not directly transferable to inform planners about surrogate performance for freshwater biodiversity in other regions, it is likely that coarse-filter surrogates will poorly represent fish species when species assemblages are not discrete, and for species with low prevalence in a region.

This novel contribution to the field of freshwater systematic conservation planning has the potential to influence conservation decisions. Planners need to give further consideration to their choice of surrogates when undertaking conservation plans. Both the type of surrogate used and the taxonomic group that the surrogate is tested for can influence the perceived surrogate effectiveness (Grantham et al. 2010). In addition, the method used to test surrogate effectiveness can also influence their apparent effectiveness. Given that conservation planners currently have a poor understanding of the effectiveness of coarse-filter surrogates there is a growing need for them to address the limitations associated with using these surrogates. Planners also need to evaluate the effectiveness of coarse-filter surrogates for representing rare species and multiple taxa before basing comprehensive conservation plans on surrogates that may well be ineffective at representing taxa of interest. Consequently, there is need for further research to identify the ecological factors that limit the effectiveness of coarse-filer surrogates for multiple taxa.

Objective 3: Develop methods to evaluate the effectiveness of invasive species management.

The effectiveness of management investments is not commonly evaluated in the conservation planning literature. This is likely due to the poor reporting of actions that are implemented as a result of systematic planning and the fact that few straightforward methods exist for quantifying effectiveness. The application of this approach to the Wet Tropics was motivated by a clear need, and by the availability of data and willingness of decision makers to be involved in the development of new approaches that could inform them and the funding bodies that invest in invasive species management. Because of the Cassowary Coast Regional Council's long-term investment in aquatic invasive plant management I was able to use readily available data on the distribution and abundance of olive hymenachne to demonstrate that predicted environmental suitability of an invasive species consistently relates to species abundance, and that the residual values from this relationship can be used to quantify the effectiveness of management investments (Chapter 5).

I found that *ad hoc* management investments were less effective than 2 or 5 year management investments at reducing olive hymenachne abundance. There was increasing reduction in olive hymenachne abundance for two and five years of invested management, with the greatest reduction occurring with five years invested. My results provide evidence not only of management effectiveness at reducing olive hymenachne abundance, but also of the day-to-day issues faced by managers. For example, if managers are to effectively manage invasive species they require access to long-term funding, which would allow them to maintain on-going management presence in the landscape, and likely improve the effectiveness of their actions. However, current funding for invasive species management in the Wet Tropics and other regions of Australia are limited to one- or two-year instalments. The invasive characteristics of olive hymenachne (e.g. 15 year seed bank viability) as well as other species that are declared invasive do not conform to the current short-term funding provided for their control and/or eradication. Therefore, short duration funding does not allow managers to establish and maintain management programs that are effective at reducing and/or minimizing additional spread of an invasive species. To do so managers require long-term access to funding, and the smart use of funds, using systematic approaches to identify the most cost effective solutions (Simberloff 2009, Chapter 6).

The Wet Tropics data used for this study were adequate to demonstrate the effectiveness of a single management method (spray control); however, the limitations of the data did not allow me to evaluate the effectiveness of other management actions commonly used in the region (e.g. spray + revegetation). With additional data on spray control and other types of management I could build the evidence needed to inform managers about the effectiveness of alternative management actions (e.g. restoration) that may be more effective at maintaining reduced abundance of olive hymenachne over a longer time period, as well as contributing additional ecological values to freshwater ecosystems (e.g. providing shade and food sources for fish species dependent on terrestrial fruit and insects). In addition, knowledge gained from evaluating alternative management actions could be used to inform other managers targeting olive hymenachne in this and other regions (e.g. south Florida).

This research is a novel contribution to the field of freshwater systematic conservation planning. The methods I used could be adapted to address most questions related to management effectiveness, not only for invasive species but also for other conservation investments where the objective is to reduce or gain species abundance.

Objective 4: Integrate management costs into systematic conservation planning for invasive species.

The application of systematic approaches to resource allocation questions extending beyond the selection of reserves, and the inclusion of management costs, are two areas where gaps remain in the field of freshwater systematic conservation planning. Apart from my research (Chapter 6), there appear to be no examples of systematic approaches to resource allocation questions for invasive species management. Data availability and willingness of decision-makers provided the opportunity to identify cost-effective solutions for aquatic invasive species management through a novel application of systematic conservation planning.

This research demonstrated the benefits of accounting for cost in systematic conservation planning, and the benefits (reduction in cost) that are gained from using systematic approaches over *ad hoc* approaches in selecting areas for management investment. When selecting priority areas for invasive species management, I accounted not only for the ecological values that would be gained by removing olive hymenachne, but also for costs associated with undertaking three different invasive species management actions. To demonstrate the benefits of using a systematic approach I established five management prioritization scenarios.

I demonstrated the cost-effectiveness of systematic solutions to invasive species management, and the cost-effectiveness and reduced likelihood of invasion in solutions when ecosystem connectivity is accounted for. I showed that the problem of prioritizing invasive species management is too complex to be solved with non-systematic methods, and demonstrated that by explicitly accounting for connectivity between infestations and management costs, systematic approaches are more effective than non-systematic approaches.

While I applied this approach at a catchment scale and for a single invasive species, it could also be useful in guiding conservation at different scales and for informing decision making for multiple invasive species. For example, this approach could be applied at a regional scale to help regional decision makers identify priority areas for invasive species management across multiple local government jurisdictions, or it could be used at a finer scale within sub-catchments to help local government and communities decide how and where to cost-effectively manage invasive species on private lands. In addition, this approach could be adapted to tackle resource allocation questions for multiple aquatic invasive species, for areas where such data are available.

At the local scale this approach could be expanded to account for social data, which has yet to be done in freshwater systematic conservation planning. Identifying an approach to account for landholder willingness to be involved in invasive species management programs on their properties would greatly advance the field, as well as improve the likelihood of successful conservation outcomes on private lands. Using this approach, managers could identify a subset of private lands where invasive species management would be the most effective by gaining the greatest ecological benefit, with highest cost-efficiency and social acceptability.

One major limitation to my approach is that my solutions were ‘static’, meaning that the priorities selected by Marxan were only based on a snapshot in time. In reality, the ecological and economic processes that influence the selection of areas for management investment are dynamic and likely to change over time as the invasive species continues to spread. Dynamic conservation planning is complex, and the associated dynamic data are often not available (Visconti et al. 2010). Dynamic conservation planning is a relatively new area of research and, with no known examples in the freshwater realm, there is considerable work to be done.

Future research priorities

The knowledge gained through answering the questions addressed in this thesis has raised yet more questions. In addition, there are areas of freshwater systematic conservation planning that are still under development and remain research priorities. In the above section I discussed research needs relevant to each specific research objective. Here, I discuss more general research priorities in the field of freshwater systematic conservation planning, some of which have been raised in this thesis. These include: 1) improving understanding of how well fresh waters are protected under existing protected area networks, 2) improving methods for understanding the limitations of using coarse-filter surrogates in freshwater systematic conservation planning, 3) accounting for socioeconomic factors in freshwater systematic conservation planning, 4) improving methods to account for dynamic processes in systematic conservation planning, and 5) implementing systematic conservation approaches to address alternative conservation actions.

Protection of fresh waters

Protected areas have been the core element of conservation efforts for well over a century (Margules & Pressy 2000), particularly for terrestrial habitats and species. The past two decades have seen a rise in the number of marine protected areas established globally (Abell et al. 2007), with new areas continually being proposed. However, the protection of fresh waters for their intrinsic values has received much less attention. There have only been a handful of studies that have quantified the effectiveness of this protection (e.g. Keith et al. 2000, Abellán et al. 2007, Nel et al. 2007, Herbert et al. 2010; Turak et al. 2011; Chapter 3).

One major limitation to conducting a global analysis of the incidental protection of freshwater ecosystems and species within terrestrial protected areas is the paucity of data on freshwater ecosystems. Furthermore, the reliability and spatial accuracy of data that is available have raised concerns about the inaccuracies that could arise from conducting such analyses (Abell et al. 2007; Herbert et al. 2010). Given the limitations associated with global scale data on freshwater ecosystems and species there is a need for regional gap analyses to provide a better understanding of the limitations associated with depending on terrestrial protected areas to afford protection to fresh waters (Nel et al. 2007). Since the idea of effective freshwater protected areas (Abell et al. 2007) emerged there have been four peer-reviewed publications (plus my study described in Chapter 3) which have evaluated the effectiveness of existing terrestrial protected areas in representing freshwater ecosystems. This is an important area of researcher that can assist planners to better understand the effectiveness as well as the limitations (e.g. pollutants entering protected areas from upstream) of terrestrial protected areas for protecting freshwater ecosystems and species (see for example, Nel et al. 2009).

Coarse-filter surrogates

Conservation planners often use a combination of available abiotic and biotic datasets to represent ecosystems and biodiversity (Ban 2009). The effectiveness of using these surrogates is rarely investigated, and in freshwater systematic conservation planning there have been no assessments of surrogate effectiveness apart from the work presented in Chapter 4. This demonstrates a major research gap in the systematic conservation planning literature. While there have been previous assessments of surrogate effectiveness in both terrestrial (e.g. Grantham et al. 2010) and marine (e.g. Ban 2009) realms, the conclusions drawn from these studies are not necessarily directly applicable to other regions or realms (Grantham et al. 2010). The effectiveness of surrogates has been shown to depend on a number of factors, including the type of surrogate, the spatial scale of the data, differences between study regions, the method used to evaluate effectiveness and the target features (species/ecosystems for which the surrogate is meant to serve) in question (Grantham et al. 2010). Therefore, while some general conclusions can be drawn from various studies about the effectiveness of surrogates, for example, that ecological classifications have limited value as surrogates for rare or threatened species (Grantham et al. 2010), there remains a need to identify the influence of each of several factors (above) on the effectiveness of surrogates. Without testing the effectiveness of surrogates conservation planners do not have a complete understanding of the limitations associated with the data they are using to derive conservation solutions.

Socio-economic factors

The explicit accounting of socioeconomic factors in freshwater systematic conservation planning is a new area of research (Nel et al. 2011). For freshwater ecosystems, the process of examining conservation costs is complex because of the range of upstream, downstream and catchment dependencies of any wetland or stream reach. Fresh waters are often in public tenure, so direct acquisition costs for conservation are seldom considered in freshwater planning. In addition, applying conservation actions for freshwater ecosystems could also require extensive changes to land cover and use in catchments and along riparian zones. All of these changes come with costs associated with acquisition, lost opportunities for extraction or development, or of the various actions being undertaken (e.g. restoration).

In particular, conservation planners and managers of fresh waters in large catchments must deal with complexities of access and ownership, as well as multiple, overlapping jurisdictions and many levels of governance and biophysical links (Linke et al. 2011). To effectively account for socioeconomic factors, much of the ground work must be done in early stages of the planning process to ensure that key stakeholders are informed and have the opportunity to provide input to the planning process.

Generally, the economic aspects of socioeconomic information have received considerably more attention than the social aspects (e.g. Adams et al. 2010; Carwardine et al. 2008). The research presented in Chapter 6 is the first attempt to explicitly account for the costs associated with establishing management actions for freshwater conservation. There appear to have been no other explicit attempts to account for costs of opportunities and constraints related to ownership and governance in freshwater systematic conservation planning. By considering costs related to ownership and governance conservation planners can minimize the impacts felt by all stakeholders involved in the planning exercise.

Freshwater planning exercises that have explicitly considered people and their activities have generally been limited to assessments of condition or future threat (e.g. Linke et al. 2007; Nel et al. 2007). These examples and studies from other realms are mostly directed towards consideration of demographic, land-use and socio-economic data (e.g. Ban et al. 2009; Klein et al. 2009b). However, these data alone are not sufficient for choosing conservation areas. Conservation also depends on the presence of many other broad classes of social data, such as development trends, environmental values, landholder willingness to be involved in conservation, beliefs and sense of place, and enabling conditions (Pasquini et al. 2010). Accounting for all these social values in freshwater planning will be challenging due to the longitudinal, lateral and vertical connectivity of freshwater ecosystems and the many stakeholders that depend on these systems. Therefore, effective planning outcomes will require involvement of many stakeholders, some of whom have distant connections to freshwater ecosystems of immediate concern for conservation (Ban et al. in press). Explicit accounting for socioeconomic factors in freshwater systematic conservation planning could have a strong influence on how conservation decision making is carried out for these ecosystems in the future.

Accounting for dynamic processes

One of the significant challenges facing freshwater systematic conservation planning is dealing with the dynamic nature of ecological and socioeconomic systems. In Chapter 6, I demonstrated static solutions to the resource allocation question for invasive species management. However, such solutions do not inform managers about the best sequence of actions over time. Similarly, when planning for dynamic processes such as weed invasion, there is a need for methods that can evaluate the performance of the solutions for achieving conservation objectives. In the case of the work presented in Chapter 6, the results of a scheduling exercise could be used to illustrate the limitations of current budget allocations to achieve effective on-ground management in a reasonable time. In addition to scheduling management actions and invasive species there are also a number of the ecological processes that are currently poorly accounted for in freshwater systematic conservation planning, these include: aquatic migrations, population persistence and the dynamics associated with flow regimes as well as ephemeral systems. Advancing this area of research will improve the relevance of systematic plans through methods that capture both spatial and temporal dynamics of freshwater ecosystems and their dependent species.

Further consideration of alternative conservation actions

In this thesis I have focused on identifying areas for the protection of freshwater biodiversity, and identifying priority areas for the management of invasive species on both public and private lands. However, there are several other strategies beyond reserves and invasive species management that are used to conserve freshwater biodiversity (e.g. riparian restoration, fire management, environmental water allocations and the management of pollutants). Although none of these strategies are new in practice, the use of systematic conservation planning methods to address resource allocation and the spatial prioritization of these actions across landscapes are new and emerging applications. Despite the generality of the conservation resource-allocation problem, the application of systematic conservation planning to problems outside of reserve design is in its infancy. The work presented in

Chapter 6 is the first application of systematic conservation planning methods to address a resource allocation question for invasive species management, and one of the first examples expanding these methods beyond questions related to reserve design.

Some of the emerging applications of systematic conservation planning methods beyond reserve design are the prioritization of environmental water flows (Nel et al. 2011) and the application of systematic conservation planning methods to address ecological restoration planning (e.g. McBride et al. 2010). For example Crossman et al. (2007), Crossman & Bryan (2009) and McBride et al. (2010) have demonstrated how the steps and stages presented in Figure 1.1 can be adapted to the resource allocation question concerning the prioritization of restoration actions. The discipline of systematic conservation planning offers the theory and methods needed to address the resource allocation problem for restoration, which entails the prioritisation of funds across an array of conservation areas or actions in time and space (Margules & Pressey 2000).

While some ecological restoration can be achieved with limited expense, it can also entail costly management of invasive species, reintroductions of rare species, replanting of diverse plant communities, and/or the creation of specific ecological niches (Hobbs & Norton 1996). The likelihood of restoration being a success can also be linked to the cost and relative intensity of the restoration activity selected (e.g. Dorrough et al. 2008; Chapter 6). Where financial resources are limited (which is normally the case), decisions need to be made about which areas to restore, while considering opportunities and constraints, and when, and what methods to use (e.g. Hyman & Leibowitz 2000; McAllister et al. 2000).

Focusing on a freshwater example, the Wet Tropics offers a unique opportunity to identify riparian restoration priorities, because the majority of land not already under protection in the WTWHA is cultivated for agricultural and horticultural production or urban development. In these highly productive landscapes, with small remaining fragments of native vegetation occurring along waterways, riparian restoration is more likely to be accepted than purchasing areas for further protection. However, implementing broad-scale riparian restoration is constrained by the costs. Effective restoration outcomes in the Wet Tropics require strategic deployment of conservation resources. The major focus of funding, research and management in the Wet Tropics has been to improve downstream water quality entering the GBRWHA, with freshwater ecosystems being neglected. Therefore, it is timely to take effective and cost-efficient approaches to prioritize riparian restoration to mitigate disturbances such as weed invasions and to restore important terrestrial habitat upon which a number of endemic fish species (e.g. jungle perch, *Kuhlia rupestris*) are dependent. Below I demonstrate how the stages outlined in Figure 1.1 can be adapted to the riparian restoration resource allocation problem.

Figure 1.1 outlined the stages that should be considered when undertaking a systematic plan. Here I discuss how these stages can be used to develop a systematic approach to riparian restoration at regional scale. First, to be systematic, the approach used to identify riparian restoration priorities must account for the ecological assets which will receive benefit from the restoration action being undertaken. In the case of riparian restoration, this could include both terrestrial (e.g. birds or frogs) and freshwater (e.g. fish) dependent species. Second, clearly defined quantifiable objectives about the desired outcomes from the riparian restoration must be identified. An example of a quantifiable objective is to restore and maintain 100 km^2 of riparian vegetation in the Wet Tropic region. Third, every systematic plan requires a list of the areas of conservation interest and their spatial dependencies. This could include all stream reaches in the Wet Tropics, or a subset of stream reaches in a particular catchment. This step also requires defining the spatial connectivity of the planning areas, and allows the planner to spatially relate the areas to ensure their connections are accounted for in the planning process. Fifth, a list of management actions (e.g. planting, maintenance, monitoring) is required, and an understanding of how these actions contribute towards achieving the defined objectives. An example of a management action for riparian restoration would be forest replanting. This action would have an associated cost and contribute to the overall objective of the plan, which in this case is to restore 100 km^2 of riparian vegetation in the Wet Tropics. Finally, socioeconomic information related to the plan must be considered. A simplistic example in the case of restoring riparian vegetation in the Wet Tropics would be to account for the cost of implementing each action and, preferably, a budget. However, real-world planning processes are never straightforward, as discussed above. In order for systematic approaches to be effective, and to be useful for informing on-ground management, consideration must be given to socioeconomic information extending beyond economic factors. Therefore, at this stage it may be important to identify the availability of social data, and consider the types of social information (e.g. landholder willingness to be involved in conservation programs, land tenure, and landholder goals) that would be useful in guiding effective riparian restoration outcomes on both public and private lands.

As discussed in Chapter 1, there are additional factors such as regional and local goals (e.g. government, community or individual landholder goals) that should be considered when undertaking a systematic conservation plan. This is critically important when planning for conservation actions such as riparian restoration, which will likely need to be carried out on private lands. There are also additional constraints and opportunities such as human-induced disturbances, willingness of stakeholders, access to the land or water and condition of the existing landscape that need to be considered, but for which data may not always be readily available. Finally, local priorities, opportunities and constraints that may not be identified during the regional planning process are likely to become evident once actions identified as regional priority areas are investigated on-ground. Regional-scale priority areas can therefore ignore unforeseen constraints and opportunities at the local scale, which may lead to regional designs being difficult to apply. One of the biggest challenges for conservation planners and decision makers is to evaluate the advantages of aligning local priorities with the regional design (scaling up) against those of altering the regional design as new data become available (scaling down) (Mills et al. 2010). Yet, as has been shown in the marine realm, adjusting conservation actions to local information, departing to some extent from regional design, is likely to increase local support and compliance with resource regulation (e.g. Green et al. 2009). In the terrestrial (e.g. Knight et al. 2010) and marine realms (e.g. White et al. 2005) issues related to regional design and local action are beginning to be addressed, and it is likely that this area of research will be an emerging topic in freshwater systematic conservation planning as the field develops and regional-scale plans begin to be implemented.

Concluding remarks

Conservation initiatives in the Wet Tropics have been strongly focused on terrestrial and marine realms. As I demonstrated in Chapter 3, the protection of fresh water ecosystems in this region is far below the level of protection afforded to terrestrial ecosystems, and requires improved conservation initiatives that not only focus on protection but on a whole-catchment approach that considers ecosystem connectedness. The lack of protection and high number of human-induced disturbances influencing the ecological condition of fresh waters in this region demonstrates what many freshwater ecologists and conservation planners have been trying to convey about the global status of freshwater ecosystems. In addition, the major disturbances (e.g. habitat degradation, species invasions) influencing the condition of freshwater ecosystems in the Wet Tropics are similar to those highlighted in current literature (e.g. Dudgeon et al. 2006). In Chapters 5 and 6, I presented methods to improve the efficiency and effectiveness of managing aquatic invasive species, one of the human-induced disturbances contributing to the decline of freshwater diversity worldwide. The results of these studies offer evidence that on-going investment in invasive species management can result in effective outcomes, and that linking management actions, constraints and objectives in a transparent and defensible manner can result in more cost-effective solutions than *ad hoc* approaches to invasive species management. Given that all four of the case studies undertaken in this thesis addressed questions highly relevant to the advancement and application of systematic approaches to conservation, the knowledge and tools generated from this thesis will inform conservation decision making for fresh waters globally

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Appendix A

Chapter 3 supporting information

Table S3.1 Wetland type and conservation status definitions from Queensland Department of Environmental Resource Management (DERM 2009).

Wetland Type	Definition
Riverine	Riverine wetland or fringing riverine wetland. These are wetlands with an open, non-vegetated channel.
Lacustrine	Lacustrine (lakes). These are generally larger than 8 ha, situated in a topographic depression or dammed river channel and have < 30% vegetation cover.
Palustrine	Palustrine (swamps, marshes etc). These are generally non-tidal areas dominated by vegetation (> 30% cover) or, if lacking vegetation, area < 8 ha.
Estuarine	Estuarine wetlands. Intertidal areas such as mangroves and salt flats.
Conservation Status	**Definition**
Endangered	The area of remnant vegetation for the regional ecosystem is < 10% of the pre-clearing extent of the regional ecosystem; or the area of remnant vegetation for the regional ecosystem is 10-30% of the pre-clearing extent of the regional ecosystem and < 10 000 ha.
Of concern	The area of remnant vegetation for the regional ecosystem is 10- 30% of the pre-clearing extent of the regional ecosystem; or the area of remnant vegetation for the regional ecosystem is > 30% of the pre-clearing extent of the regional ecosystem and < 10 000 ha.
Least concern	The area of remnant vegetation for the regional ecosystem is > 30% of the pre-clearing extent of the regional ecosystem and > 10 000 ha.

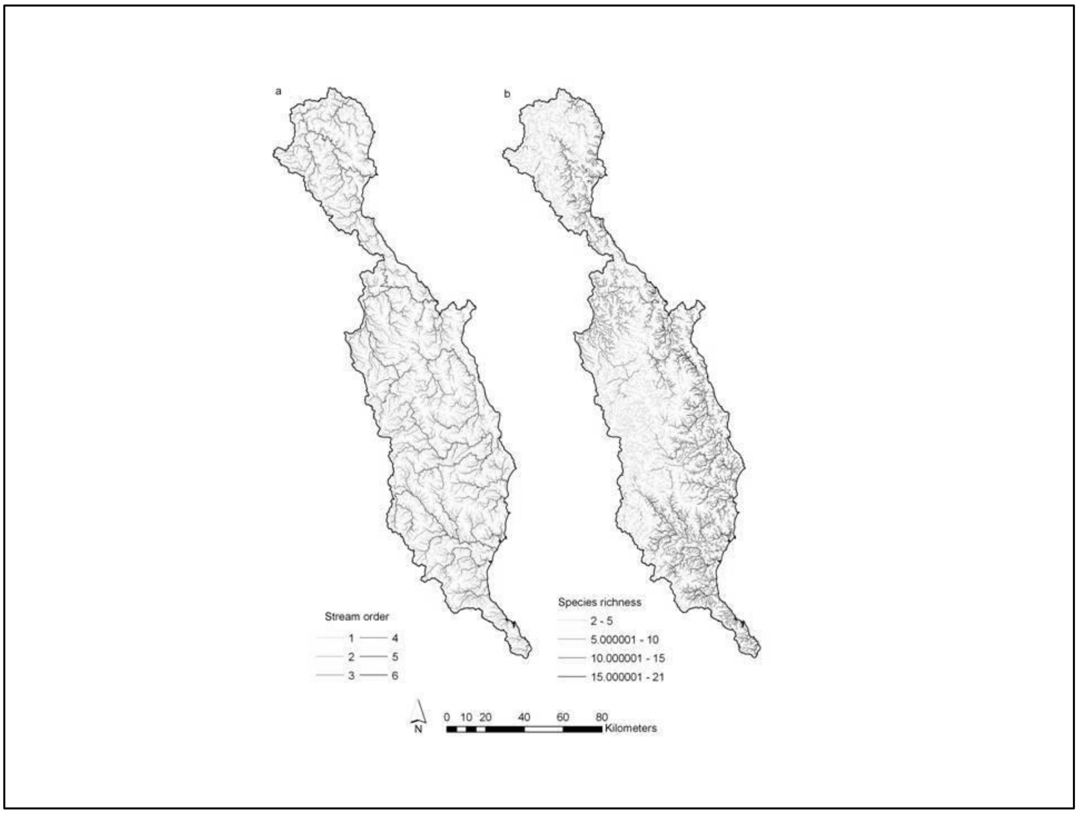

Figure S3.1 Distribution of a) Strahler stream orders 1-6 and b) fish species richness by stream reach (n = 7210), based on modelled distributions for 45 fish species.

Table S3.2 The Area Under the Receiver Operator Characteristic curve (AUC) for distribution models established for 45 freshwater fish species. * = species endemic to the Wet Tropics.

Species	AUC
Ambassis agassizii	0.89
Ambassis agrammus	0.80
Ambassis miops	0.89
Amniataba percoides	0.72
Anguilla obscura	0.85
Anguilla reinhardtii	0.97
Awaous acritosus	0.82
Bunaka gyrinoides	0.85
*Cairnsichthys rhombosomoides**	0.80
Craterocephalus stercusmuscarum	0.78
Eleotris fusca	0.84
Eleotris melanosoma	0.88
Glossamia aprion	0.72
Glossogobius sp. 1	0.81
*Glossogobius bellendenensis**	0.85
Glossogobius giurus	0.94
Giurus margaritacea	0.85
Hephaestus fuliginosus	0.75
*Hephaestus tulliensis**	0.78
Hypseleotris compressa	0.91
Kuhlia rupestris	0.80
Lates calcarifer	0.90
Lutjanus argentimaculatus	0.86
Leiopotherapon unicolor	0.93
Megalops cyprinoides	0.87
Mesopristes argenteus	0.91
Melanotaenia maccullochi	0.86
Melanotaenia splendida	0.71
*Melanotaenia utcheensis**	0.85
Mogurnda adspersa	0.76
Mugil cephalus	0.91
Nematalosa erebi	0.82
Neosilurus ater	0.83
Neosilurus hyrtlii	0.96
Notesthes robusta	0.79
Ophisternon gutturale	0.89
Oxyeleotris aruensis	0.79
Oxyeleotris lineolatus	0.85
Pseudomugil gertrudae	0.86
Porochilus rendahli	0.89
Pseudomugil signifer	0.89
Redigobius bikolanus	0.77
*Schismatogobius sp.**	0.82
Tandanus tandanus	0.73
Toxotes chatareus	0.91

* = endemic to the Wet Tropics.

Appendix B

Chapter 4 supporting table

Table S4.1 The Area Under the Receiver Operator Characteristic curve (AUC) for distribution models established for 28 freshwater fish species.

Species	AUC
Ambassis agrammus	0.78
Ambassis miops	0.87
Anguilla reinhardtii	0.72
Awaous acritosus	0.74
Bunaka gyrinoides	0.85
Cairnsichthys rhombosomoides	0.76
Craterocephalus stercusmuscarum	0.75
Eleotris fusca	0.79
Eleotris melanosoma	0.88
Giurus margaritacea	0.84
Glossamia aprion	0.71
Glossogobius sp. 1	0.77
Glossogobius bellendenensis	0.80
Hephaestus fuliginosus	0.65
Hephaestus tulliensis	0.73
Hypseleotris compressa	0.91
Kuhlia rupestris	0.80
Lates calcarifer	0.89
Leiopotherapon unicolor	0.94
Lutjanus argentimaculatus	0.82
Melanotaenia splendida	0.65
Mogurnda adspersa	0.74
Neosilurus ater	0.83
Notesthes robusta	0.76
Oxyeoleotris aruensis	0.71
Pseudomugil signifer	0.87
Redigobius bikolanus	0.74
Tandanus tandanus	0.68

Appendix C

Characterizing errors in digital elevation models and estimating the financial costs of accuracy

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Characterizing errors in digital elevation models and estimating the financial costs of accuracy

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Digital topographic models are the foundation of more advanced modeling applications and ultimately inform planning and decision making in many fields. Despite this, the error associated with these models and derived attributes is commonly overlooked. Little attention has been given in the scientific literature to the benefits gained from having less error in a model or to the corresponding cost associated with reducing model error by choosing one product over another. To address these gaps in knowledge we evaluated the error associated with five digital elevation models (DEMs) and derived attributes of slope and aspect relative to the same attributes derived from LiDAR data. We also estimated the acquisition and processing costs per square kilometer of the five test models and the LiDAR models. We used three measures to characterize model error: (1) root mean square error, (2) mean error (and standard deviation), and (3) area of significant elevation error. We applied these measures to DEM products that are used extensively across a range of applications for planning and managing natural resources. We depicted the relationship between model accuracy (the inverse of error) and cost in two ways. One was accuracy/cost ratio for each model. The other used separate data on accuracy and cost to better guide potential users in choosing between models or deciding on necessary expenditure on models. The main conclusion of our work was that accounting for error in DEMs can inform choice of models and the need for financial outlays.

Keywords: data error; cost; error distribution; root mean square error; mean error

1. Introduction

Primary topographic attributes play a critical role in decision making for many planning and management fields. Understanding both natural and anthropogenic patterns and processes across a landscape requires techniques that can accurately represent complex topographic features (Holmes *et al.* 2000). Topographic models and derived attributes such as slope and aspect form the foundation for more advanced applications such as hydrological modeling and climate change scenarios, and ultimately influence applications and decisions in many aspects of planning and investment (Veblen 1989, Burrough and McDonell 1998). Depending on the application, even small elevation errors can greatly affect the utility of derived products (Holmes *et al.* 2000). For example, small topographic model errors can lead to inaccurate slope, aspect, and curvature derivatives, in

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turn leading to inaccurate predictions of slope failures (Holmes *et al.* 2000), inaccurate depiction of stream flow directions (Wise 2000), and dramatic misrepresentation of hydrological features (Lee 1996).

For research and management projects, digital elevation models (DEMs) are sometimes developed by the research teams that will use them for further modeling. More commonly, DEMs are acquired either by purchasing or by obtaining publicly available products (Holmes *et al.* 2000). When DEMs are produced by users, the local and global accuracies are known and the methods used to derive the product are understood and often well documented. In contrast, preprocessed models often are not supplied with information on data collection, methods for processing, or distribution of errors (Aguilar *et al.* 2007). In these cases, users have little understanding of the spatial distribution of errors associated with topographic models because measures of model error, beyond the root mean square error (RMSE) and mean error (ME), are not readily available (Darnell *et al.* 2008). In addition, it can be difficult to re-create the spatial patterns of errors for preprocessed DEMs. Consequently, there is a need for more supporting data and documentation to be made available to users. These data should include better estimates of inherent errors so that users can characterize and understand the implications of errors in derived data and applications (Wechsler 2007).

In countries such as Australia, as the resolution of data increases, institutional barriers tend to prevent access to users such as academic researchers, students, and nongovernmental organizations. The fine-resolution data required for local studies are usually scarce, held by local governments or private agencies, and expensive for other users to acquire. If high cost reflects the greater accuracy of fine-resolution data, then cheaper products often come with more uncertainty and error (Wechsler 2007). Important questions about this trade-off remain unsolved. One concerns accuracy: what are the most informative ways of measuring the accuracy of topographic models so that their utility for different applications can be understood by potential users? A second question is: what are the acquisition and processing costs associated with spatial data for research, management, and decision making in countries such as Australia where accurate high-resolution data come with a heavy price tag and less accurate coarse-resolution data are more readily obtained?

The work presented here addresses these questions and is directed at DEM end users. One of our major aims is to enable users of DEMs to better appreciate inherent errors in topographic models and their effects on subsequent applications as well as the corresponding costs associated with different models. A second aim is to suggest to potential users ways of balancing the costs and benefits of different topographic models. To represent the range of data sources that are either free or available for purchase in our region of northeastern Queensland, Australia, we use five different test DEMs derived from topographic, orbital, and satellite data. We present straightforward, repeatable methods for characterizing local and global errors in the test DEMs using two light detection and ranging (LiDAR) data sets as surrogates for 'true' elevation and use them to derive 'true' slope and aspect. We then measure the costs associated with acquiring and processing the five test models compared to the two high-resolution LiDAR models available for parts of our region. To depict the relationship between model accuracy and cost, we sum the cost in Australian dollars needed to acquire and process each product, and then present the relationship between cost and accuracy in two different ways. The first is the accuracy/cost ratio. The second is with disaggregated plots of model cost and model accuracy. This complements the ratios by allowing potential users to identify thresholds of accuracy required for their purposes and then to find the most cost-effective topographic model.

2. Methods

2.1. Study area and data

Our two study areas are within the Tully–Murray and Daintree catchments of northeastern Australia (Figure 1). Their extents are approximately 9 and 3 km^2, respectively. The Tully–Murray study area lies in a low-relief landscape, between 0 and 10 m elevation, near the confluence of the Tully and Murray Rivers. It is mainly deforested and covered by sugarcane with remnant patches of floodplain vegetation along waterways. The Daintree study area lies in a higher-relief section of the Daintree catchment, varying from 2 to 325 m elevation. The landscape within and surrounding the Daintree study area is predominantly native rainforest.

For our comparisons, we assumed that two LiDAR data sets represented spatial patterns of ‘true’ elevations, slopes, and aspects. True elevation values were represented by the two LiDAR models (Tully–Murray: mean = 10.911 m, SD = 2.08, n = 9936 and Daintree: mean = 93.84 m, SD = 89.51, n = 3132). We used three types of source data to derive five test DEMs to investigate the extent and distribution of DEM error. Two DEMs (1:100K and

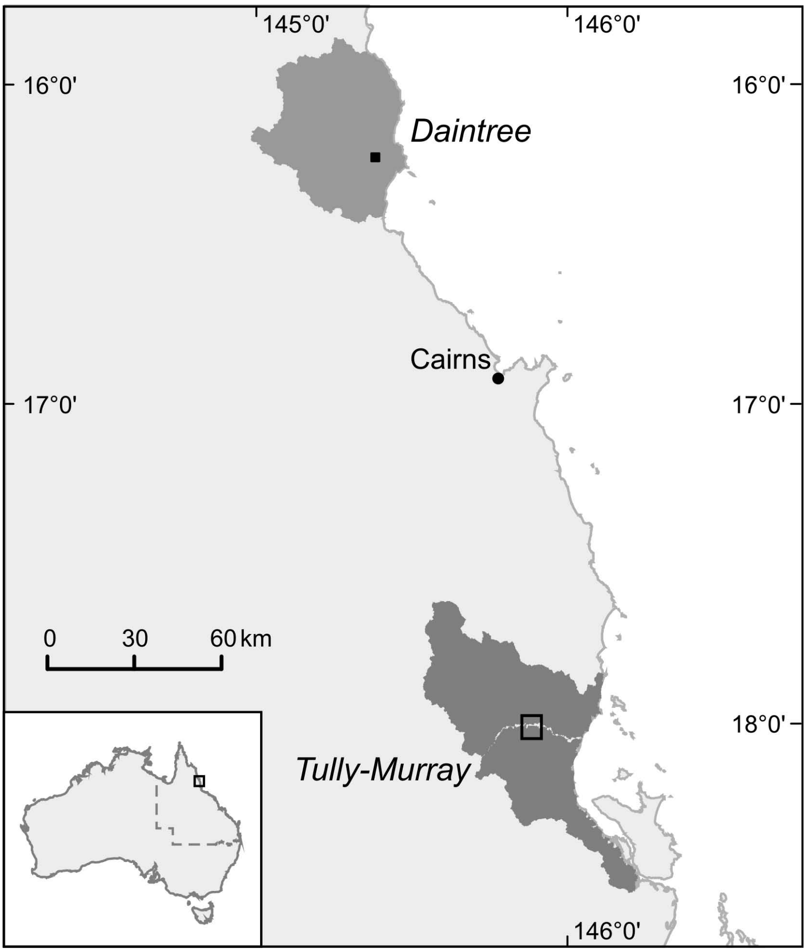

Figure 1. Location of the Tully–Murray and Daintree study areas (rectangles), within their respective catchment areas (shaded) in northeastern Queensland, Australia.

1:50K) were derived from 25 m contour topographic map sources, one DEM was derived from orbital (space shuttle) data (SRTM DTED 1), one DEM was derived from satellite data (SPOT HRS DTED 2, referred to subsequently as SPOT), and one DEM was a combined model (SRTM DTED 1 + 1:50K) from both topographic and orbital sources (Appendix A).

We received several models, including both LiDAR models, in different spatial resolutions and/or geographic coordinate systems (Appendix A). Therefore, to effectively compare models, we interpolated them to a common 30 m resolution using spline interpolation in ANUDEM 5.2 (Hutchinson 2006) as well as projecting them into the local coordinate system (MGA GDA 1994 zone 55) using ArcGIS 9.2 (ESRI 2006). We selected 30 m resolution for the comparison of models because this was the most appropriate resolution for our larger conservation planning project, based on the 1:50K and 1:100K scale of the topographic maps and the resolution of other spatial data available for our study region.

2.2. Distribution of cell elevation error

To determine the overall distribution of elevation error for each test model, we extracted and created a vector of center point elevation values for each 30 × 30 m cell. We then subtracted respective LiDAR center point elevation values from test model centre point elevation values to give error values of individual 30 × 30 m cells for each test model, and plotted those in relation to true elevation and slope. For each test model, we then determined the spatial correlation (Pearson's correlation coefficient) between elevation error and both true elevation and slope for both study areas using the 'cor' package in R statistical software, Version 2.8.0 (R Development Core Team 2008).

2.3. Root mean square error for elevation

We selected the RMSE as one measure of topographic model error because it is a common, if contested, way of comparing different DEM products (e.g. Burrough and McDonell 1998, Willmott and Matsuura 2006). The RMSE is a quadratic scoring rule that measures the average magnitude of error and incorporates both random and systematic errors introduced during data production (Appendix B). Because the error values are squared to obtain the RMSE, the measure weights large errors more heavily than small errors. However, because of the complex relationship between squaring error values of individual 30 × 30 m cells and averaging this relationship across all cells in the entire model, it is difficult to interpret the relative importance within RMSE of ME, defined below, and spatial variability of error (Willmott and Matsuura 2006).

It can be useful to calculate the difference between ME and RMSE, rather than the RMSE value alone. Because the RMSE is always greater than or equal to ME, larger differences between the two measures indicate larger spatial variation in individual cell errors across the model. However, these differences alone cannot provide the DEM user with an estimate of how well each cell in the DEM represents true elevation, which requires an additional, spatially explicit, measure of individual cell error (below). Here we apply the RMSE measure to our test models for comparative purposes to emphasize the need for DEM end users to consider alternative and complementary measures of error when evaluating products.

2.4. Mean elevation error and standard deviation

As a second measure of topographic model error, we determined ME (Appendix B) for each of the five test models in the two study areas, using center point values of individual

30 × 30 m cells estimated in Section 2.2.Unlike the RMSE, the ME is a linear score to which all individual cell errors contribute in direct proportion to their individual error values. We used ME and standard deviation in addition to the RMSE to describe overall model error for all test models. For some comparisons, we calculated the unsigned mean error (UME) values because we were interested only in the magnitude (not direction) of error. We used a paired t-test to determine if each of the test models was significantly different from the respective LiDAR models using R statistical software.

2.5. Area of significant elevation error and spatial correlation between models

We were also interested in identifying the spatial distributions of error, accounting for each 30 × 30 m cell in each test model and the extent to which error was spatially correlated between models. Because neither RMSE nor ME is spatially explicit, we needed two additional analyses. As the number of cells in both study areas was quite high (n = 9936, Tully–Murray; n = 3132, Daintree), we assumed a normal distribution of cell error. Therefore, to calculate the area of significant elevation error, we used the 'pnorm' function in R statistical software. Given the error values for each cell in each test model, the 'pnorm' function determines the probability that a normally distributed random number will be less than or equal to the error value of each cell (Appendix B). We then identified those 30 × 30 m cells that deviated significantly from the assumed normal distribution of error ($P < 0.05$, two-tailed test) for each test model, then mapped these cells and measured their total extent in each study area. We also determined the percentage of each study area with significant elevation error so that we could compare study areas. We used Pearson's coefficient to measure the spatial correlation of elevation error between all the 30 × 30 m cells in the test models within each study area.

2.6. Mean and standard deviation of errors for derived attributes

We were also interested in determining if models with the highest ME in estimated elevation were also the models with the highest ME in estimated slope (degrees) and aspect (degrees). For each study area, we used ArcGIS 9.2 to derive slope and aspect for all test models and the LiDAR models (Appendix B). Assuming that LiDAR gave 'true' slopes and aspects, we then measured the mean (signed) and standard deviation of error in slope and aspect for each test model after subtracting LiDAR center point values from the center point values of the test models. Finally, for each study area, we used the Spearman's ranked correlation coefficient to measure the match in rankings of test models according to error in elevation, slope, and aspect.

2.7. Benefit–cost analysis of test models

We defined the total cost of each test model and the LiDAR models as the sum of acquisition and processing costs in Australian dollars (AUD). We considered acquisition costs to be any costs associated with acquiring or purchasing either data sources or the models directly. We considered processing costs to be those related to the production of each model. Extensive postprocessing is involved in preparing LiDAR data. For this study we accessed LiDAR data that had already been postprocessed and requested time estimates from the providers to estimate the processing cost. Postprocessing of the test DEMs involved several kinds of analyses, such as visual inspections, identifying and correcting areas in the topographic data where contours were incorrectly numbered, and identifying and repairing spurious sinks and peaks for all DEMs. To standardize the production cost, we used the hourly pay rate for a research assistant at James Cook University, Australia.

To measure the 'benefit' of each test model and the LiDAR models, we used two measures of accuracy. These were both defined as the inverse of elevation error to more intuitively convey to end users the gain in return for cost. We derived our first measure of accuracy from the UME. For each study area, we subtracted each test model's UME from the maximum UME of any test model (produced by the 1:50K model in the Tully–Murray and the SPOT model in the Daintree). The least accurate model therefore had zero accuracy. Our second measure of accuracy was the percentage area without significant elevation error for each model (i.e. the complement of percentage area with significant error from Section 2.5). For LiDAR, which we assumed gave true elevation, accuracy was the full extent of each study area.

3. Results

3.1. Distribution of model elevation error in relation to true elevation and slope

Elevation error in the Tully–Murray was significantly correlated with true elevation and slope (Figures 2a and 3a), except for the 1:100K model which was not correlated with true slope. For test models in the Tully–Murray, elevation error of 30 × 30 m cells was evenly distributed between about 7.5 and 15.0 m true elevation (Figure 2a) and concentrated below 0.8° of true slope (Figure 3a). Errors from the SRTM DTED 1, SPOT, and SRTM DTED 1 + 1:50K models were positively correlated with true elevation but negatively correlated with true slope. Errors from the 1:100K and 1:50K models were positively correlated with true elevation, but only the 1:100K model produced errors that were positively correlated with true slope.

In the Daintree, elevation error in all models increased markedly above about 50 m true elevation (Figure 2b) and was concentrated between 0 and about 35° slope (Figure 3b). Elevation error from the SRTM DTED 1 and SRTM DTED 1 + 1:50K models was not correlated with true elevation. However, elevation error from the 1:100K, 1:50K, and SPOT models was correlated with true slope (Figure 2b). The 1:100K, SRTM DTED 1, and SRTM DTED 1 + 1:50K were negatively correlated with true elevation, while the 1:50K and SPOT were positively correlated. Error from the 1:100K and SRTM DTED 1 + 1:50K models was not correlated with true slope, but error from the other three models was (Figure 3b). All model elevation errors, except the 1:100K, were negatively correlated with slope.

3.2. Parameters of model elevation error

We used three parameters – RMSE, ME (with standard deviation), and area of significant error – to characterize the extent and distribution of elevation error across all the 30 × 30 m cells in the five test models.

In the Tully–Murray study area, RMSE values for all models were similar, although that for the 1:100K model was the highest (Table 1). The 1:100K model also produced the greatest difference between RMSE and UME, indicating that it had the greatest spatial variance in elevation error (and see Figures 2a and 3a). The difference between the RMSE and UME values for the 1:50K model was the lowest in the Tully–Murray and the correspondingly low spatial variance in error is apparent in Figures 2a and 3a. RMSE values were more variable in the Daintree (Table 1). The SRTM DTED 1 had both the highest RMSE value and the greatest difference between the RMSE and UME, corresponding to strong variation in individual cell error values (Figures 2b and 3b). The SPOT model had the

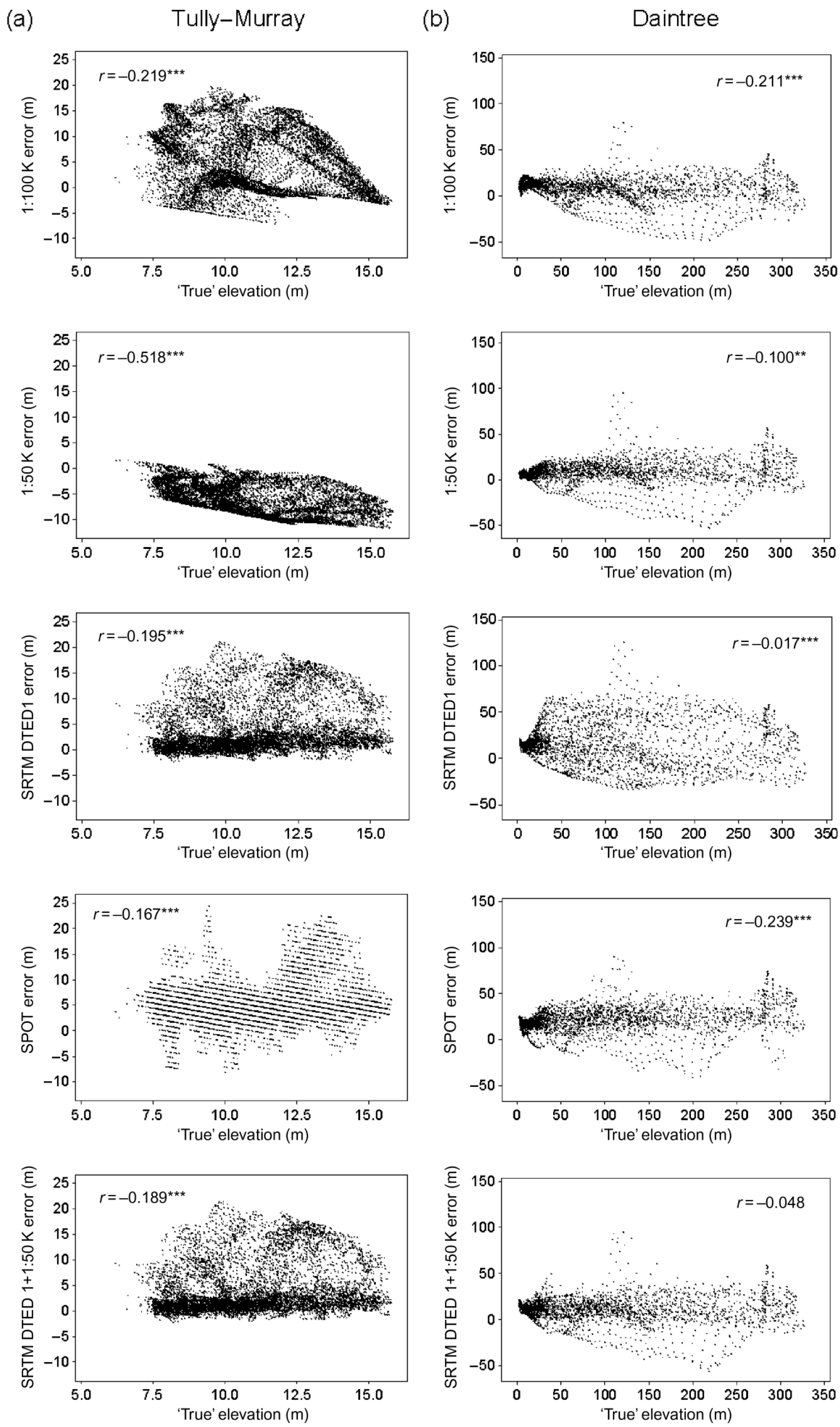

Figure 2. Scatter plots showing the distributions of individual cell elevation error (m) for the five test models relative to true elevation (LiDAR elevation values): (a) Tully–Murray and (b) Daintree study areas. Models are arranged by source data type (i.e. topographic, orbital, satellite, and topographic + orbital). Asterisks indicate the level of significance: $^{**}P < 0.01$, $^{***}P < 0.001$.

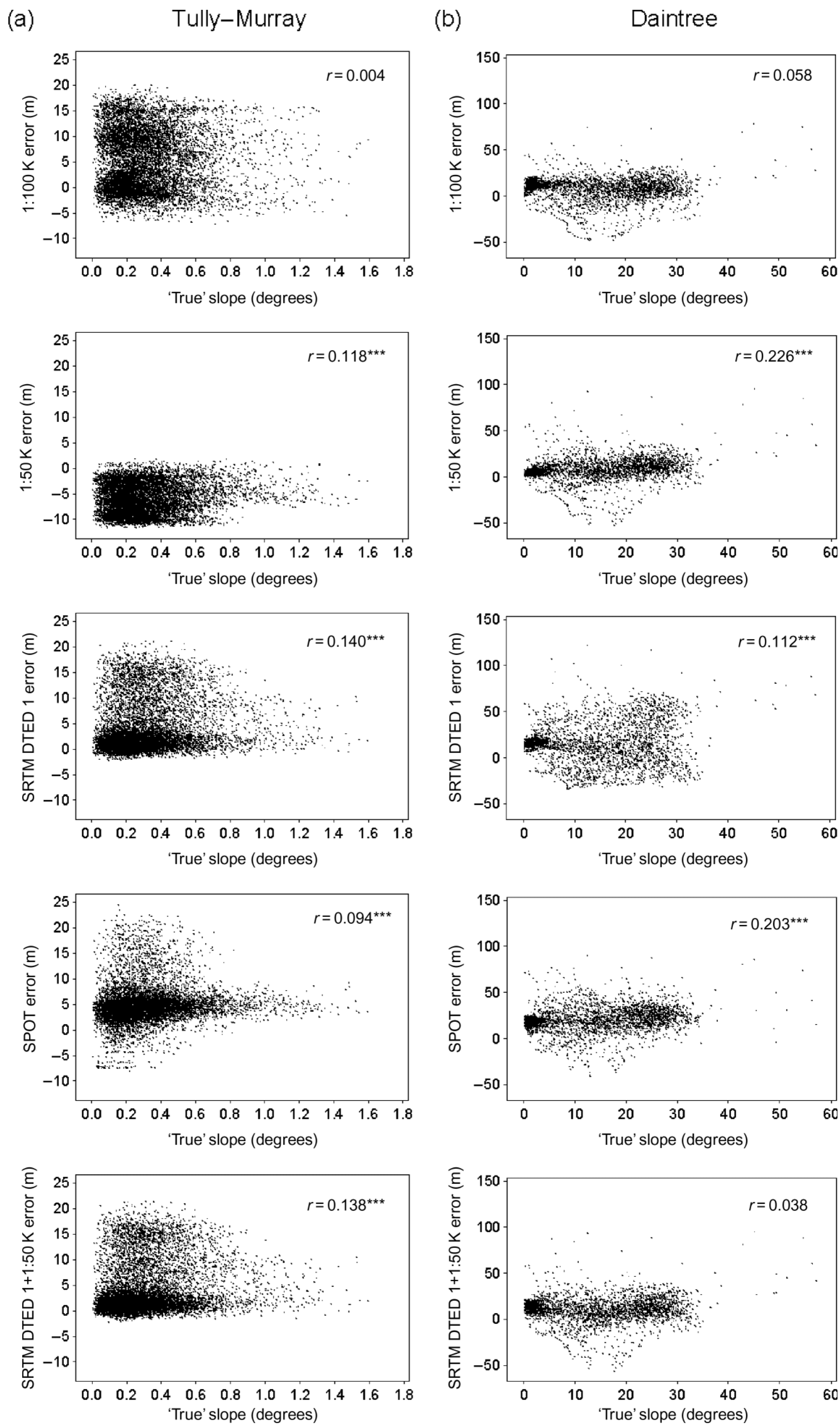

Figure 3. Scatter plots showing the distribution of individual cell elevation error (m) for the five test models relative to true slope (LiDAR slope values): (a) Tully–Murray and (b) Daintree study areas. Models are arranged by source data type (i.e. topographic, orbital, satellite, and topographic + orbital). Asterisks indicate the level of significance: $**P < 0.01$, $***P < 0.001$.

Table 1. Three measures of elevation error of test models: root mean square error (RMSE), unsigned mean error (UME), and area of significant elevation error (percentages of study areas with significant elevation error in parentheses).

Measure	Study area	1:100K	1:50K	SRTM DTED 1	SPOT	SRTM DTED 1 + 1:50K
RMSE (m)	Tully–Murray	7.84	6.57	6.22	6.15	6.31
	Daintree	15.01	14.82	27.52	24.9	17.53
UME (m)	Tully–Murray	5.19	5.84	3.93	4.99	4.01
	Daintree	8.46	8.42	16.39	21	11.29
Area of significant elevation error (sq km)	Tully–Murray	0.6021 (6.7%)	0.3906 (4.3%)	1.0071 (11.2%)	1.017 (11.3%)	0.5814 (6.5%)
	Daintree	0.0621 (2.1%)	0.1089 (3.4%)	0.1989 (6.6%)	0.09 (3.0%)	0.1269 (4.2%)

All measures are relative to true elevations as indicated by LiDAR values. Models are arranged by source data type (i.e. topographic, orbital, satellite, and topographic + orbital).

second highest RMSE error value in the Daintree but the least difference between RMSE and UME, indicating both larger errors but relatively little variance (and see Figures 2b and 3b).

In the Tully–Murray the 1:50K model had the highest UME and the range between highest and lowest UME was only about 1.9 m (Table 1). In the Daintree there were larger differences between models in UME values with more than 12 m separating the highest (SPOT) and lowest (1:50K).

Respectively, the SPOT and SRTM DTED 1 models had the largest and second largest areas of significant elevation error in the Tully–Murray and the 1:50K model had the smallest (Table 1). These values ranged up to 11.3% of the study area. In the Daintree, the SRTM DTED 1 model had the largest area of significant elevation error (6.6% of the total area), while the 1:100K model had the smallest (2.1% of the study area). Overall, the percentages of study areas occupied by cells with significant elevation error were consistently lower in the Daintree study area (Table 1).

3.3. Rankings of models according to different parameters of elevation error

Correlations between rankings of models for RMSE, UME, and area of significant error (Table 2) indicate the extent to which one of the measures of error can inform choice of models for the other two. In the Tully–Murray, none of the correlations were significantly different from random and two were negative, indicating that rankings were different between all pairs of measures. In the Daintree, rankings for RMSE were significantly but imperfectly correlated with those for area of significant elevation error. Overall, however, there is no indication that any one measure of error is a reliable guide to choice of models with respect to other measures.

3.4. Spatial correlations of elevation error between models

Mainly because of the large number of cells in the correlations (9936 in the Tully–Murray, 3132 in the Daintree), all spatial correlations were significant (Table 3). Nonetheless, there were large differences in the sizes of coefficients. In the Tully–Murray, there was a virtually exact fit between the SRTM DTED 1 and the SRTM DTED 1 + 1:50K models and smaller, but still substantial, spatial matches between each of these models and the SPOT model. The

Table 2. Spearman's correlation coefficients between rankings of the five test models according to the three parameters of elevation error – root mean square error (RMSE), unsigned mean error (UME), and area of significant error – in the Tully–Murray and Daintree study areas.

Comparison	Spearman's coefficient
Tully–Murray	
RMSE|UME	–0.40
RMSE|area of significant elevation error	–0.50
UME|area of significant elevation error	0.70
Daintree	
RMSE|UME	0.20
RMSE|area of significant elevation error	0.90*
UME|area of significant elevation error	0.50

*$P < 0.05$.

Table 3. Pearson's correlation coefficients between models in the Tully–Murray and Daintree study areas based on elevation error for all 30 × 30 m cells.

	1:50K	SRTM DTED 1	SPOT HRS	SRTM DTED 1 + 1:50K
Tully–Murray				
SRTM DTED 1	–0.12***			
SPOT	–0.14***	0.54***		
SRTM DTED 1 + 1:50K	–0.11***	1.00***	0.53***	
1:100K	0.35***	–0.09**	–0.06*	–0.09**
Daintree				
SRTM DTED 1	0.73***			
SPOT	0.76***	0.51***		
SRTM DTED 1 + 1:50K	0.91***	0.80***	0.67***	
1:100K	0.84***	0.69***	0.62***	0.85***

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

poorest, and almost nonexistent, match was between the 1:100K and SPOT models. These relationships are also reflected in the distributions of areas of significant error (Figure 4) with strong coincidence of these areas between the SPOT and SRTM DTED 1 + 1:50K models and almost no coincidence of areas between the 1:100K and SPOT models. Correlation coefficients were generally larger in the Daintree than in the Tully–Murray, with six values larger than 0.7 and all larger than 0.5 (Table 3). These larger values are reflected by mostly greater coincidence between models in terms of areas of significant error in the Daintree than in the Tully–Murray (Figure 4). Pairs of models with largest and smallest correlation coefficients were not the same for the two study areas.

3.5. Mean error and standard deviation for elevation and derived attributes

In the Tully–Murray four of the five models overestimated mean elevation, while the 1:50K model underestimated mean elevation (Table 4). In the Daintree, all five test models overestimated mean elevation, and the SPOT model had the greatest ME. In both study areas, models with largest MEs were not necessarily those with highest standard deviations (see Section 3.2 and Figures 2 and 3).

In the Tully–Murray, the SPOT model had the largest mean slope error and the 1:50K model had the lowest (Table 4). All models in the Daintree had negative mean slope error values (Table 4). The size of mean slope errors was generally comparable between the two

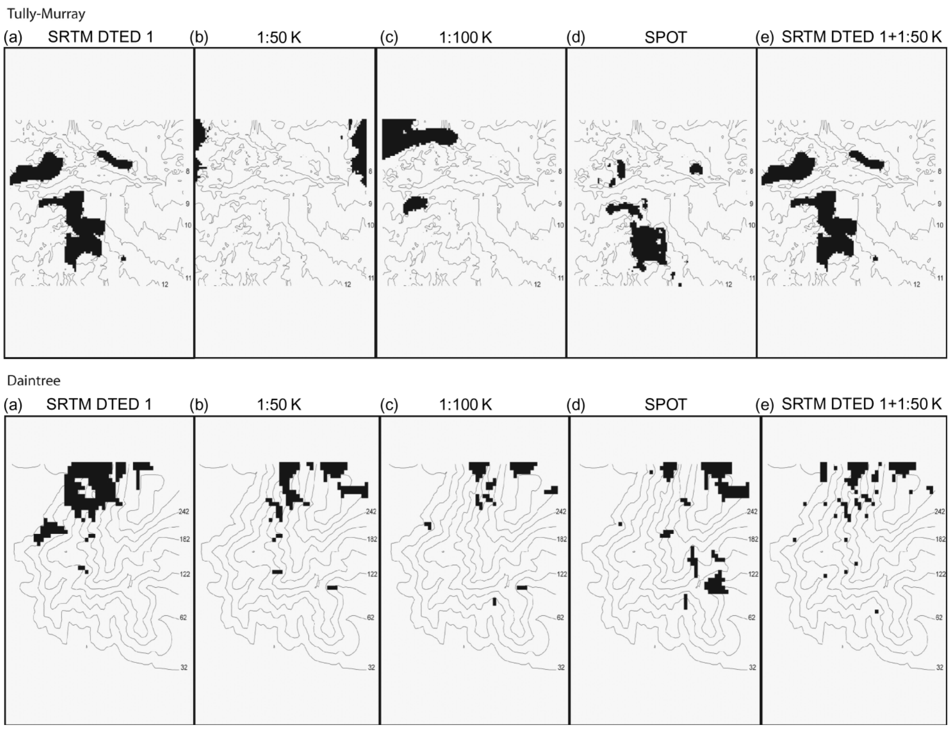

Figure 4. Spatial distribution of individual 30 × 30 m cells with significant elevation error for each of the test models: (a) SRTM DTED 1; (b) 1:50K; (c) 1:100K; (d) SPOT; (e) SRTM DTED 1 + 1:50K in the Tully–Murray and Daintree study areas. Contours represent true elevation (LiDAR models).

Table 4. Mean error and standard deviation for elevation (m), slope (degrees), and aspect (degrees) for the five test models in the Tully–Murray and Daintree study areas. Models are arranged by the source data type (i.e. topographic, orbital, satellite, and topographic + orbital).

	Tully–Murray		Daintree	
	Mean error	Standard deviation	Mean error	Standard deviation
Elevation (m)				
1:100K	5.19	5.88	8.46	12.40
1:50K	–5.84	3.02	8.42	12.20
SRTM DTED 1	3.93	4.82	16.39	22.11
SPOT	4.99	3.60	21.00	13.39
SRTM DTED 1 + 1:50K	4.01	3.60	11.29	13.42
Slope (degrees)				
1:100K	0.77	0.99	–1.15	6.05
1:50K	–0.05	0.22	–0.62	5.48
SRTM DTED 1	1.39	1.45	–1.79	6.20
SPOT	1.82	1.79	–0.45	6.59
SRTM DTED 1 + 1:50K	1.41	1.53	–0.11	6.32
Aspect (degrees)				
1:100K	–1.04	151.10	–2.81	44.08
1:50K	–10.74	147.50	–2.13	46.40
SRTM DTED 1	23.19	159.40	–3.45	57.02
SPOT	5.18	159.90	–0.99	63.51
SRTM DTED 1 + 1:50K	–154.50	119.50	–9.65	68.84

Table 5. Spearman's correlation coefficients between rankings of the five test models according to elevation, slope, and aspect unsigned mean error (UME) in the Tully–Murray and Daintree study areas. None of the coefficients was significant.

Comparison	Spearman's coefficient
Tully–Murray	
Elevation UME|slope UME	0.13
Elevation UME|aspect UME	–0.73
Daintree	
Elevation UME|slope UME	–0.10
Elevation UME|aspect UME	–0.10

study areas but standard deviations were consistently larger in the Daintree. In neither study area were the rankings of test models for elevation and slope error correlated (Table 5), indicating that the size of elevation errors does not necessarily indicate the extent to which these will propagate into mean slope errors.

Mean aspect error varied strongly in the Tully–Murray (Table 4) with the SRTM DTED 1 + 1:50K model having a very large error. Mean aspect errors were more uniform in the Daintree, although the SRTM DTED 1 + 1:50K model again had the largest value. Only the SRTM DTED 1 and SPOT models had positive mean aspect error in the Tully–Murray. All other models in both study areas had negative mean aspect error. Standard deviations were consistently larger in the Tully–Murray than in the Daintree (Table 4). Like the slope results, there were no significant correlations between rankings for test models according to mean elevation and aspect error (Table 5).

3.6. Model accuracy and cost

Accuracy/cost ratios varied strongly between models, study areas, and measures of accuracy (Figure 5). Ratios for LiDAR and SPOT were consistently low and ratios for SRTM DTED derived models tended to be high. Ratios based on UME produced very different rankings of models between the Tully–Murray and Daintree study areas (Figure 5a). In particular, the 1:50K model had the lowest ratio of any model in the Tully–Murray but one of the highest in the Daintree. Ratios based on percentages of study areas without significant error were similar between study areas and distinctly grouped, with LiDAR lowest, followed by SPOT, then the topographically derived models, then the SRTM DTED derived models.

Separate plots for accuracy and cost help to explain the results for accuracy/cost ratios but also add information that is not discernible from the ratios. Figures 6 and 7 show why SPOT generally had lower ratios than other test models: this model provided lower or comparable accuracy but at substantially higher cost. For accuracy based on UME, ratios for SRTM derived models were higher than for other test models in the Tully–Murray and relatively high in the Daintree (Figure 5a) because these models gave the highest accuracies (Tully–Murray) or comparable accuracies (Daintree) for very low cost. Ratios based on areas without significant error (Figure 5b) were higher in the Daintree than in the Tully–Murray because of consistently higher accuracies in the Daintree (Figure 7).

Figures 6 and 7 also emphasize the nonlinear relationship between cost and accuracy. For accuracy based on UME in the Tully–Murray study area, the cheapest model (SRTM DTED 1) gave 33% of the benefit for 2% of the cost relative to the LiDAR model (Figure 6a). Similarly, in the Daintree and considering the percentage of study area without significant

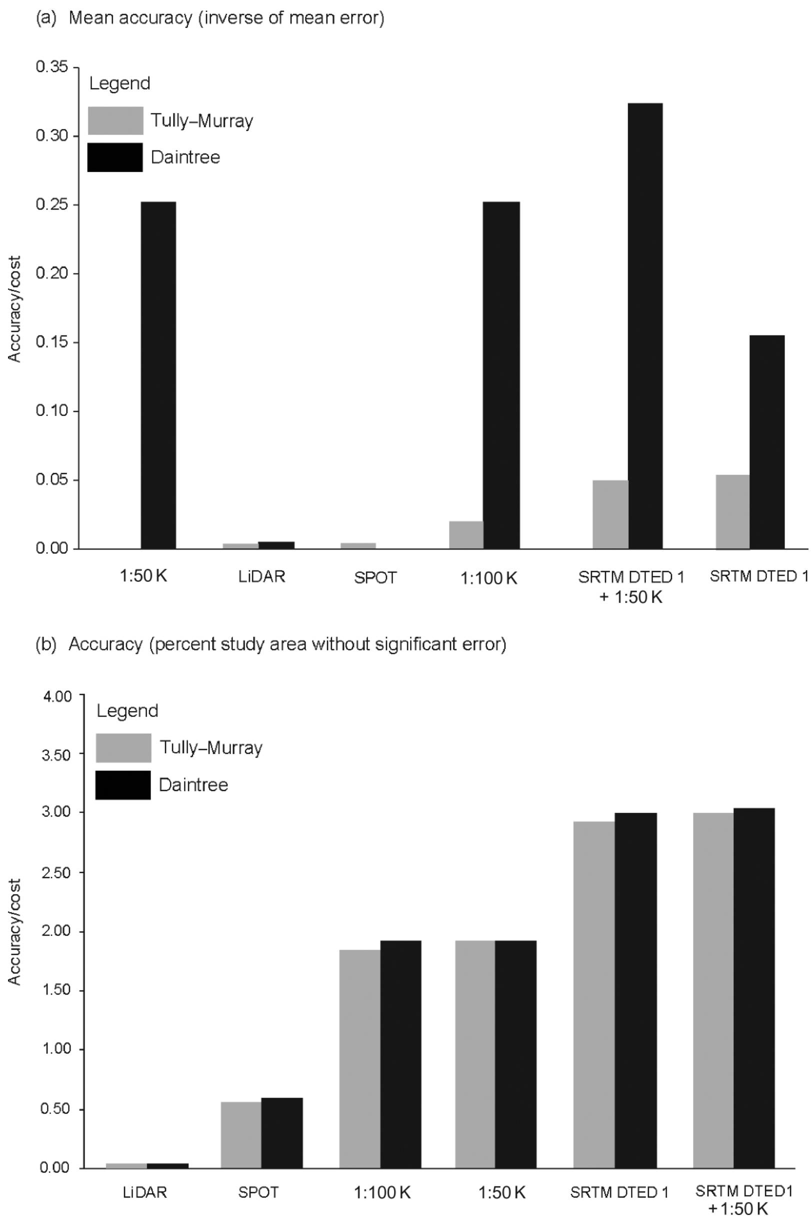

Figure 5. Accuracy/cost ratio for LiDAR models and five test models in the Tully–Murray (gray bars) and Daintree (black bars) study areas: (a) mean accuracy (inverse of mean error) and (b) accuracy (percent study area without significant error). Note that ratios in part (a) are not comparable between study areas. Models are arranged by increasing accuracy/cost ratio for the Tully–Murray study area.

elevation error (Figure 7b), the cheapest model (SRTM DTED 1) had only 4% less accuracy than the LiDAR but 98% lower cost (Figure 7b).

Nonlinear trade-offs between accuracy and cost lead to consideration of minimum standards for accuracy. In the Daintree, for example, two test models (1:50K and 1:100K) had accuracy values from UME within 9 m of true mean elevation (Table 1, Figure 6b),

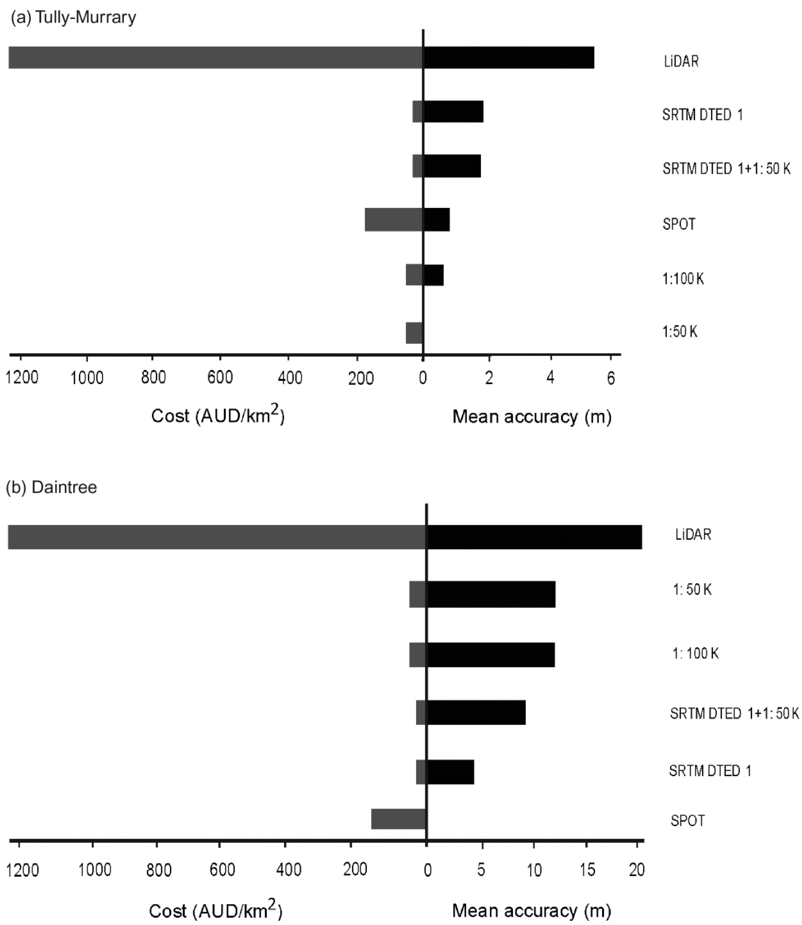

Figure 6. Bar plots depicting cost (AUD/km^2) and mean accuracy (inverse of UME; m) for LiDAR and five test models in the (a) Tully–Murray and (b) Daintree study areas. Note that accuracy values in this figure are not comparable between study areas. Models are arranged in decreasing order of model accuracy.

which might be acceptable for regional-scale environmental planning. These could then be compared according to costs (which are similar) and other criteria. For the Tully–Murray, the best test models according to UME accuracy (derived from SRTM) were within about 4 m of true elevation (Table 1, Figure 6a). Because of the flat terrain, however, this figure represents a large percentage of both mean (37%) and standard deviation (190%) of true elevation. Together with relatively large percentage areas of significant elevation error (Table 1), these results indicate that users would either have to settle for considerable uncertainty in their topographic model or seek funds for LiDAR to improve accuracy.

4. Discussion

This work arose from our interest in evaluating the DEM products available in our region to understand topographic model error and its potential influence on conservation planning and management of natural resources. Specifically, this project was motivated by our need for

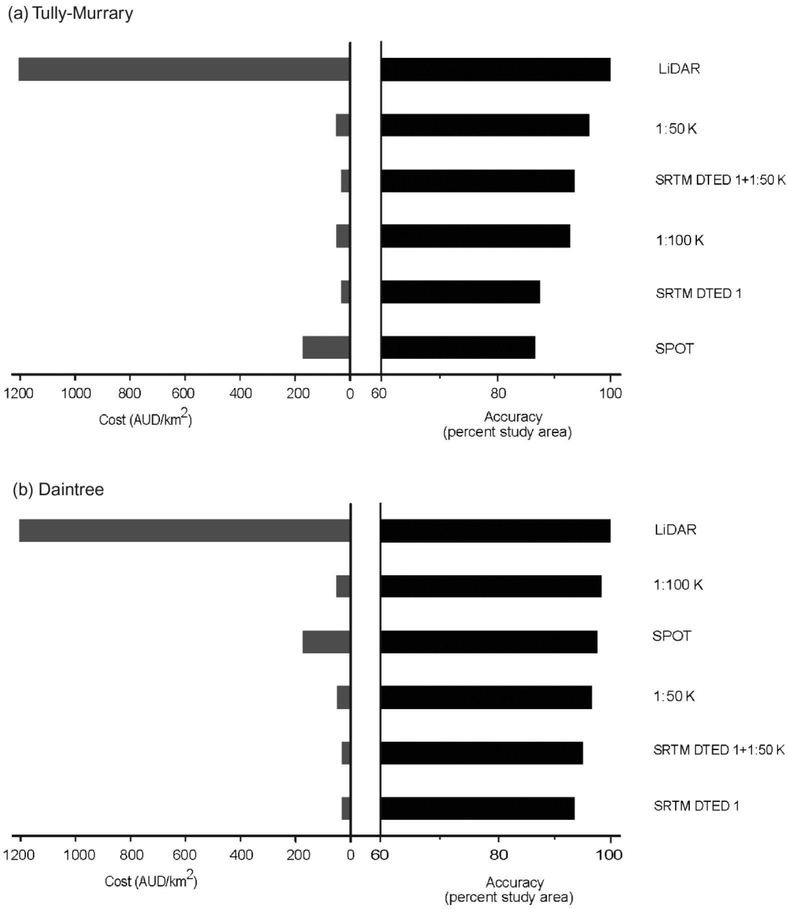

Figure 7. Bar plots depicting cost (AUD/km^2) and accuracy (percent study area without significant error) for LiDAR and five test models in the (a) Tully–Murray and (b) Daintree study areas. Note that accuracy values in this figure are comparable between study areas. Models are arranged in decreasing order of model accuracy.

topographic models on which to base hydrological modeling for stream classification and conservation planning in north-eastern Queensland.

We demonstrated that elevation error in DEMs varies between models and has variable relationships with 'true' elevation and slope. Our results align with those of Holmes *et al.* (2000) and Thompson *et al.* (2001), who noted variable relationships between elevation error and true elevation and slope when evaluating the implications of DEM error on terrain modeling. With only two exceptions, our models produced elevation errors that were significantly correlated with true elevation in both study areas. We found that some models were susceptible to elevation error in low-relief areas such as the floodplain of the Tully–Murray. This is particularly true of the models (1:100K and 1:50K) derived from topographic data with 20 m contour lines. Although the interpolation method was effective (Appendix A), these models could not adequately represent elevation between or below 20 m contours.

Importantly, our three measures of elevation error ranked test models differently. Each measure conveyed different information about the distribution of error, accounting for all the

30×30 m cells in each study area, and our results provide little confidence that any single measure can serve as a surrogate for the others. Put another way, our results emphasize the need for several complementary measures to adequately characterize error, unless potential users of models are very clear about what single aspect of elevation error they wish to minimize. In particular, combining measures of RMSE and UME can be informative about the spatial variation of error in models (and see Willmott and Matsuura 2006). Our comparisons therefore help to underline the limitations of RMSE as a sole measure of error, even though it is commonly reported alone, because it confounds the magnitude of error across a model with the model's spatial variation in error (Willmott and Matsuura 2006). We also demonstrated the value of complementing both RMSE and ME with a spatially explicit measure. Our area of significant elevation error conveys additional information and comes with the potential to map the locations of cells that deviate strongly from true elevation. This adds to interpretation of error by allowing users to relate significant error to attributes of their study areas and to identify the implications of error for particular applications.

We also showed that larger errors in models of elevation do not necessarily propagate to larger errors in models of slope and aspect (and see Holmes *et al.* 2000, Thompson *et al.* 2001). Rankings of our test models according to these kinds of errors were uncorrelated in both study areas, so elevation error is not a reliable predictor of error in derived attributes. End users need to consider this when evaluating the type of error that could influence the reliability of their management decisions.

Although accuracy/cost ratios might be intuitively appealing when evaluating alternative topographic models, our results highlighted a key advantage in considering accuracy and costs separately: the ability to consider threshold requirements of accuracy based on one or more measures relevant to the intended applications. Someone interested in very high accuracy across a landscape with low relief (e.g. Rayburg *et al.* 2009) will have different expectations of ME (e.g. less than 1 m) than someone interested in modeling regional-scale threats to coastal systems (e.g. Cooper and McLaughlin 1998). Alternatively, upper limits on possible expenditure might limit achievable accuracy and inform users about the uncertainty inherent in their topographic models.

While accuracy/cost ratios for LiDAR were very low compared to all or most test models, depending on the study area, the accuracy/cost ratios hid the potential gains in accuracy from these models. This could, depending on the intended application, be a compelling reason for a large investment. The most extensive LiDAR purchases in north-eastern Queensland have been for regional disaster management focused on flat coastal lowlands where very high accuracy is required to assess the potential for large economic impacts of events such as floods, storm surges, and tsunamis. Our sample of these data from the Daintree was atypical in covering an area of high relief. Similarly, CSIRO purchased our small LiDAR sample in the Tully–Murray study area for detailed hydrological modeling on the floodplains.

Many users of topographic models are land-use planning professionals, who depend on DEMs and their derivatives to guide local, regional, and national initiatives in managing natural resources. Yet, while it is critical to understand the limitations of DEM products to inform land-use decisions, there remains a general acceptance that end users cannot afford the time needed to explore DEM error (Wechsler 2003). It is apparent from our study and previous ones (e.g. Wise 2000; Sindayihebura 2008) that accounting for error in topographic models can inform choice of models and the need for financial outlays. Ideally, these analyses will also extend to understanding the implications of observed error for specific applications. This presents a new set of analytical challenges that we are just beginning to address in our work across the Wet Tropics of Queensland. While there is little scope to purchase LiDAR across the entire region, its availability for small parts of the region with very different terrains, and the assumption that topographic attributes from LiDAR are ‘true’, allows us to extrapolate errors in our selected models across the entire region. We will use the results presented here to account explicitly for the propagation of error in elevation, slope, and aspect from test models into classification of stream reaches and decisions about priorities for conservation action.

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Appendix A. Detailed model descriptions

A.1. Spline interpolation

Source data used for the spline interpolation included (1) contour lines derived from 1: 100K topographic maps (Queensland Department of Environment and Resource Management 2008); (2) contour lines derived from 1: 50K topographic maps (Australian Army); (3) center points derived from SRTM DTED Level 1; and (4) SRTM DTED 1 Level center points + contour lines derived from 1:50K topographic maps. These four DEMs were created using ANUDEM 5.2 (Hutchinson 2006).

Shuttle Radar Topography Mission (SRTM) is a single-pass synthetic aperture radar technique based on the interference of radar returns at two separate antennas (Farr *et al.* 2007). This works by radiating a pulse from one antenna and measuring the difference in phase of the signal returns from each respondent antenna. The recorded vertical error budget for one pass of the SRTM was 16 m, or 90% accuracy at mean sea level (Farr *et al.* 2007).

SRTM derived DTED has unique properties compared to photogrammetrically derived DTED (Farr *et al.* 2007). Photogrammetric post heights are defined as a measured height at a given post, whereas synthetic aperture radar interferometry post heights are derived from the measured mean height of the pixels around the post. SRTM DTED is a measure of the reflective surface, which can penetrate into the tree canopy but does not reach soil surface (Farr *et al.* 2007). SRTM data error is dominated by random error and flat surfaces can exhibit a 'popcorn' appearance (Rodriguez *et al.* 2006). White speckles on the face of some mountains are holes in the data caused by steep terrain. Phenomena called layover and shadowing are responsible for these gaps. In addition, vertical obstruction (VO) data consists of man-made cultural features such as buildings and power pylons and remain in the DTED data. The near-global data set covers between 60° N and 56° S latitudes (Farr *et al.* 2007).

We used the SRTM DTED 1 and SRTM DTED 1 + 1:50K as input to ANUDEM 5.2 as data having mostly spot heights. We set the roughness penalty for the selected model at 0.5 for potential and 0 for profile curvature. We set horizontal and vertical units in meters for both models. We set cell size at 30 m and a grid margin of 600. We set the lowest elevation bound at 0 m and the highest at 1700 m because the highest known point in the region occurs just below 1700 m. We set the first elevation tolerance to 5 m and the second at the default of 6 times the first elevation tolerance (30 in this instance).We set the positional error settings to 1.0 for the RMS factor and 0.25 for the vertical standard error. We used the default settings of 0.2 for cliffs and a value of 0 for stream positional errors because there were no stream lines burnt into these DEMs. The interpolated SRTM DTED 1 (30 m) DEM had a vertical accuracy of 27.5 m in higher-relief areas and 6.22 m in low-relief areas. The SRTM DTED 1 + 1:50K model had a vertical accuracy of 17.53 m in higher-relief areas and 6.31 in low-relief areas.

Positional accuracy (both horizontal and vertical) for the 1:100K digital topographic data was 34 m on the ground. The 1:50K topographic data had a 20 m positional (horizontal and vertical) accuracy. We considered the input data to be mainly contours with both roughness penalties set to 0 because this is the suggested setting for contour data in ANUDEM 5.2. We set both horizontal and vertical units in meters and the cell size at 30 × 30 m with a grid margin of 600. Similar to all models generated for this study area, we set the elevation bounds between 0 and 1700 m. We set the first elevation tolerance to one half the contour intervals (20 m for both models respectively). Therefore, both the 1:50K and 1:100K topographic contour derived models had a tolerance of 10 m. We set the discrete RMS factor to 1 and the vertical standard error to zero. The 1:50K and 1:100K topographic contour derived models had a vertical accuracy of 14.82 and 15.01 m, respectively, in high-relief areas. In low-relief areas, we determined a vertical accuracy of 6.57 and 7.84 m, respectively.

A.2. SPOT HRS DTED 2

The SPOT HRS DTED 2 (SPOT) is designed and built by SPOT Image Corporation and the French National Cartographic Institute (IGN) using HRS collected stereo pairs (SPOT Image Corporation 2008). The Reference3D is a worldwide accurate DEM database generated from HRS sensors onboard

SPOT 5 without any ground control points. Some assessments performed worldwide have shown that the Reference3D met its standard specifications (SPOT Image Corporation 2008). The database is composed of three information layers: (1) DEM of 1″ resolution (≈30 m), (2) orthoimages at 5 m resolution, and (3) documented and traceable metadata. SPOT has documented 90% circular error vertical accuracy between 10 and 30 m (slope dependent) and absolute horizontal accuracy of 10 m at slope less than 20 m. SPOT is the only documented DEM providing detailed information on the identification and location of the kind of residual errors (gaps/artifacts) found in all DEM products generated by automatic correlation (SPOT Image Corporation 2008). The documented vertical accuracy of SPOT for our study region was stated to be below 10 m when slope was less than 20°. The results of our work support this. We determined a low-relief (<2° slope) RMSE of 6.15 m for the SPOT model.

A.3. LiDAR – Tully–Murray

The LiDAR imagery collected for the Tully–Murray study region was collected on a Diamond Aircraft ECO-Dimona flying 400 m above the surface. Approximately four data points were collected per square meter. We derived center points from the original 3 m grid cells using ArcGIS 9.2 and input them to ANUDEM 5.2. We used the same spline technique explained above to interpolate from 3 m to a 30-m-spaced grid. The resulting vertical accuracy was 40 cm and the horizontal accuracy was 50 cm for the 30 m LiDAR model.

A.4. LiDAR – Daintree

The LiDAR imagery for the Daintree study area was donated to this project by the Cairns City Council. The documented vertical accuracy reported here is determined only for this study area, and does not reflect the accuracy of the model used by Cairns City Council. We used raw LAS files converted to multipoint files using ArcGIS 9.2 to generate four raster grids for the study area. We took output point files from ArcGIS 9.2 and input them to ANUDEM 5.2 and used the same spline technique to interpolate the 5-m-spaced grids of the raw LiDAR to a 30-m-spaced grid. The resulting vertical accuracy was 40 cm and the horizontal accuracy was 50 cm for the 30 m LiDAR model.

Appendix B. Equations

B.1. RMSE

We calculated RMSE as follows:

$$\mathrm{RMSE} = \sqrt{\left[\frac{1}{n}\sum_{i=1}^{n}\left(z(x_0) - \hat{Z}(x_0)\right)^2\right]}$$

where z is the elevation value for each cell (x_0) in each test model, and $\hat{Z}$ is the true elevation value for each cell (x_0) in the LiDAR model.

B.2. ME

We calculated ME as follows:

$$ME = \frac{1}{n}\sum_{i=1}^{n}\left[z(x_0) - \hat{Z}(x_0)\right]$$

where z is the elevation value for each cell (x_0) in each test model, and $\hat{Z}$ is the true elevation value for each cell (x_0) in the LiDAR model.

B.3. Normal distribution of error

We determined the probability of any 30 × 30 m cell error value being equal to the mean distribution of error using a probability density function. For a normal distribution, the probability density function was

$$p(x) = \frac{1}{\sqrt[\sigma]{2\pi}} \exp\left(- \frac{(x-\mu)^2}{2\sigma^2} \right)$$

where μ is the mean, σ is the standard deviation, and exp is the exponential function.

B.4. Slope

We calculated slope (degrees) for each 30 × 30 m cell in ArcGIS 9.2. The equations used in ArcGIS 9.2 to determine slope (degrees) are

$$\frac{\text{Rise}}{\text{Run}} = \sqrt{\left(\left[\frac{\Delta z}{\Delta x}\right]^2 + \left[\frac{\Delta z}{\Delta y}\right]^2 \right)}$$

$$\text{Slope(degrees)} = \arctan\left(\frac{\text{Rise}}{\text{Run}}\right) \times 57.29578$$

where Δz is the rate of change of the surface, Δx is the horizontal direction change, and Δy is the vertical direction change from the center of each 30 × 30 m cell in a 3 × 3 roving window.

B.5. Aspect

We calculated aspect (degrees) for each 30 × 30 m cell in ArcGIS 9.2. In ArcGIS 9.2, aspect is calculated using a moving 3 × 3 window that visits each 30 × 30 m cell. For each cell in the center of the window an aspect value is calculated incorporating the values of the cell's eight neighbors. Each of the eight cells surrounding the center cell is assigned a letter from *a* to *i*. The center cell is identified as *e*, as displayed below:

a	*b*	*c*
d	*e*	*f*
g	*h*	*i*

The rate of change Δ, in *x*-direction for cell '*e*', is calculated as follows:

$$\frac{\Delta z}{\Delta x} = \frac{(c + 2f + i) - (a + 2d + g)}{8}$$