Conservation and ecology of wetland birds in Africa

Submitted by

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I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

Signature: ……………………………………………………………..

Abstract

Conservation managers worldwide are increasingly faced with the challenges of managing and protecting fragmented landscapes, largely as a consequence of human activities. Over recent decades, ecological theory has made a significant contribution to the development of landscape-scale conservation and practice. However, recommendations accounting for what is practically achievable in the modern-day landscape are currently lacking, while criteria for conservation planning and prioritisation continue to neglect the role of habitat networks at the required spatial scale for the long-term persistence of biodiversity. In this thesis, I test and apply ideas surrounding the complexities of managing and conserving species in a landscape context, using a suite of bird species endemic to papyrus (*Cyperus papyrus*) swamps in East and Central Africa as a model system. In the face of large-scale habitat loss and degradation, practical measures that account for the fragmented nature of this system, the needs of multiple specialist species, and the reliance on this habitat by local people, are urgently required. I first review the concepts originating from reserve design theory to provide a decision-making framework for those involved in landscape-scale conservation amid 21st century challenges to biodiversity, highlighting the key principles to be considered for informed choices to be made. Second, I show that the needs of local people can be compatible with conservation planning in the tropics, and may play an important part in maintaining habitat quality for species residing in historically disturbed landscapes. Third, I develop a novel framework to make an explicit link between metapopulation dynamics and conservation planning. Despite differences in the patch-level dynamics of individual species, areas of habitat where populations of multiple species are resistant to extinction, and resilient because of high chances of (re)colonization can be identified, highlighting where resources could be invested to ensure species have the capacity to respond to future change. Finally, I simulate the metapopulation dynamics of the papyrus-endemic birds to demonstrate that the optimal conservation strategy for the long-term persistence of all species residing in a network depends on the characteristics of individual species, and the total area that can be protected. Overall, this thesis develops and tests the ecological theory used in spatial conservation planning, emphasising the importance of habitat disturbance and interspecific ecological differences for the effective management of habitat

networks. The results increase the evidence base for the conservation of wetland birds in Africa, as well as for species residing in fragmented landscapes more generally.

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All photos contained in this thesis are © Lynda Donaldson.

Forward: As Chapters 2-5 are written as distinct research papers, and include published research (see Publications), reference to the first-person plural has been retained for these sections.

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Chapter 1:
General introduction

Habitat destruction and degradation from human activities (Newbold et al. 2015) are among the greatest threats to biodiversity worldwide (WWF 2014, 2016). The destruction of habitat comprises both habitat loss (a decrease in the amount of habitat available) and habitat fragmentation (a change in the configuration of habitat) (Fahrig 2002, 2003; Liao et al. 2013); thus, specialized species with localized habitat distributions are particularly sensitive to the spatial changes in habitat experienced across the landscape (Devictor, Julliard & Jiguet 2008). Among the international agreements established to combat these threats, the Convention on Biological Diversity (CBD), established at the United Nations Conference on Environment and Development in 1992, was arguably one of the most fundamental steps towards the conservation of global biodiversity (Gaston & Spicer 2004). Habitat extent and condition were used as indicators for the 2010 Biodiversity Targets (Butchart et al. 2010), agreed during the 6th Conference of the Parties (The Hague, 2002). Following failure to achieve these goals (CBD 2010), at the tenth meeting of the Conference of the Parties, countries were called upon to implement the 2011-2020 Strategic Plan for Biodiversity, including the current Aichi Biodiversity Targets (CBD 2011). Among these targets, the need to significantly slow habitat loss and reduce degradation continues to be acknowledged (target 5), alongside another 19 targets under 5 strategic goals, based around recognising the causes of biodiversity declines, reducing threats, and improving the status of biodiversity by 2020. However, current progress towards these targets is slow, suggesting that attaining the desired results by 2020 is unlikely (Tittensor et al. 2014), while the conservation funding available to meet the set goals is inadequate (McCarthy et al. 2012). Thus, strategic conservation planning is paramount to ensure resources are used wisely, and encourage the most chance of success for global biodiversity this time around.

Conservation planning and prioritisation

Protected areas are regarded as the backbone for conservation management (Watson et al. 2014), aiming to be representative of biodiversity, and ensure its long-term persistence (Margules & Pressey 2000). These are recognised as an integral part of *in situ* conservation (Article 8 of the text of the CBD) and form part of the Aichi targets; aiming to increase the coverage of these areas to 17% of terrestrial and inland water, and 10% of coastal marine areas by 2020 (CBD 2011). Various priority sites have also been established in an attempt to ensure that resources are invested in the most important areas, focusing on hotspots with high species richness, endemism, pristine habitat or levels of threat, such as Centres of Plant Diversity (WWF & IUCN 1994-1997), Key Biodiversity Areas (Eken et al. 2004), Biodiversity Hotspots (Myers et al. 2000) and Major Tropical Wilderness Areas (Mittermeier et al. 1998). In theory these priority sites can be used to assist with the designation of protected areas, though arguably have had little success in encouraging conservation implementation (Brooks et al. 2006). However, following an increase in the level of fragmentation occurring across landscapes, combined with added pressures from climate change, pollution and invasive species (Millennium Ecosystem Assessment 2005), the implications of site-based approaches to conservation, i.e. focusing on the protection of a particular place (Coppolillo et al. 2004), have become apparent. Rather than managing and preserving sites in isolation, it is now widely recognised that conservation should focus on networks of habitat for the persistence of biodiversity (Lawton et al. 2010).

Landscape-scale conservation

Theoretical work has vastly enhanced our understanding of the response of species to the spatial configuration of habitat and, in turn, played a pivotal part in guiding the conservation management of fragmented landscapes and reserve design at landscape scales (Diamond 1975). The theory of island biogeography (MacArthur & Wilson 1967) built on the species-area and species-isolation relationships (Hanski 1994a), stating that the number of species an island can hold is a function of its size and distance from a mainland population. The theory of metapopulation dynamics developed these concepts further; the processes of extinction and colonization are still central to this theory, but there is no mainland population, and all patches (or “islands”) show constant turnover (Hanski & Gilpin 1991).

Originally defined by Levins (1969) as a “population of populations”, a metapopulation consists of a set of local populations that are vulnerable to extinction through stochastic events (Thomas 1994), but the balance of extinction and recolonization means that the metapopulation as a whole can still persist (Figure 1.1). Interest in modelling the metapopulation dynamics of species has increased substantially over the past few decades, following the demand for managing plant and animal populations in fragmented landscapes (Hanski & Gilpin 1991), alongside the development of models that can be applied to real metapopulations (Hanski & Gilpin 1991; Hanski 1999a; Ovaskainen & Hanski 2001), and with readily available ecological field data (Hanski 1994b). To reside as a classical metapopulation, a species must exist in spatially distinct habitat patches, all local populations must be at risk of extinction, patches should not be too isolated to prevent (re)colonization, and dynamics should be sufficiently asynchronous so that simultaneous extinction is unlikely (Hanski et al. 1995a). Metapopulation models have been applied to a variety of taxa (see Hanski & Thomas 1994) and shown their potential to identify key areas for investment (Hanski et al. 1996), predict the response of species to changes in their environment (Hanski & Thomas 1994; Lindenmayer, McCarthy & Pope 1999; Moilanen 2004), and note threshold levels of fragmentation for persistence (Bulman et al. 2007). Based on the assumptions associated with the rate of colonization and extinction for most spatially-realistic metapopulation models (Figure 1.1), metapopulation theory has played a key part in informing the design of ecological networks, and the importance of habitat size, quality and levels of connectivity for species persistence across the landscape (e.g. Lawton et al. 2010).

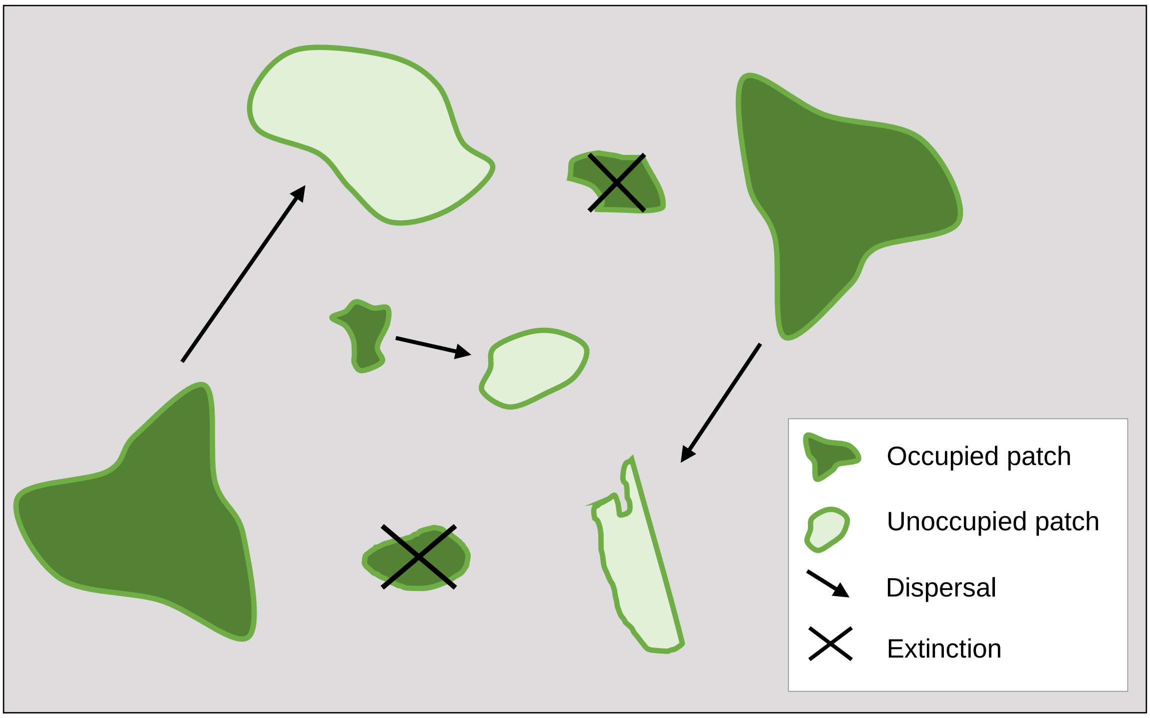

Figure 1.1. Simplified illustration of a ‘real’ metapopulation: occupied (dark green) and unoccupied patches (light green) surrounded by unsuitable habitat (grey). Arrows signify the colonization of unoccupied habitat and crosses indicate extinction events at occupied patches. In spatially-realistic metapopulation models, the rate of colonization is often modelled as a function of the distance to occupied patches, and the rate of extinction as a function of population size derived from patch area (Hanski 1994b), or can be scaled with habitat quality (Thomas et al. 2001; Franken & Hik 2004).

Practical considerations for conserving landscapes

Site-based approaches to conservation traditionally adopted the top-down management model that typically excluded people (Hutton, Adams & Murombedzi 2005). However, with a growing human population (WWF 2016) and demand for land (Defries, Foley & Asner 2004), conservation at the landscape-scale inevitably involves people. The invariable link between biodiversity conservation and human wellbeing is now generally recognised; the Millennium Ecosystem Assessment (2005) was based on a framework involving the dynamic interaction between people and the status of the ecosystem, while the CBD also agrees that human wellbeing and ecosystem management should be integrated

(Berkes 2007). However, the compatibility of biodiversity conservation and human welfare is still questioned (Wilkie et al. 2006), and they remain viewed as separate entities. Conservation management is designed to enhance habitat quality in a bid to support bigger populations of species (Hodgson et al. 2011b). Often this involves strict limits on the disturbance caused by people (Hodgson et al. 2009b), but fails to explore the extent to which maintaining habitat quality for biodiversity may explicitly involve people. International agreements recognise that the requirements of resources by local communities should be respected (CBD 2011), thus such needs should be fully considered and incorporated into conservation thinking and planning.

Wetland conservation

Wetland habitats and ecosystems typify many of the threats to biodiversity and challenges facing conservation biologists today. Evidence suggests that wetlands are declining at a particularly rapid rate, with 64-71% lost globally since 1900 AD (Davidson 2014). Agricultural conversion is the greatest threat (Junk et al. 2013), driven primarily by high population growth, lack of food security among the rural poor, poor governance (Mitchell 2013), and ill-defined property rights (Adger & Luttrell 2000). As a result, recent assessments suggest that freshwater species (including those of wetlands) are more threatened than terrestrial species (WWF 2016). Wetlands are well known for their biodiversity (Russi et al. 2013), especially in the tropics (Gopal, Junk & Davis 2000). But as a result of their high productivity (Kansiime, Saunders & Loiselle 2007), large populations of people, predominantly the rural poor (Mitchell 2013), are dependent on the ecosystem services and resources they provide (see references in Hartter & Ryan 2010). This mutual dependency between biodiversity and people in wetlands exemplifies the need to manage and preserve ecosystems in a way that minimises the trade-off between poverty and conservation (Senaratna Sellamuttu, de Silva & Nguyen-Khoa 2011). However, very few studies have investigated how this might be achieved in practical terms, enabling the involvement of local communities, as opposed to exclusion (Morrison et al. 2012).

The conservation of wetlands is primarily based on the preservation of important sites (Amezaga, Santamaría & Green 2002). International wetland policy is largely driven by the Ramsar Convention (Iran, 1971) (Junk et al. 2013), with an overarching purpose of ensuring “the conservation and wise use of wetlands through local and national actions and international cooperation, as a contribution towards achieving sustainable development throughout the world” (http://www.ramsar.org/). The benefit of wetlands for both people and nature is recognised through the ‘wise use’ philosophy, though does not guarantee that sustainable management will be effective in participating countries (van Dam et al. 2011). As part of becoming a signatory to this convention, parties are required to designate at least one site for the list of wetlands of international importance (Ramsar sites), based on criteria such as hosting rare or unique wetland types, populations of important species or ecological communities, or high numbers of water birds, fish or other taxa (Ramsar Convention Secretariat 2010). As with other site-based approaches, designation considers wetlands in relative isolation (Amezaga, Santamaría & Green 2002). However, wetlands are a naturally fragmented habitat, becoming increasingly so (Hartter & Southworth 2009), and are degraded in size and quality as a result of the threats placed on them (Hartter & Ryan 2010). Not only are wetlands connected hydrologically (Amezaga & Santamaría 2000), their discrete fragmented nature means that many of the species residing in these habitats would fulfil metapopulation criteria (see above), and conservation management would benefit from a consideration of metapopulation dynamics.

In this thesis, I study the metapopulation dynamics of specialist birds of papyrus swamps in East Africa as a model system, to understand the implications and applications of metapopulation biology for landscape-scale conservation.

Papyrus swamps

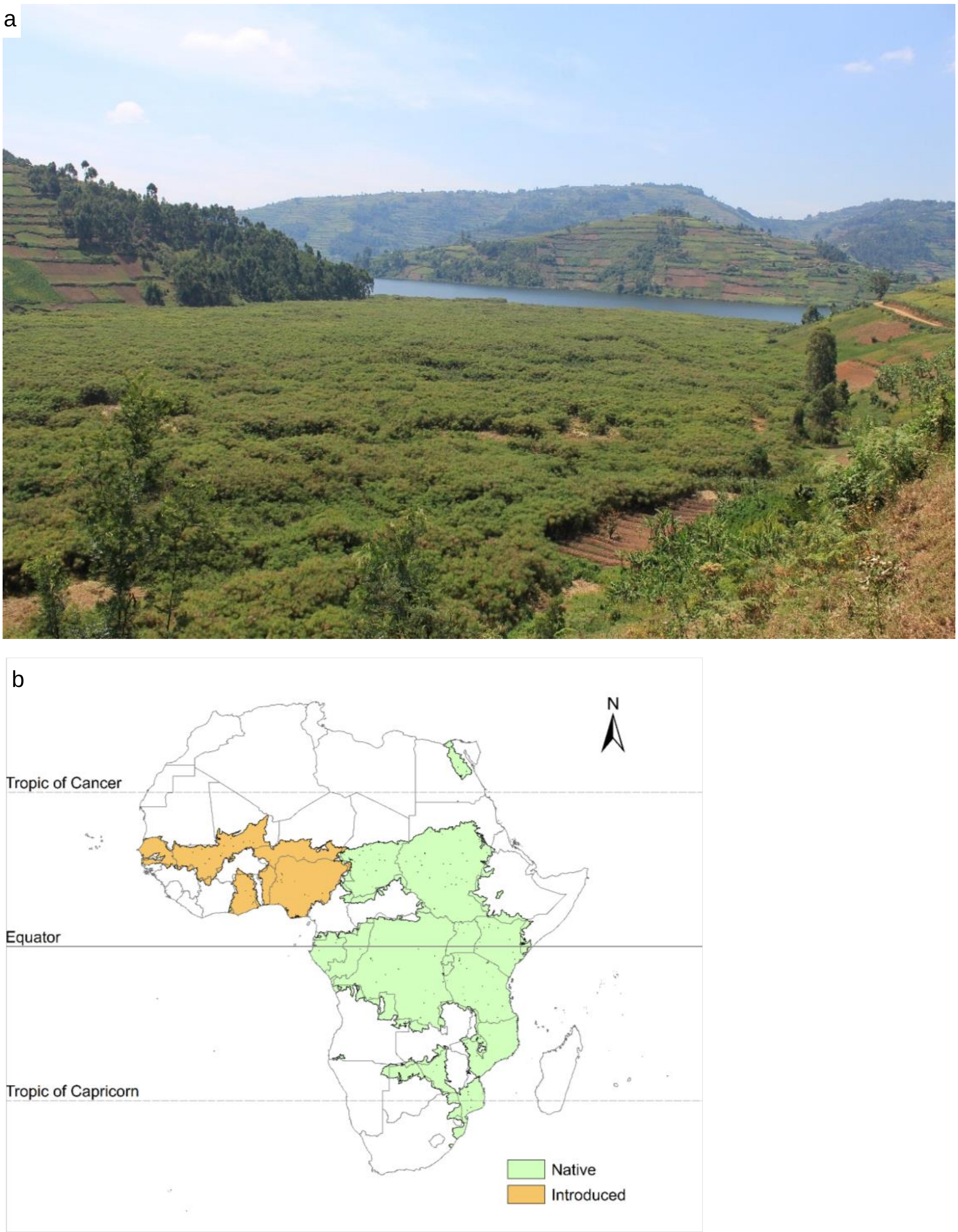

Figure 1.2. Papyrus (Cyperus papyrus): a) Papyrus swamp (Kagoma) at Lake Bunyonyi, south-west Uganda; b) Distribution across Africa (IUCN 2017a; displayed using ArcGIS v 10.2.2).

Papyrus (*Cyperus papyrus*) is a fast-growing freshwater sedge typically reaching 4-5m in height, either rooted in waterlogged substrate along deep river valleys and lake edges (Figure 1.2a), or detached from the ground to form floating mats

(Kipkemboi & van Dam 2016). It grows to form patchy, widespread networks of swamps (Owino & Ryan 2006), individually ranging from very large (tens of km's in length) to very small in size (<1ha) (Southworth et al. 2010; Jacob et al. 2014). These wetlands are distributed across large parts of Africa (Figure 1.2b), from sea level to over 2000 masl (metres above sea level) (Jones & Muthuri 1985). Particularly high densities of papyrus are found across equatorial regions that make up its native range (Figure 1.2b), predominantly the upper Nile and Congo basins, with the most extensive tracts of swamp situated in the Sudd, South Sudan (Kipkemboi & van Dam 2016), while it has been introduced to parts of West Africa (Figure 1.2b), the Mediterranean, USA and India (see Terer, Triest & Muasya 2012). Although formally widespread in the Nile Delta until the early 1700's, only traces remain in this area following regulated flooding regimes and human activities (Kipkemboi & van Dam 2016).

As a result of the high productivity of papyrus compared to other emergent macrophytes (Terer et al. 2012), primarily due to the C4 photosynthetic pathway (Boar, Harper & Adams 1999), papyrus swamps support the livelihoods of millions of people through the provision of a variety of ecosystem services. Amongst these are the ability to purify water, act as flood barriers, provide sediment traps, offer grazing habitat for livestock, assist with climate regulation through carbon storage and high rates of evapotranspiration, and provide a habitat for fish that can be sold locally, or provide a vital source of protein for the rural poor (Maclean *et al.* 2003c; d; van Dam *et al.* 2011; Terer *et al.* 2012; Triest, Sierens & Terer 2014; Ryken *et al.* 2015; Kipkemboi & van Dam 2016). People have also been reliant on papyrus as a natural resource for several millennia. First used to make paper by the Ancient Egyptians (Terer, Triest & Muasya 2012; Gaudet 2014), papyrus continues to supply the raw materials required for making handicrafts, building features such as thatched roofs, fences and outbuildings, and as a source of fuel (Maclean et al. 2003d; Terer et al. 2012; Figure 1.3). But combined with its importance for people, papyrus also hosts a unique biodiversity. Approximately 187 species of various biota have been documented in papyrus swamps (see Kipkemboi & van Dam 2016) including various mammals, such as the rare sitatunga antelope (*Tragelaphus spekii*) and hippopotamus (*Hippopotamus amphibious*), as well as numerous fish, reptiles, amphibians (Kipkemboi & van Dam 2016), and multiple bird species (Maclean et al. 2003a).

Although the diversity of papyrus swamps is low in comparison to other tropical ecosystems (Dirzo & Raven 2003), they support unique species ranging from various arthropods (Sutton & Hudson 1981), dragonflies (Clausnitzer et al. 2012), and a group of endemic passerines (Britton 1978) (see below).

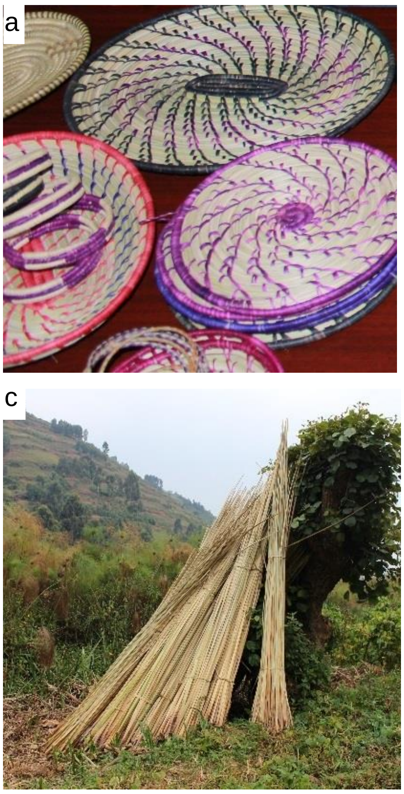

Figure 1.3. Example of papyrus resource use: a) handicrafts for sale at local market; b) small outbuilding constructed from papyrus; c) papyrus bundles used for thatching roofs or fences.

Threats & protection

As with wetlands around the world, papyrus swamps have been suffering from high rates of drainage and destruction over the past few decades (van Dam et al. 2011; Figure 1.4). Human population growth and an associated shortage of land force people to drain swamps (permanently or temporarily [Maclean, Boar & Lugo 2011]) to gain access to space on which to farm crops (Carswell 2002), while entire swamp networks have been drained for commercial purposes (Maclean, Boar & Lugo 2011; Figure 1.4a). Over recent years, large intact areas of wetland, such as Yala swamp in Kenya and Lake Kyoga in Uganda, have been threatened by further plans for rice farming operations (Maclean, Bird & Hassall 2014). Climate change will likely exacerbate such threats, with uncertainty in rain-fed agriculture potentially leading to further localised drainage of swamp land

(Kipkemboi & van Dam 2016), and alterered hydrological regimes can impact the regeneration and resilience of papyrus stems during periods of drought (Triest, Sierens & Terer 2014). Moreover, a lack of a legislative framework to guide sustainable use has led to the overexploitation of this resource (Kipkemboi & van Dam 2016; Figure 1.4b); potentially facilitated by lower water levels in the future (van Dam *et al.* 2014). High population densities of people in rural parts of Africa derive their income from these swamps on a subsistence scale (Maclean et al. 2003c), with the poorest people in society estimated to receive the most benefit from harvesting this resource (Maclean et al. 2003d). Research has highlighted that the economic value of wetlands themselves is higher than that obtained from wetland conversion (van Dam *et al.* 2014). Maclean *et al.* (2003c), for example, quantified the conversion of swamps for cultivation in an area of south-west Uganda to be US $21-181/ha, compared to US $1226 – 1615/ha for low intensity use from harvesting and fishing (Maclean, Boar & Lugo 2011). As a result, the loss and degradation of papyrus impacts the lives of local people, not only through a loss of ecosystem services, but from the goods extracted from the swamps themselves, and the economic value they provide. However, policies designed to regulate use are scarce and poorly enforced (Maclean, Boar & Lugo 2011), and need to recognise the balance between the functioning of wetlands and their use for people’s livelihoods (Osumba, Okeyo-Owuor & Raburu 2010). From the 47 African countries that are signatories to the Ramsar Convention, 28 have papyrus swamps (van Dam et al. 2014). Some of these are Ramsar sites (van Dam et al. 2014), though most lack any conservation or protection status (Kipkemboi & van Dam 2016).

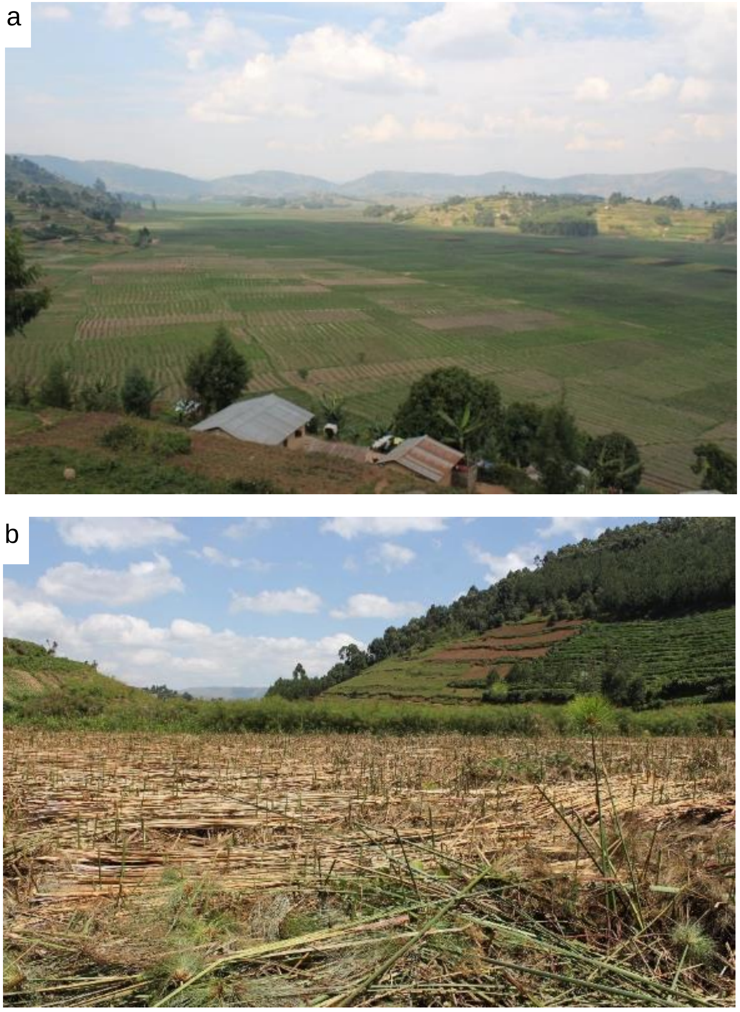

Figure 1.4. Threats to papyrus swamps:

a) Wetland drainage for agricultural conversion, Kabale district;
b) Large harvested area, Kacoco swamp, Lake Bunyonyi; Uganda

Papyrus-endemic passerines

Papyrus swamps are home to a group of generalist bird species that regularly use these wetlands (Maclean et al. 2003a), but also host a group of passerines which are endemic or near-endemic to this habitat (Britton 1978; Vande weghe 1981). These specialist species are distributed across parts of East and Central Africa; listed as “Lake Victoria biome species”, with ranges restricted to swamps and marshes within the Lake Victoria basin (Byaruhanga, Kasoma & Pomeroy 2001), although a small isolated population of white-winged swamp-warbler (*Bradypterus carpalis*) is also found in north-west Zambia (Maclean, Bird & Hassall 2014). Following recent taxonomic assessments, papyrus yellow warbler (*Calamonastides gracilirostris*) has recently moved from the genus *Chloropeta*, and the population located in Zambia, bordering with south-east Democratic Republic of Congo (DRC), split to the Zambian yellow warbler (*Calamonastides bensoni*) (del Hoyo & Collar 2016). The population of this species in a remote part of western Kenya has also been questioned due to the documented differences in appearance, biometrics and vocalization from the population in Uganda/Rwanda (Maclean et al. 2003b), though currently remains as one species.

As a result of the threat placed on the habitat on which they depend, papyrus-endemic passerines have been described as some of the most threatened and inadequately protected in the region (see references in Maclean et al. 2006). Currently papyrus yellow warbler is listed as Vulnerable on the IUCN (International Union for the Conservation of Nature) Red List because it has declined rapidly and continues to decline owing to extensive habitat loss, while papyrus gonolek (*Laniarius mufumbiri*) is Near Threatened because it is estimated to be in moderate decline from papyrus drainage and degradation (IUCN 2017b). Nevertheless, recent evidence suggests that all papyrus-endemic species are declining at an even faster rate than their habitat, primarily as a result of the geographical overlap with areas subjected to the most agricultural conversion, and fragmentation effects (Maclean, Bird & Hassall 2014).

Despite the evident threats placed on these birds, they have been subject to little investigation. The impacts of landscape alteration on their populations remain relatively unknown (Maclean et al. 2006), but given the dependence on this resource by local people, investigating the habitat requirements of these species and the extent to which their conservation conflicts with sustaining human livelihoods, is crucial. Very few papyrus swamps in East Africa are protected (Fanshawe & Bennun 1991; Kipkemboi & van Dam 2016). Some are designated as Ramsar sites, and/or Important Bird and Biodiversity Areas (IBAs) based on the presence of these globally threatened (Criterion A1) and biome-restricted (Criterion A3) papyrus-endemic birds (Fishpool & Evans 2001). Although there is recognition that networks of priority sites, such as IBAs, should be extended (Maclean, Bird & Hassall 2014), the data available for such designations is scarce, and has not yet considered the consequences of a naturally fragmented habitat for conservation. To date, patch-level and regional dynamics of these species have not been formally tested, and could have important implications for where resources are channelled (Maclean, Wilson & Hassall 2011). Spatial aggregations of these species have been recorded (Maclean et al. 2006), and they are known to move infrequently between patches (Britton 1978), though the impact of fragmentation on their dispersal has been recognised (Owino & Oyugi 2008). Combined with the knowledge that these species reside in distinct habitat patches, and dynamics do not appear to be synchronous (Maclean et al. 2006), a metapopulation framework is appropriate to explore the dynamic processes operating (Hanski et al. 1995a), and determine the importance and consequences of considering networks of habitat, rather than investing in sites in isolation, as is common in wetland conservation (see above).

Ugandan wetland policy

Uganda has been described as “mainstreaming” the way for wetland conservation in East Africa through specific wetland policies and designated conservation agendas (Mitchell 2013). Wetland conversion was officially banned in 1986 (Wetlands Inspectorate Division 2001), and a National Wetlands Programme developed in 1989, to ensure the sustainable use of resources and protection where needed (Huising 2002). After becoming a signatory to the Ramsar convention, Uganda was the first country in Africa and the second in the world, to establish a National Wetlands Policy (1995), which prohibits any activity that excludes water from wetlands (see references in Hartter & Ryan 2010). The Ministry of Water, Lands and the Environment prepared a Wetland Sector Strategic Plan from 2001-2010, which aimed to provide direction and an action plan for those involved in wetland management and conservation (Wetlands Inspectorate Division 2001). The National Environmental Management Authority (NEMA) is the government body responsible for all environmental issues in Uganda, and officially protects all permanent wetlands in the country (Hartter & Ryan 2010). However, following the development of a national decentralization policy in 1995, rights and responsibilities were devolved to the local level (Hartter & Ryan 2010). The Constitution (1995) and Local Governments Act (1997) gave power to the Local Councils to manage resources, and ultimately led people to recognise wetlands as significant components for their livelihoods rather than the “wastelands” they were once made out to be (Hartter & Ryan 2010).

Despite the development of numerous policies and government agencies assigned to help manage wetlands in Uganda, coordination and implementation has proved difficult (see references in van Dam et al. 2011; Pomeroy, Tushabe & Loh 2017). Confusion over property rights remains (Wetlands Inspectorate Division 2001; Maclean *et al.* 2003c), alongside competing interests and an underestimation of importance in some parts of the region (van Dam et al. 2011). Given population pressure and a scarcity of land, wetlands continue to be cultivated (Huising 2002) and exploited at unsustainable levels (Chapman et al. 2001). Many seasonal wetlands remain unprotected, while only 1% of wetlands are estimated to fall within protected area boundaries (Pomeroy, Tushabe & Loh 2017). Unprotected wetlands are commonly viewed as unclaimed or unused, and local people often adhere to the “use it or lose it viewpoint (Hartter & Ryan 2010)”, leading to the continued cultivation present today. As a signatory to the CBD, Uganda has an obligation to reduce the loss and degradation of natural habitats by 2020, and reduce the threatened status of its species (CBD 2011). However, weak implementation of the National Wetlands Policy combined with a distinct lack of resources, has cast doubt over the ability of Uganda to meet these biodiversity targets (Pomeroy, Tushabe & Loh 2017).

Thesis aims and objectives

The overarching aim of this PhD is to test and apply theory associated with landscape-scale conservation in fragmented habitats, using papyrus endemic birds in East Africa as a model system. In turn, I hope that this work will enhance the evidence-base for ensuring conservation resources are targeted most effectively across today’s landscapes, whilst assisting with conservation prioritisation for wetland birds in Africa, and species residing in fragmented habitats globally. The main objectives of this work are to:

i. Review existing theory associated with landscape-scale conservation to assist with modern-day conservation prioritisation
ii. Examine the extent to which the needs of local people are compatible with conservation planning

iii. Investigate the importance of the spatial configuration of wetland patches for species' persistence, and determine the implication of this for multi-species conservation prioritisation

iv. Explore approaches associated with conservation planning to design effective protected networks for multiple species

Study system

Study site

Research was carried out in a network of papyrus swamps surrounding Lake Bunyonyi, south-west Uganda (Figure 1.5). This is a steep sided lake, located approximately 1950 masl (Denny 1973). Agriculture has been practiced here for centuries and is the main economic activity for local people, growing a range of crops including cabbages, sweet potatoes, peas, beans, sorghum, Irish potatoes and maize (Kizza et al. 2017). It can rain throughout the year in this region, though it rains less between December – January and July – August (Maclean et al. 2003d), and the mean annual temperature is estimated to be 16.1˚C (Kizza et al. 2017). The shoreline extends for approximately 114km (Denny 1973) and is fringed by a narrow band of vegetation, including papyrus. Larger wetlands are found in sheltered lake inlets and grow along deep valleys, dominated by papyrus and other types of emergent vegetation, including *Phragmites*, *Typha* and *Cladium* spp. (Denny 1973). Rates of wetland loss in the south-west of Uganda are amongst the highest in the region (Huising 2002; Maclean, Wilson & Hassall 2011), although habitat loss at Lake Bunyonyi is mostly associated with edge encroachment (Maclean et al. 2003d). Wetland soils are regarded as more fertile and provide a crucial source of water during the dry season (Kizza et al. 2017). At this time, the elevated farmed land dries up, forcing people to retreat to swamp areas to grow crops (Maclean et al. 2003d). Lake Bunyonyi is estimated to be approximately 40m deep and compared to other lakes across East Africa (e.g. Boar et al. 1999), the water level remains stable here all year round (Denny 1973). Due to the depth of the lake and thus large volume of water, water availability and polluted drinking water are not issues experienced by rural people residing within proximity to the lake (Maclean *et al.* 2003d). As a result, papyrus swamps in this area are limited in their value to provide service benefits such as trapping sediment, purifying water and providing a habitat for fish (Maclean *et al.* 2003c). The main service provided by the swamps to local people here is the provision of raw materials, which are harvested and used to make personal items, such as sleeping mats, or is sold locally at markets as a source of income (see Chapter 3). Tourism at the lake has escalated over recent years, increasing the demand for papyrus and other wetland vegetation to fence campsites, and thatch roofs for holiday cottages (S. Katungi *pers. comm*).

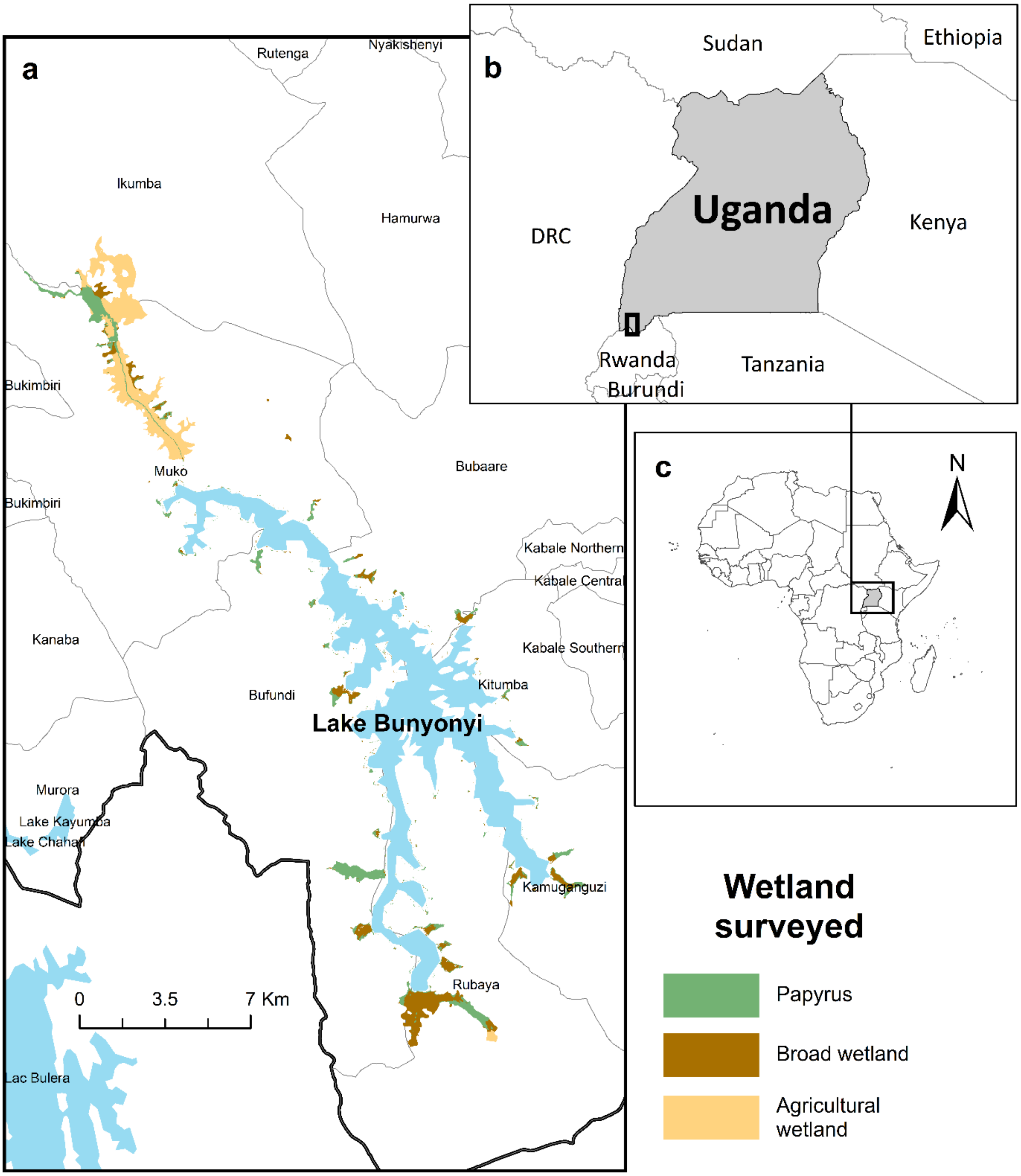

Figure 1.5. Map of the study area: a) Lake Bunyonyi with wetland areas surveyed; b) Uganda (▯ shows location of study site); c) Location of Uganda in Africa. Displayed using ArcGIS v 10.2.2.

Study species

Relatively high densities of five species of papyrus-endemic passerines are found in wetlands surrounding Lake Bunyonyi: greater swamp-warbler (*Acrocephalus rufescens*), white-winged swamp-warbler, Carruthers's cisticola (*Cisticola carruthersi*), papyrus yellow warbler, and papyrus canary (*Crithagra koliensis*[1]) (Maclean, Bird & Hassall 2014; Figure 1.6). Global distributions for all species include parts of Burundi, DRC, Kenya, Rwanda, Tanzania and Uganda (IUCN 2017b). Although greater swamp-warbler resides within various wetland types distributed across sub-Saharan Africa (BirdLife International 2017a), race *foxi* is primarily confined to papyrus within this part of region (Vande weghe 1981). Papyrus gonolek does not occupy swamps above 1680 masl (Maclean et al. 2006), thus are absent from wetlands in the study area. Currently all species, with the exception of papyrus yellow warbler, are listed as Least Concern (Table 1.1). However, data available on population size and trends is limited (Table 1.1), and assuming an ongoing decline in the extent of habitat across East Africa, these species could warrant uplisting to threatened status in the future (Criterion A2c; Maclean, Bird & Hassall 2014).

The suite of papyrus-endemic birds studied are described as insectivorous, although papyrus canary is often seen feeding outside of swamps in nearby crops (Britton 1971). Britton (1978) observed evidence of vertical zonation, particularly with those warbler species most similar in size (white-winged swamp-warbler and greater swamp-warbler; ~18-29g) during a mist-net study in western Kenya. White-winged swamp-warbler evidently forages lowest in the papyrus, while papyrus canary is mostly associated with the upper canopy level (Vande weghe 1981). Breeding and moulting corresponds most closely with rainfall and subsequent food availability following the rainy seasons (Britton 1978). Papyrus yellow warbler and Carruthers's cisticola are known to reside in broader wetland vegetation types at higher altitudes, often when closely associated with papyrus (Vande weghe 1981). Papyrus yellow warbler is restricted to papyrus in drier parts of its range, while Carruthers's cisticola is confined to papyrus primarily at lower altitudes, where it experiences competition with winding cisticola (*Cisticola*

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[1] Recently moved from the genus *Serinus* (del Hoyo & Collar 2016)

marginatus) (Vande weghe 1981). Within the study region, Carruthers's cisticola can also inhabit wetland areas adjacent to some larger swamps around the lake which have recently been cleared for agriculture (Figure 1.5).

Figure 1.6. Papyrus-endemic birds studied: a) greater swamp-warbler (*Acrocephalus rufescens*); b) white-winged swamp-warbler (*Bradypterus carpalis*); c) papyrus yellow warbler (*Calamonastides gracilirostris*); d) Carruthers's cisticola (*Cisticola carruthersi*); e) papyrus canary (*Crithagra koliensis*) (del Hoyo & Collar 2016).

Table 1.1. Summary table of Red List category and population data available for the study species, obtained from IUCN (2017b) and Maclean, Bird & Hassall (2014).

Species	**Red List category**	**Criterion**	**Extent of occurrence (km^2)***	**Number of adults†**	**Population trend**
Greater swamp-warbler‡	LC	NA	12,300,000	Unknown	Stable
White-winged swamp-warbler	LC	NA	809,000	3,289,029	Decreasing
Papyrus yellow warbler	VU	A2c + A3c+ A4c (past and future rapid population decline)	235,000	90,151	Decreasing
Carruthers's cisticola	LC	NA	307,000	370,225	Decreasing
Papyrus canary	LC	NA	261,000	415,192	Decreasing

*IUCN (2017b); †best estimate from Maclean, Bird & Hassall (2014); ‡Refers to global *Acrocephalus rufescens* population as data for race *foxi* only are not available; LC = Least Concern, VU = Vulnerable

Currently one site at Lake Bunyonyi, Nyamuriro Swamp, has been designated as an IBA due to holding a significant component of these biome-restricted species (Criterion A3), and significant numbers of a globally threatened species: the papyrus yellow warbler (Criterion A1) (BirdLife International 2017b). Despite this, Nyamuriro is not included in any national or international protected area categories (NatureUganda 2010). Meanwhile, previous work by Maclean et al. (2014) recommends the network of IBA's in the Kigezi district are extended, since the swamps in this region are among the most important for populations of papyrus yellow warbler. Data to support such assessments is currently lacking; the following work will help provide the basis for future designations.

Thesis structure

This thesis comprises of six chapters. Chapters 2-5 are written as distinct research papers; Chapters 2 and 3 are published in peer-reviewed journals (see Publications above), while Chapters 4 and 5 are written in preparation for submission.

Chapter 2 reviews the widespread existing theory associated with conservation planning in fragmented landscapes, incorporating new perspectives that were not conventionally considered following the origin of reserve design. We consider the trade-offs between the four axes of reserve design (bigger, better, more and more joined sites), and collate the extensive literature available to provide a simplified framework for prioritising among the key strategies, when faced with modern-day challenges. This chapter provides the backbone for the remaining parts of the thesis; detailing the theory that is later applied and tested using my study system.

Chapter 3 investigates the compatibility of habitat quality and local livelihoods. Specifically, this chapter determines the threat placed on biodiversity from human habitat use, examining the physical aspects of swamps that drive the densities of papyrus passerines. The outcomes of this chapter are incorporated as measures of habitat quality in Chapter 5.

Chapter 4 explores the factors influencing the persistence of multiple species occupying the same habitats, in line with traditional theory. I use a novel framework in the context of metapopulation theory to quantify the resistance and resilience of populations to extinction, based on their probability of survival and reestablishment. This enhances our understanding of why species occupy particular habitat patches, the extent to which these differ between species, and how these dynamic processes can be used to prioritise resources for conservation with consideration of the need to adapt and respond to future change. This chapter uses knowledge of turnover at the patch-level over the short-term, to develop metapopulation models for the network as a whole in Chapter 5.

Chapter 5 investigates the optimal conservation strategy for ensuring the long-term persistence of specialist species'. I use metapopulation models to predict the response of the study species to the range of conservation planning approaches reviewed in Chapter 2, and examine the potential to design effective networks for multiple species with overlapping habitat requirements.

Chapter 6 collates the outputs from Chapters 2-5, highlighting the implications of this work for the conservation of wetland birds in East Africa, as well as the wider applications for species residing in fragmented landscapes more generally. I suggest future directions as a result of this research, and emphasize the contribution made to the field of landscape-scale conservation planning and prioritisation.

Chapter 2:

Old concepts, new challenges: adapting landscape-scale conservation to the 21st century

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Donaldson, L., Wilson, R.J., & Maclean, I.M.D. (2017) *Biodiversity & Conservation,* **26**, 527–552.

Abstract

Landscape-scale approaches to conservation stem largely from the classic ideas of reserve design: encouraging bigger and more sites, enhancing connectivity among sites, and improving habitat quality. Trade-offs are imposed between these four strategies by the limited resources and opportunities available for conservation programmes, including the establishment and management of protected areas, and wildlife-friendly farming and forestry. Although debate regarding trade-offs between the size, number, connectivity and quality of protected areas was prevalent in the 1970s-1990s, the implications of the same trade-offs for ongoing conservation responses to threats from accelerating environmental change have rarely been addressed. Here, we reassess the implications of reserve design theory for landscape-scale conservation, and present a blueprint to help practitioners to prioritise among the four strategies. We consider the new perspectives placed on landscape-scale conservation programmes by 21st century pressures including climate change, invasive species and the need to marry food security with biodiversity conservation. A framework of the situations under which available theory and evidence recommend that each of the four strategies be prioritized is provided, seeking to increase the clarity required for urgent conservation decision-making.

Introduction

After failing to meet the 2010 Convention on Biological Biodiversity (CBD) targets (Butchart et al. 2010), the global community has been offered a second chance to halt biodiversity declines by 2020 through the CBD's Aichi targets (CBD 2011). Current financial resources available to meet these targets are insufficient (McCarthy et al. 2012) and in consequence there is urgent need for conservation planners and practioners to have sufficient information to select and employ efficient, cost-effective actions (Williams, ReVelle & Levin 2005). Nevertheless, there is much debate regarding the most effective means for adapting conservation to accelerating environmental change (Hodgson et al. 2009b), leading to an extensive literature that presents some apparently conflicting messages to those involved in conservation planning and decision-making.

Classical approaches to increase the effectiveness of protected area designation and management have drawn upon the theories of island biogeography (MacArthur & Wilson 1967) and metapopulation dynamics (Levins 1969; Hanski & Gilpin 1991; Hanski 1999a). In these approaches, the four main trade-offs among the size, number, quality and connectivity of protected areas can be summarised by Diamond's (1975) outline of geometric principles for the design of nature reserves (Figure 2.1). Since the 1990s, however, conservation actions have evolved from a primarily reserve-based approach to give greater consideration to landscape-scale processes (Opdam & Wascher 2004; Watts et al. 2010), partly because climate change and increased habitat fragmentation have led to increasingly dynamic patterns of colonization and extinction (Heller & Zavaleta 2009). Landscape-level conservation initiatives include the Pan-European Ecological Network (Jongman et al. 2011) and "greenways" in the USA (Ahern 2004). In England, the recent "*Making Space for Nature*" report (Lawton et al. 2010) summarized the recommendations of a now substantial scientific literature to increase the effectiveness of protected area networks in fragmented landscapes in four simple words: "more, bigger, better and joined". The report recommended, in a priority hierarchy: 1) improving the quality of habitat, 2) increasing the size and 3) number of sites, and 4) enhancing connectivity among sites for conservation. In the UK, these recommendations are incorporated into biodiversity policy (Department for Environment, Food and Rural Affairs (DEFRA)

2011) and increasingly inform planning and management by conservation agencies and organisations working to maintain and restore habitats in the UK's highly fragmented landscapes.

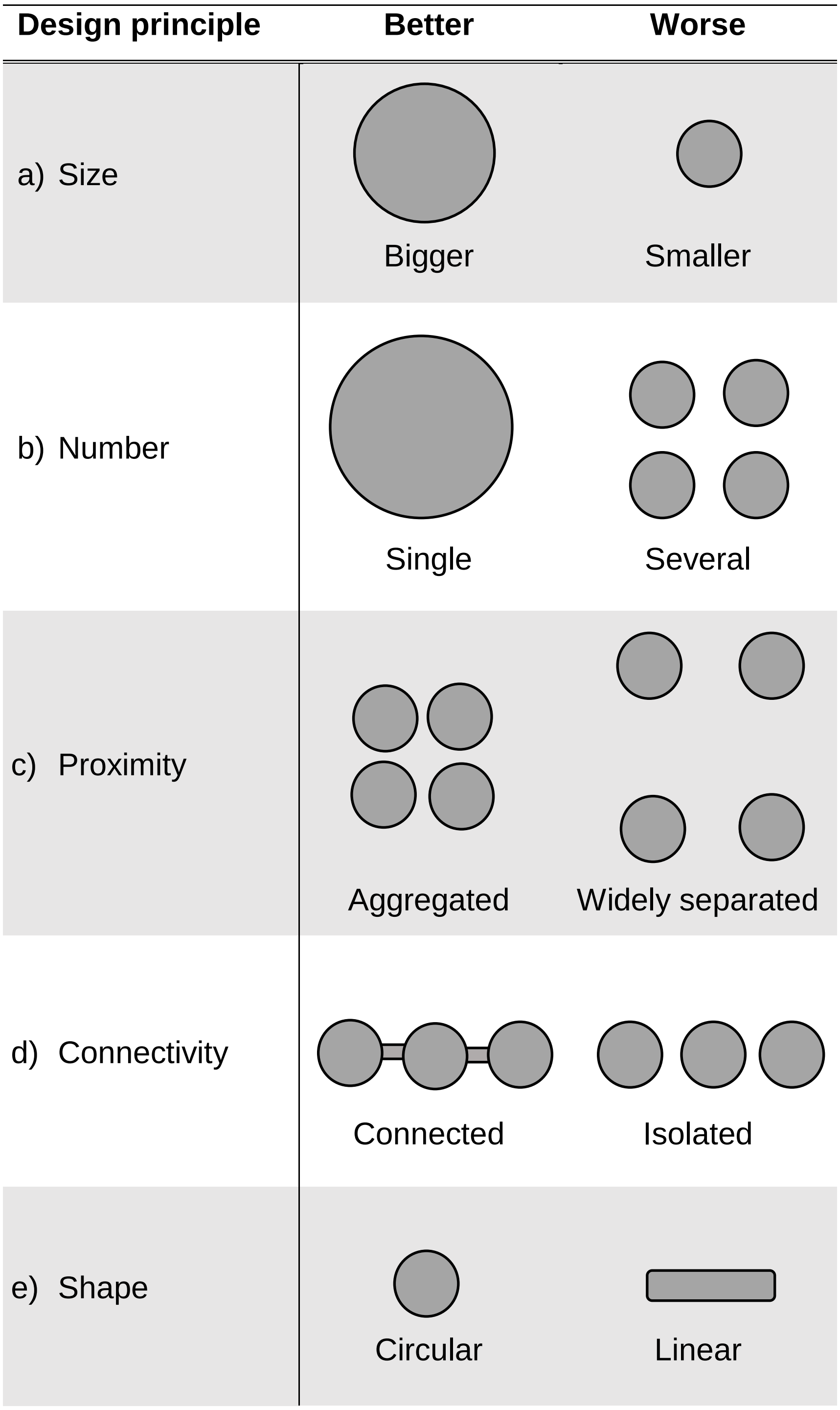

Figure 2.1. Suggested geometric principles for nature reserve design derived from Diamond (1975). In all cases, species extinction rate would be expected to be lower on the left (better) than on the right (worse).

The Lawton et al. (2010) report provides valuable recommendations regarding the UK's network of protected sites, but global variation in land-use history, levels of fragmentation and biogeographic context drive a need to determine more widely for conservation practitioners the circumstances under which increasing the area, number, connectivity and quality of conservation sites is most effective. Published research seldom tackles trade-offs among all 4 approaches together to assist with the transition from theory to practical application (but see Hodgson et al. 2011a). Moreover, since the origin of the principles of reserve design, the challenges faced by biodiversity have evolved from emphasis on land use change in the 20th century (Sala et al. 2000), to include a rapid rise in impact from climate change, invasive species and pollution, alongside continuing pressures from overexploitation in the 21st century (Millennium Ecosystem Assessment 2005; Urban 2015). The ability of the natural environment to provide ecosystem services is declining as a result of increasingly degraded habitats (Millennium Ecosystem Assessment 2005) which, coupled with increasing human populations, impacts the ability to marry food security with conservation. These pressing issues necessitate a shift in focus from the simplistic interpretation of what was originally thought to be best; effectively factoring new challenges into decision making from a reemphasis of original ideas, to modifying classical theory to adapt to a world of accelerating environmental change. To our knowledge, research to date has not addressed these challenges alongside their impact on assumptions from classical reserve design.

Here, we synthesize concepts associated with landscape-scale approaches to conservation, and offer a practical blueprint for effective decision making, highlighting how our priorities change in the context of 21st century challenges including climate change, the spread of invasive species and food security, which were largely unforeseen when the original approaches were devised (Table 2.1). We present the four axes of reserve design in the order of decreasing importance as proposed by Lawton et al. (2010), but consider trade-offs first associated with habitat quality, then between size and number of reserves, and finally consider the importance of connectivity and how to achieve it. The nexus between conservation theory and modern-day application is invariably tangled by complexities and practicalities. We aim to provide conservation decision-makers with the information they need to make informed choices on the most effective action given, and plot a path through some of this tangle.

Table 2.1. Overview of the main considerations and summary of evidence from key supporting references associated with the most effective strategy between better, bigger, more and more-connected sites.

Consideration				**Recommended strategy**	**Summary of evidence**
Goal	Multiple spp.			*Heterogeneity*	Greater species diversity with habitat variety (Rosenzweig 1995) e.g. (see Benton et al. 2003; Báldi 2008)
				Bigger	Species Area Relationship states that larger sites hold more species (MacArthur & Wilson 1967; Diamond 1975) through habitat diversity, area per se, concentration of resources, edge effects (Connor & McCoy 2001) e.g. (Brückmann, Krauss & Steffan-Dewenter 2010)
				More sites	High rates of immigration (Fahrig 2003) and wide variety of habitat (Dover & Settele 2009; Oliver et al. 2010), supporting a range of species
				More connected	Both area and isolation influences the number of species a site can hold (Diamond 1975) e.g. plants (Damschen et al. 2006), butterflies (Brückmann, Krauss & Steffan-Dewenter 2010)
	Single sp.	Habitat preference	Interior	*Bigger*	Less edge; higher area: edge ratio (Bender, Contreras & Fahrig 1998)
			Edge	*Homogeneity*	Availability for colonization (Thomas et al. 2012)
				More sites	Edge effects (Bender, Contreras & Fahrig 1998)
				More connected	Corridors provide high edge: area ratio (Haddad 1999; Haddad & Tewksbury 2005)
			Specialist	*Homogeneity*	Specific habitat requirements (Ye, Skidmore & Wang 2013) e.g. birds (Root 1998; Devictor, Julliard & Jiguet 2008), butterflies (Dennis et al. 2013)
				Bigger	Matrix habitat not suitable, negatively affected by habitat fragmentation, avoid edge (see Brückmann et al. 2010); e.g. butterflies (Dover & Settele 2009; Brückmann, Krauss & Steffan-Dewenter 2010) and plants (Dover & Settele 2009)
				More connected	Less likely to occur in matrix than generalists (Brückmann, Krauss & Steffan-Dewenter 2010) e.g. butterflies (Haddad 1999; Brückmann, Krauss & Steffan-

Consideration				**Recommended strategy**	**Summary of evidence**
					Dewenter 2010; Dennis et al. 2013) and plants (Brückmann, Krauss & Steffan-Dewenter 2010)
			Generalist	*Heterogeneity*	Less sensitive to quality (Ye, Skidmore & Wang 2013) e.g. birds (Devictor, Julliard & Jiguet 2008), butterflies (Oliver et al. 2010)
				More sites	Occur in matrix, occupy smaller isolated patches (Dennis et al. 2013)
				Less connected	More likely to exist in matrix between sites (Lees & Peres 2009; Brückmann, Krauss & Steffan-Dewenter 2010)
		Habitat requirements	Migratory	*Heterogeneity*	Buffers variation in resources through time (Benton, Vickery & Wilson 2003)
				More sites	Move between sites to meet habitat requirements (Bender, Contreras & Fahrig 1998)
				More connected	Move between sites to meet habitat requirements (Benton, Vickery & Wilson 2003; Donald & Evans 2006)
		Range size	Large	*Bigger*	Less prone to extinction in larger sites (Di Minin et al. 2013) and less at risk from human-wildlife conflict (Abele & Connor 1979; Woodroffe & Ginsberg 1998)
				More connected	Enable movement between sites (Rosenberg, Noon & Meslow 1997; Donald & Evans 2006; Lawton et al. 2010) and increase recolonization rates (Di Minin et al. 2013)
			Small	*Heterogeneity*	More vulnerable to environmental change, buffers these effects (Oliver et al. 2010)
				More sites	Smaller sites are sufficient for range requirements (Abele & Connor 1979)
		Body size	Large	*Bigger*	Larger bodied species have larger range sizes (Abele & Connor 1979; Cardillo et al. 2005)
			Small	*More sites*	Smaller range sizes thus smaller sites are sufficient (Abele & Connor 1979; Cardillo et al. 2005)
		Dispersal capability	High	*More sites*	Capacity to move between sites (Nicol & Possingham 2010)
				Less connected	Links would have limited worth (Bennett 2003)

Consideration				Recommended strategy	Summary of evidence
			Intermediate	*Bigger*	Lower mortality rate associated with less emigration and failure to locate site (Thomas 2000)
				More connected	Assist with locating patches (Thomas 2000), especially matrix restoration (Donald & Evans 2006)
			Very poor/ sedentary	*Homogeneity*	Require good quality habitat (Ye, Skidmore & Wang 2013)
				Bigger	Less need for movement (Öckinger & Smith 2006; Nicol & Possingham 2010)
				More connected	Assist with dispersal, providing within dispersal range (Doerr, Barrett & Doerr 2011)
		Dispersal mode	Animal-borne	*More connected*	Assists with animal movement (Brudvig et al. 2009)
			Wind-borne	*More sites*	More edge to reach non-target habitat (Brudvig et al. 2009)
				Less connectivity	Unaffected by direct connectivity (Brudvig et al. 2009)
		Population viability	High	*More sites*	Metapopulation persistence (higher turnover of local extinction and recolonization) (Drechsler & Wissel 1998)
				More connected	Persistence of metapopulation (Drechsler & Wissel 1998)
			Low	*Homogeneity*	Higher population growth (Thomas et al. 2001; Griffen & Drake 2008; Ye, Skidmore & Wang 2013)
				Bigger	Greater population carrying capacity (Griffen & Drake 2008)
Landscape attributes[a]		Fragmented		*Heterogeneity*	Less vulnerable to climate change and extreme events in fragmented landscapes (Opdam & Wascher 2004)
				More sites	Species will be more adapted to live in fragments (Schnell et al. 2013)
				More connected	Movement between habitats is important (Isaak et al. 2007; Dennis et al. 2013)
		Continuous		*Bigger*	Species are poorly adapted to live in small fragments (Schnell et al. 2013)

Consideration		**Recommended strategy**	**Summary of evidence**
Climate variability (risk of disease/ environmental disturbance) and vulnerability to climate change[a]	High variability + low vulnerability	*Heterogeneity*	Buffers stochastic extinctions from environmental disturbance (Opdam & Wascher 2004; Hopkins et al. 2007; Piha et al. 2007; Dover & Settele 2009), stabilizes populations (Oliver et al. 2010)
		More sites	Spreads risk of extinction (Groeneveld 2005; Dover & Settele 2009; Oliver et al. 2010) and encourages recolonization through “stepping stone” habitat (Schnell et al. 2013)
		Less connected	Spreads risk of extinction and reduce impact (Simberloff & Cox 1987; Williams, ReVelle & Levin 2005)
	Low variability + high vulnerability	*Homogeneity*	Location for colonization and thus range shift (Hodgson et al. 2011a; Thomas et al. 2012)
		Bigger	Larger source populations to facilitate range shift (Hodgson et al. 2009b, 2011a)
		More sites	Promote rapid movement through stepping stone habitat (Hodgson et al. 2012; Magris et al. 2014)
		More connected	Higher probability of colonization and thus range shift (Heller & Zavaleta 2009; Hodgson et al. 2012; Lawson et al. 2012)
	Low variability + low vulnerability	*Homogeneity*	Strong patch quality-occupancy relationship in static habitat (Hodgson, Moilanen & Thomas 2009)
		More connected	Strong connectivity-occupancy relationship in static habitat (Hodgson, Moilanen & Thomas 2009)
Economics & ownership[a]	Limited funds	*Homogeneity*	Protect currently intact environments, restoring habitat is financially expensive and time consuming (Possingham, Bode & Klein 2015)
		Bigger	Lower unit/area management costs (Simberloff & Abele 1976; Radchuk, Wallisdevries & Schtickzelle 2012) since rely on natural processes (Lawton et al. 2010) and require low maintenance (Williams, ReVelle & Levin 2005)

Consideration		**Recommended strategy**	**Summary of evidence**
		More connected	Balance costs associated with Single Large or Several Small (SLOSS) sites with corridors between network of small refuges (Simberloff & Abele 1976); and cost effective to use existing natural connections or man-made structures (Lawton et al. 2010)
	Surrounding land ownership	*More sites*	Enlarging sites not possible (Dover & Settele 2009; Doerr, Barrett & Doerr 2011)
		More connected	Discourage species use of neighboring habitat (Hartter & Southworth 2009)
	No surrounding land ownership	*Bigger*	Encourage protection of more space for nature (Dover & Settele 2009)

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[a] Evidence for the strategy to adopt amid new challenges not conventionally considered

Quality in a changing world

Enhancing habitat quality has traditionally been a crux of reserve-based conservation (New et al. 1995). Numerous studies demonstrate that improved habitat quality reduces the amount of habitat needed to sustain populations of species (Lawton et al. 2010) and following the shift in focus to reserve configuration and connectivity promoted by metapopulation biology, many others highlight the role of habitat quality in enhancing metapopulation persistence in fragmented landscapes (e.g. Verboom et al. 1991; Thomas et al. 2000; 2001; Fleishman et al. 2002; Resetarits and Binckley 2013). In the face of climate change, improving habitat quality through better *in situ* management is now generally regarded as the most important step for biodiversity conservation (Lawton et al. 2010; Hodgson et al. 2011a; Resetarits & Binckley 2013; Greenwood et al. 2016). Enhancing quality can also effectively enhance connectivity by increasing the number of potential dispersers (Hodgson et al. 2009b), and promote the ability of species to shift in response to a warming climate (Hodgson et al. 2009b, 2011a; Lawson et al. 2013). Simply preserving intact habitat, as opposed to enhancing its quality can also be an effective approach when time and money is serverly limited (Possingham, Bode & Klein 2015).

Homogeneity or heterogeneity?

Two broad approaches have been suggested as means of enhancing quality: providing more optimal habitat (homogeneity) or increasing heterogeneity, generally achieved through restoration of existing degraded habitat, or managing intact areas. The existing trade-offs between these two approaches have seldom been recognised, yet influence the outcome and overall effectiveness of management. Studies have demonstrated the positive influence of creating more optimal habitat on population size (Thomas et al. 2001; Ye, Skidmore & Wang 2013), dispersal success (Ye, Skidmore & Wang 2013), and population growth (Griffen & Drake 2008). In turn, providing more optimal habitat can influence extinction and colonization rates (Thomas et al. 2001, 2012; Fleishman et al. 2002; Franken & Hik 2004; Lawton et al. 2010; Resetarits & Binckley 2013; Ye, Skidmore & Wang 2013), providing source populations and habitats for colonization, which enhance the capacity of species to shift with climate change (Thomas et al. 2012). In contrast, greater habitat heterogeneity buffers the effect of environmental fluctuation compared to homogenous habitats, encouraging population stability (Opdam & Wascher 2004). Since the frequency of extreme climate events is likely to increase (IPCC 2007), the buffering effects of habitat heterogeneity could now be important for climate change adaptation (Piha et al. 2007; Maclean et al 2015). Moreover, irrespective of changes in the frequency of extreme events, the suitability of various habitat types for species is likely to change with climatic change. Thus providing greater habitat variety is viewed as a particularly effective adaptation strategy, over and above homogeneity, within a dynamic environment (Oliver et al. 2010).

Given these contrasting approaches towards *in situ* management and supporting evidence for each method particularly in the face of environmental change, evidence and understanding of the circumstances under which approach to follow is key. This decision partly depends on whether the primary conservation objective is single species conservation versus the protection of multiple species. Although many conservation programmes and the direct outcomes through which their success is measured tend to be single-species oriented, contingent on funding and/or legislation, an underlying assumption is that these measures will benefit other species or the community as a whole through umbrella or focal species effects (Bennett et al. 2015). The habitat characteristics that signify high quality are likely to be species-specific (Mortelliti, Amori & Boitani 2010) and so for individual species conservation programmes, habitats with high quality resources geared towards the focal species represent the preferred approach. However, this is only true in more stable environments (Johnson 2007), or by ensuring that habitat management itself offsets climatic changes (Greenwood et al. 2016). If the stated goal is to conserve multiple species, enhancing heterogeneity, and thus habitat variety, is likely to be more effective (Oliver et al. 2010). Field mosaics, for example, have been shown to benefit various species of birds and invertebrates, and the loss of heterogeneity through agricultural intensification is one of the reasons for biodiversity declines on farmland (see Benton et al. 2003). Amid the modern-day landscape, however, an increase in habitat variety can also lead to an increase in species richness of invasive species (Pyšek, Jarošík & Kučera 2002) which can result in undesirable effects on the community structure of native species (Levine et al. 2003). It should also be recognised that optimal quality can promote range shifts for other (non-focal) species and thus could still form part of multiple species conservation in the face of climate change (Lawson et al. 2013), and can be a benefical approach even if a particular focal species is replaced by non-target species as ranges move (Hodgson et al. 2009b).

Alternatively, if concentrating efforts on a single species, the requirements of that species and location within its geographic range are important. Specialist species are often more threatened than generalist species, more sensitive to within-patch variation in quality, and thus benefit from more homogeneous environments (Devictor, Julliard & Jiguet 2008; Ye, Skidmore & Wang 2013). Nevertheless, if specialist species also have small geographic ranges and restricted populations, they are more vulnerable to environmental change (e.g. Davey et al. 2012) and could benefit from the buffering effects of habitat heterogeneity (Oliver et al. 2010), as has been shown to be the case for birds (e.g. Root 1998) and species of British butterflies (Dennis et al. 2013). For those with different habitat requirements at varying stages of their lifecycle, habitat variability may be beneficial or essential (Johnson 2007; Oliver et al. 2010); though in this context, heterogeneity can be considered a component of optimal habitat quality.

In terms of location, the position of a species in its range and within the landscape influences levels of exposure to temporal fluctuations in conditions and resource availability that can be buffered by spatial heterogeneity (Opdam & Wascher 2004; Dover & Settele 2009). Populations at the edge of species' ranges or in anthropogenically fragmented landscapes typically occupy smaller and more isolated areas of habitat. If dispersal between populations and rescue/recolonization are inhibited (Opdam & Wascher 2004), then promoting persistence through enhanced local habitat heterogeneity may be particularly pertinent (Lawton et al. 2010). Nevertheless, prevailing conditions at the edges of species' geographic ranges are expected to represent the environmental limits at which populations can persist, so ensuring some optimal areas of habitat are present both in reserves (Thomas et al. 2001) and at the edge of the species range to allow for recolonization (Thomas et al. 2012), is essential. Finally, for species residing in fragmented landscapes consisting of networks of smaller patches (Moilanen & Hanski 1998), the effects of habitat quality on colonization and extinction may be less important than area and isolation. In this case, the creation of bigger, more connected sites will be more effective than simply improving patch quality.

Space for nature

Traditionally the theories of island biogeography (MacArthur & Wilson 1967; Simberloff & Abele 1976) and metapopulation dynamics (Moilanen & Hanski 1998; Hanski 1999a) emphasize the role of habitat area in influencing local population viability, and have contributed to the prioritization of larger reserves over smaller ones in conservation planning (Williams, ReVelle & Levin 2005; Lawton et al. 2010). Nevertheless, there is conflicting evidence suggesting that several small reserves may be more effective than a single large one of equivalent total area (see Ovaskainen 2002). The “SLOSS” (Single Large or Several Small) debate between these two perspectives originated in the 1970s and remains contentious despite numerous attempts at resolution (Tjørve 2010). In the current context of challenges now faced by biodiversity, each strategy continues to offer different pros and cons depending on the challenge in question.

Larger sites have classically been favoured for their greater carrying capacities (Hanski 1999a) and consequently, are less vulnerable to extinction from environmental and demographic stochasticity (Diamond 1975; Huxel & Hastings 1999; Franken & Hik 2004; Griffen & Drake 2008). Since climate change is coupled with an increase in extreme weather events (IPCC 2007), buffering the impact of this with larger population sizes is an effective strategy. In the ringlet butterfly (*Aphantopus hyperantus*), for example, larger sites were less sensitive to droughts and promoted faster population recovery (Oliver, Brereton & Roy 2013). Larger sites also offer a reduced risk of inbreeding (Groeneveld 2005) and loss of genetic variability due to drift (Jarvinen 1982), potentially increasing intrinsic adaptability to environmental change (see Merilä 2012). The main appeal for larger sites within modern-day landscape-scale conservation, however, is the capacity to enhance range shift. Large source populations in reserves enhance colonization of surrounding habitat, supporting metapopulation persistence in highly fragmented landscapes (Wilson et al. 2002; Lawson et al. 2012), thus facilitate range shifts in the face of climate change (Hodgson et al. 2011b). Moreover, large sites have been advocated for their ability to support greater species richness (e.g. Connor & McCoy 2001; Lees & Peres 2006; Hartter & Southworth 2009; Lawton et al. 2010; Dennis et al. 2013) and may enhance the capacity of natural areas to provide ecosystem services such as pollination (Kremen et al. 2004; Palmer et al. 2004; Klein et al. 2007).

Nevertheless, contrary to classical theory, creating bigger sites is not consistently effective when accounting for modern-day challenges to biodiversity. Landscapes are becoming increasingly threatened with large correlated environmental disturbances (Huxel & Hastings 1999) and exposed to frequent disease epidemics (Jarvinen 1982), under which the presence of a large continuous block of habitat can increase extinction risk and reduce the chance of recolonization from surrounding populations (Groeneveld 2005; Schnell et al. 2013). Whilst large protected area size can reduce propagule pressure from invasive species because of a reduced perimeter:area ratio (Hulme et al. 2014), effective monitoring and control of invasive species can be more difficult to achieve in larger protected areas (Foxcroft et al. 2013). There are also social and cultural constraints to the designation of protected areas that were not considered by original solutions to the SLOSS debate (Williams, ReVelle & Levin 2005), such that increasing habitat area for conservation is often not possible within modern landscapes (Doerr, Barrett & Doerr 2011).

In contrast, immigration rates to multiple smaller conservation sites can often be higher (Fahrig 2003), the landscape-scale risk of extinction lower (Hartley & Kunin 2003; Groeneveld 2005; Nicol & Possingham 2010) and the variety of habitat greater (Dover & Settele 2009; Oliver et al. 2010). Consequently, landscapes with several smaller sites can hold more species than a single large site (Simberloff & Abele 1976; Groeneveld 2005; Báldi 2008; Rybicki & Hanski 2013), but could be missing habitat specialist or interior species with large body size (Cardillo et al. 2005) or resource and area requirements (e.g. Oertli et al. 2002; Ye et al. 2013). Whether or not conservation managers are directly focusing on single or multiple species, recognition of the dynamic responses of populations and metapopulations to environmental change calls for the siting of reserves to support the persistence of species rather than simply the representation of as many as possible (see Margules and Pressey 2000; Kukkala and Moilanen 2013). Planning tools have been developed to examine how the area and configuration of reserves can optimise both persistence and the complementarity of species protected (e.g. Moilanen et al. 2005).

In terms of specific implications of accelerating environmental change for the SLOSS debate, studies frequently fail to specify the extent to which invasive species contribute to the increased richness of landscapes with multiple smaller sites (Pyšek, Jarošík & Kučera 2002). However, providing an increased number of so-called “stepping stone” habitats or protected areas can enhance the speed of colonization of new landscapes, increasing the ability of species to track climate change (Hodgson et al. 2012), both in terrestrial (Lawson et al. 2012) and potentially marine environments (Magris et al. 2014).

Bigger or more?

In reality, many factors influence whether one large or several small reserves are more effective for achieving conservation goals (Soul & Simberloff 1986), so a more useful question for conservation decision-making concerns the circumstances in which each approach is favoured (Williams, ReVelle & Levin 2005; Tjørve 2010). If the aim is to protect multiple species, both approaches can enhance species richness as described above, with the expectation that the lower the proportional overlap in species among sites, the more effective is a multi-reserve approach (Connor & McCoy 2001; Tjørve 2010). However, the dynamic and transient responses of species distributions to rapid environmental change add some new provisos to this general guideline. For example, a greater number of species are expected to suffer delayed extinctions following habitat loss in landscapes with smaller rather than larger reserves (Kuussaari et al. 2009) and under climate change, one must also factor in the location of these sites and whether they remain climatically suitable for their focal species (Hodgson, Moilanen & Thomas 2009; Hodgson et al. 2009a). Where sites are forecast to remain climatically suitable, large reserves will benefit species with poor dispersal capability (Hodgson, Moilanen & Thomas 2009; Hodgson et al. 2009a). Conversely, for species with high dispersal rates, it is recommended to focus on patch number initially before increasing area (Nicol & Possingham 2010), enabling species to utilise the “stepping-stones” and shift in response to warming temperatures (Hodgson et al. 2012).

In the context of increasing extreme weather events, the distinction between the benefit of large reserves for habitat-interior species and small patches for edge species is exacerbated (Bender, Contreras & Fahrig 1998). Edge species are often more vulnerable to climate variability, especially when confined to small fragments of remaining habitat exposed to extreme weather events (e.g. Powell and Wehnelt 2003). Though larger reserves can be viewed as disadvantageous for species residing in ecotones or edge habitats (Bender, Contreras & Fahrig 1998), this is only a limitation in reserves consisting mainly of homogeneous habitat. Larger sites do tend to offer high levels of heterogeneity (Connor & McCoy 2001), accommodating pockets of habitat which can create the desired “edges” for these species within the reserve itself.

For species such as the many amphibians that are vulnerable to increasingly common disease epidemics amid a warming climate (Harvell et al. 2002; Pounds et al. 2006), more, smaller sites could provide local refuges from disease. Similarly, more sites are effective for species susceptible to environmental catastrophes as the risk of extinction is spread over several locations (Groeneveld 2005) and increases the chance of recolonization from nearby sites (Schnell et al. 2013). Nevertheless, threshold effects could render smaller sites too small to act as sources for range shifts, especially for those species with highly fragmented distributions or narrow geographic ranges (Pimm et al. 2014). When reserves are too small, wide-ranging species such as carnivores can leave the sites, heightening both human-wildlife conflict and carnivore mortality (Woodroffe & Ginsberg 1998). Species which congregate in relatively small areas at varying stages of their lifecycle (e.g. see BirdLife International 2008), however, could benefit from the presence of several smaller reserves provided they are situated in locations corresponding to resources favouring aggregation. The importance of the spatial context and surroundings of sites also appear to be more important than site area for exposure to invasive species, since sites surrounded by protected landscapes can have fewer invasive species than those amongst areas with varying land-uses (Pyšek, Jarošík & Kučera 2002).

Much attention surrounding the SLOSS debate has focused on the biological benefits of each strategy (see *Space for Nature* above). But in cases where there are no clear biological grounds on which method is likely to be best, how should we determine what is most practical? The economic aspects associated with the contrasting methods were conventionally not considered by theory (Groeneveld 2005), yet adopting cost-effective approaches is fundamental to meet ambitious biodiversity targets with limited funding (McCarthy et al. 2012) whether working on a fixed budget to capture as much biodiversity as possible (maximum coverage), or aiming to conserve a set amount of biodiversity for the minimum cost (minimum set) (Albuquerque & Beier 2015). Creating large sites could be more economical in terms of creation and management (Williams, ReVelle & Levin 2005) as they start to rely on natural processes (Lawton et al. 2010) compared to managing smaller, individual sites. Overexploitation of species and habitats is a continuing challenge for biodiversity (Millennium Ecosystem Assessment 2005), thus the costs and feasibility of reserve protection against these threats will inevitably affect decisions. While the costs of internal monitoring (e.g. through transect surveys) of large sites versus small sites of equivalent area are comparable, notably less external surveillance is required for fewer, large sites with lower perimeter lengths (Ayres, Bodmber & Mittermeier 1991) and may be less at risk from poaching events (Di Minin et al. 2013). Enhancing the provision of ecosystem services promotes the ability of the environment to enhance human health and well-being, and lowers exposure to anthropogenic disturbances (Mitchell et al. 2015). But despite the expectation of greater diversity in large sites, whether large sites can enhance ecosystem function and the delivery of these services, relative to multiple smaller sites, remains equivocal. Nonetheless, with continuing land-use change leading to an increasingly fragmented landscape, there are frequently situations where it is physically not possible to create large sites due to surrounding land ownership or social and/or cultural costs of using a particular space (Williams et al. 2005). Moreover, people are altering their behaviour in response to climate change (Chapman et al. 2014), shifting agricultural regimes, modifying transport routes and building coastal defences, for example (see Segan et al. 2015). These indirect impacts of climate change can create additional barriers to creating large sites for conservation. In such cases, setting aside more, smaller sites for wildlife or opting for another strategy altogether, is often the only option.

Exploiting connectivity

Site isolation plays a fundamental role in the theories of island biogeography and metapopulation biology by determining colonization rates (MacArthur & Wilson 1967; Moilanen & Hanski 1998) and the Rescue Effect (Brown & Kodric-brown 1977). As human land conversion has greatly increased habitat isolation (Bennett 2003; Nicol & Possingham 2010), connectivity is often promoted to counteract biodiversity loss associated with habitat degradation (Williams, ReVelle & Levin 2005; Donald & Evans 2006; Lees & Peres 2008). Connectivity is now also fundamental to facilitate species range shifts in response to climatic change (Lawson et al. 2012, 2013; Thomas et al. 2012) and is thus commonly recommended for climate change adaptation (Heller & Zavaleta 2009).

But in today’s landscapes, increasing impacts from invasive species, pollution, disease and extreme weather events (Millennium Ecosystem Assessment 2005) present possible counterarguments for enhancing connectivity, given evidence that greater connectivity can lead to more rapid spread of catastrophic events (e.g. Laine 2004) and invasive species (Simberloff & Cox 1987; Dover & Settele 2009). Recent research has demonstrated that the deformed wing virus epidemic in the European honeybee *Apis mellifera*, is driven by movement of pollinator populations and spread of the mite *Varroa destructor,* and greater functional connectivity (i.e. the behavioural response of an organism to landscape features [Tischendorf and Fahrig 2000]) for the vectors of the disease therefore enhance its potential to spread to other wild pollinators (Wilfert et al. 2016). As a result, large distances between sites and regulated movement are now necessary to reduce the spread of disease, invasive species, predators, and the impacts of environmental events such as fire or hurricanes (Williams et al. 2005). Networks of sites that are well connected in terms of the dispersal capabilities of target species, but remain fragmented with respect to the transmission of disease (Huxel and Hastings 1999; Hartley and Kunin 2003; Williams et al. 2005) or susceptibility to regionally correlated environmental variation, would represent win-win situations, although providing the information required to define this optimal level of aggregation is challenging (Williams et al. 2005).

Connectivity has traditionally focused on habitat corridors, which can include natural or man-made linear features such as rivers, canals, hedgerows and railway embankments (Lawton et al. 2010). Managing the matrix between sites is often advocated as a means of making the space between pockets of protected areas amid intense land use more permeable to allow for species movement (Lees & Peres 2009). In addition, increasing the number of sites and aggregating them within the dispersal distance of focal species enhances movement, though could reduce opportunities for range expansion if not adequately spaced (Magris et al. 2014). More recently, research has begun to highlight the role of the other strategies associated with reserve design for enhancing connectivity. Local population dynamics in addition to distance between patches are essential for determining functional connectivity (i.e. potential rates of immigration). Habitat area and quality increase the size and stability of source populations for dispersal and hence rates of immigration to other patches (Hodgson et al. 2009b). Recent research has shown that stable abundance trends are more important than dispersal ability in influencing rates of range expansion in British butterflies (Mair et al. 2014), and reproductive rates of wetland vertebrates had more influence on immigration rates than species mobility (Quesnelle, Lindsay & Fahrig 2014). Thus promoting population growth through maintaining habitat quality and size is essential, and directing efforts exclusively to structural connectivity (focusing on the physical structure of the landscape [Tischendorf and Fahrig 2000]) is only beneficial under specific circumstances.

The primary purpose of enhanced connectivity (both functional and structural) is to augment species movement between sites, which is becoming increasingly more important across landscapes as range shifts are forced by climate change. Therefore, the value of increased structural connectivity alone depends on whether persistence or range expansion are limited by the dispersal ability of species relative to the existing configuration of habitats (Moilanen & Hanski 1998). The most dispersive species may not benefit from increased connectivity (Bennett 2003), but highly sedentary species may only benefit if connectivity is increased within the dispersal range of the species concerned (e.g. Doerr et al. 2011; Johst et al. 2011). With ongoing fragmentation, distances between habitats can exceed dispersal capacity for many species (Dennis et al. 2013). As a result, guidelines to identify the level of isolation of sites relative to species dispersal capacity at which enhanced connectivity most benefits regional persistence, would help to increase the effectiveness of landscape-scale conservation (Lees & Peres 2009). Such approaches could benefit the species with intermediate dispersal capabilities that have declined more than either the most sedentary or mobile species (Thomas 2000). When considering the level and capability of dispersal, it is also necessary to consider how dispersal mode differs within and between taxa (Hodgson et al. 2011a). Animal-dispersed plants, for example, can increase following the introduction of corridors for animals, whereas wind-borne dispersers may be unaffected (Brudvig et al. 2009).

Finding the space to make sites bigger across the modern human-dominated landscape is becoming increasingly problematic. As a result, enhancing connectivity may be essential for species requiring access to the resources needed (Benton, Vickery & Wilson 2003), especially those with varying needs at various stages of their lifecycles (Fahrig 2003) or with seasonal food requirements (Donald & Evans 2006), and may also encourage animals to reside within appropriate habitats, reducing human-wildlife conflict (Hartter & Southworth 2009). Establishing corridors between sites can be expensive (Dennis et al. 2013), in which case utilising man-made structures or existing natural connections is a plausible solution. Managing matrix habitat may be needed when a location offers a fragmented network of protected areas surrounded by intense land use. In return, this not only provides species with an increased capacity to shift, it enhances the ability of the environment to provide a range of ecosystem services such as pollination, human well-being and air quality. Nevertheless, in areas vulnerable to spatially autocorrelated contagion-like extinction pressures (Channell & Lomolino 2000), connectivity should be avoided; instead, opting for widely separated reserves will be more effective (Hartley & Kunin 2003).

Interplay between approaches

In reality, it is clearly not a straightforward case of selecting one approach; opting for a particular strategy can impact the ability to achieve, or even the requirement for another. Previous work has focused on the effect of habitat quality and area in enhancing functional connectivity between sites (e.g. Hodgson et al. 2009c;

Hodgson et al. 2011a but see also Doerr et al. 2011), thus choosing to develop quality or area can be an effective option for improving connectivity if required. Authors have also alluded to the fact that focusing on quality can mean there is less need to create new areas for wildlife (Lawton et al. 2010), though improving connectivity directly will ensure that species can actually reach these high quality habitats (Root 1998). In any case, enlarging sites reduces the need for connectivity (Rosenberg, Noon & Meslow 1997; Haddad 1999; Dennis et al. 2013) as these areas start to act as stand-alone reserves (Williams, ReVelle & Levin 2005), providing they reside in climatically suitable or stable areas, and also tend to offer the benefits of habitat heterogeneity when areas are sufficiently large to host a broad range of habitats. Likewise, the creation of corridors can effectively increase the size of the site (Benton, Vickery & Wilson 2003; Noel et al. 2006; Lawson et al. 2013) and so remains a useful alternative when the creation of big sites is not an option. But where the designated area of land for conservation purposes is limited in size within conservation planning, the creation of corridors could mean that the area of the sites themselves would have to be smaller to meet the overall area on offer (Rosenberg, Noon & Meslow 1997). Should more, smaller sites prove to be the best option, these areas can themselves act as stepping stones, promoting connectivity (Hodgson et al. 2009b) and simultaneously offering habitat heterogeneity (Dover & Settele 2009). Although if these sites are separated to protect against climatic disturbance, this could negatively affect the ability to suitably enhance connectivity and facilitate range shift if required (Magris et al. 2014).

Moving forward

Although context-dependent, formulating a series of generic rules would provide a much needed starting point to assist conservation practitioners involved in decision-making regarding the planning and management of protected areas amid future threats. Given the current and future constraints imposed on biodiversity and the acute shortage of funding for effective conservation, it is not always possible to implement the creation of bigger, better and more joined sites for conservation and difficult choices between these strategies will often need to be made. With increasing land-use change, for example, creating bigger sites is rarely possible within fragmented landscapes, whilst restoring increasingly degraded habitat through *in situ* management can be expensive and time consuming (Possingham, Bode & Klein 2015). Responding to an increase in invasive species, pollution and disease requires protection and management to be undertaken in widely spaced locations, bearing in mind the trajectories of climate change and routes species may follow as they shift their distributions in response (Loarie et al. 2009; Early & Sax 2011). It is now widely accepted that conservation strategies should account for climate change (Jones et al. 2016) and the inevitable need to adapt to changing temperatures, cope with environmental extremes and shift in response to climatic changes. In this case, focusing on habitat quality is the most effective strategy (Greenwood et al. 2016) but specifically how to approach this depends on a series of factors. Bigger sites and multiple smaller sites each offer benefits for climate change adaptation, whilst the functional connectivity required for this challenge can be improved through a focus on other strategies which encourage stable abundance. Indirect impacts associated with climate change have seldom been recognised in the literature (Chapman et al. 2014) but can further complicate the ability to adopt particularly strategies, or the overall effectiveness of those employed. With the potential of people to shift agricultural practices, for example, utilising numerous smaller sites may enable people to exploit areas of land in between, as opposed to entering those areas designated for wildlife (Bradley et al. 2012).

The literature associated with conservation planning has vastly progressed since the origin of reserve design theory presented by Diamond (1975). Many of the ideas proposed by classical theory still apply in the context of modern-day pressures, such as the ability of larger sites to deal with stochasticity as a result of high carrying capacities, and enhance the colonization of surrounding habitat from large source populations. Other recommendations become even more important when we factor in rapid environmental change, such as the provision of source populations provided by optimal habitat for species' range shifts, the buffering effect supplied by large populations within larger sites, and the reduced extinction risk of multiple smaller sites from correlated environmental events. Meanwhile, there are evidently cases where ideas from conventional theory no longer apply. Single large sites are prone to extinction from increasing environmental disturbances, counteracting the traditional desire to maintain structural connectivity between sites, alongside the fact that it is simply not possible in today's landscapes to create single large sites for nature where levels of biodiversity may be high, and often coincide with high human populations.

Decision-making framework

In essence, the most effective strategy in the context of 21st century pressures depends on circumstance, but by considering the goals of conservation and the characteristics of biota for which conservation is needed, it is possible to make informed choices about which strategy is likely to be best (Table 2.1). Nevertheless, practical considerations such as financial costs, reserve protection (day to day and in the future) and site monitoring are also important and are seldom considered in studies of reserve design (Groeneveld 2005). From the resulting recommendations shown in Table 2.1, size and connectivity represent the most prominent strategies amongst the considerations highlighted. However, it is noteworthy that this may not consistently be the case, particularly when focusing on issues associated with modern-day conservation including economic constraints, extent of habitat fragmentation, vulnerability to climate change and risk of disease and environmental disturbance. Upon adopting a particular conservation strategy, there are evidently multiple valid options for a particular situation (Table 2.1). Our review of the literature suggests that, amid 21st century challenges, habitat quality and area should be the priority (as in Hodgson et al. 2009c; Lawton et al. 2010); enhancing, amongst other things, the ability of species to shift in a changing climate, cope with environmental extremes and promote species richness and population viability. This offers the additional advantage of being more cost-effective than focusing on connectivity between sites, especially when protecting currently intact habitat. The exception to this rule is within existing fragmented landscapes, where area and connectivity become more important than quality (Moilanen & Hanski 1998). Since enhancing the quality and/or quantity of sites offer many of the benefits associated with connectivity, encouraging connectivity alone is only supported in a few circumstances. Despite this, more connectivity is generally considered better than isolation, aside from populations exposed to spatially contagious threats such as disease epidemics, but at low risk from climate change and hence not expected to require the ability to shift their range at least over the short-term.

The principles of this framework can effectively be used to provide solutions to 21st century issues (Box 1) where conservation continues to struggle to find answers to complex debates; highlighting the role of scientific theory in modern day conservation planning.

Box 1:

Decision making in the real world: a case study of land spare versus land share

Alongside threats from habitat change, climate change and invasive species, one of the greatest threats to global biodiversity is the need to balance the increasing demand for food security with conservation (Green et al. 2005; Donald & Evans 2006; Fischer et al. 2008; Edwards et al. 2010; Balmford, Green & Phalan 2012). Land sparing involves the preservation of natural areas for wildlife, segregated from a smaller area of land for intensive agriculture, while land sharing, or wildlife-friendly farming, involves the spatial co-occurrence of agriculture and conservation (Phalan et al. 2011; Tscharntke et al. 2012; Grau, Kuemmerle & Macchi 2013). Land sharing has been encouraged, particularly in Europe, with the support of agri-environment payments through the Common Agricultural Policy and various other certification schemes worldwide. These include the Conservation Reserve Program in the USA (Green et al. 2005; Kleijn et al. 2011; Hulme et al. 2013) and the Australian Landcare Program (Kleijn et al. 2011); aiming to cover the net losses that occur from avoiding more intensive farming methods (Lawton 2010), and provide support to those farmers who opt to make environmental improvements to their land (Donald & Evans 2006).

The land share, land spare debate epitomises the difficult choices faced in landscape-scale conservation planning: on one hand, a high quality (relatively homogenous) but smaller area of spared land for wildlife; on the other, lower quality but larger areas of heterogeneous habitat shared with farming (Green et al. 2005; Fischer et al. 2008; Adams 2012; Balmford, Green & Phalan 2012). As with the trade-offs associated with reserve design, both approaches have strengths and weaknesses (Edwards et al. 2010). Land sharing can enhance and restore connectivity by creating softer barriers to dispersal between areas of more natural habitat (Donald & Evans 2006; Fischer et al. 2008; Heller & Zavaleta 2009; Dover & Settele 2009). Sharing also encourages the creation of new wildlife sites (Donald & Evans 2006; Dover & Settele 2009; Lawton et al. 2010) although more land, potentially previously intact, must be cultivated to balance the fact that overall yield is low (Green et al. 2005; Balmford, Green & Phalan 2012; Hulme et al. 2013; Chandler et al. 2013). Nevertheless, this may mean that more land is protected in some way (Balmford, Green & Phalan 2012). In contrast, land sparing can boost species populations (e.g. Phalan et al. 2011), particularly those of greatest conservation concern (Hulme et al. 2013), and thus assist with climate change adaptation through abundant source populations. It can also increase overall species richness (Edwards et al. 2010; Chandler et al. 2013) due to more native habitat (Hulme et al. 2013) and because many wild species cannot survive in even the most wildlife friendly farmland (Tscharntke et al. 2012). However, some species are specifically adapted to agricultural landscapes (Benton, Vickery & Wilson 2003), particularly in landscapes with a long-history of disturbance (Donaldson et al. 2016). Land sparing usually produces higher yields (Grau, Kuemmerle & Macchi 2013), potentially reducing deforestation rates since there is less pressure to log other areas to meet demand (see Green et al. 2005) and more recently reported to save on greenhouse gas emissions as a result of less land conversion to meet demand for agriculture (Balmford, Green & Phalan 2012).

Amongst the confounding benefits discussed extensively in the literature, our decision-making framework can be used to demonstrate how theory associated with reserve design can help provide solution to this intensive debate (Table 2.2). The homogeneous quality associated with spared land provides benefits to specialist species, boosts populations of species vulnerable to climate warming, and provides smaller sites suitable for stationary animals with small range sizes. Providing more, smaller sites can also enhance the capacity for range shift across the landscape in response to climatic change. Meanwhile, land sharing generally enhances connectivity between sites, offering benefits to migratory species and those with low dispersal capabilities and/or large range sizes, but equally may spread the risk of extinction from correlated weather events and disease. Providing the landscape remains relatively fragmented with respect to these risks, the heterogeneity associated with land sharing can help buffer the effects of variable environmental disturbances. Land sharing is also an appealing option in areas where wildlife and low intensity forms of agriculture have coexisted for long periods of time, such as parts of Europe (Fischer et al. 2008; Hodgson et al. 2010), where species are tolerant to disturbance from such activities (Grau, Kuemmerle & Macchi 2013). Conversely, in areas with high potential agricultural activity that do not coincide with those of high biodiversity value, it is possible to zonate land and opt for a land sparing approach (Hodgson et al. 2010). However, with environmental change, crop suitability may also shift (Bradley et al. 2012) leading people to encroach on spared land. In this sense, suitable areas for people to farm with climate change could be equally as important as providing suitable areas for species' ranges to shift, or alternatively opt for a land sharing approach where both have the potential to move. Finally, this challenge highlights the importance of practical considerations (Table 2.2), with site ownership, planning and governance being amongst the most fundamental factors leading to the most appropriate option available.

Table 2.2. The prevalent factors derived from a range of scientific studies associated with the theory of reserve design influencing solutions to the land spare, land share debate.

Factor			**Land spare**[a]	**Land share**[b]	**Justification**	**Reference(s)**
Species traits	Habitat preference	Specialist	✓		Land sparing provides higher quality, natural habitat suitable for specialists, whilst generalists can exist in lower quality habitats	Green et al. 2005; Devictor et al. 2008; Fischer et al. 2008; Hulme et al. 2013; Ye et al. 2013
		Generalist		✓		
	Habitat requirements	Migratory		✓	Some species require a variety of habitats (heterogeneity), continuity (connectivity) and/or large areas to complete life cycle	Donald & Evans 2006; Johnson 2007; Fischer et al. 2008
		Stationary	✓			
	Human disturbance	Sensitive	✓		Land sparing involves less disturbance to wildlife since area is spared for them	Green et al. 2005; Grau et al. 2013
		Tolerant		✓		
	Range size	Small	✓		Land sparing involves a smaller area of high quality land designated for wildlife, while land sharing settles for a lower quality but much larger area of land for wildlife	Phalan et al. 2011; Hulme et al. 2013
		Large		✓		
	Dispersal capability	High	✓		Land sharing enhances connectivity through soft barriers to dispersal between areas of natural habitat	Donald & Evans 2006; Fischer et al. 2008; Heller & Zavaleta 2009; Dover & Settele 2009
		Low		✓		
	Population viability	High		✓	Land sparing can boost species populations	e.g. Phalan et al. 2011
		Low	✓			

Factor			**Land spare**[a]	**Land share**[b]	**Justification**	**Reference(s)**
Threats	Climatic change	High vulnerability, low variability	✓		Higher quality spared land can provide source populations for climate adaptation and assist with capacity for range shift	Phalan et al. 2011
		High variability, low vulnerability		✓	Sharing is associated with a heterogeneous landscape, thus buffers environmental disturbances (providing landscape remains relatively fragmented to spread extinction risk)	Fischer et al. 2008
Practical	Ownership	Multiple		✓	Land sparing is not possible with multiple owners	Adams 2012
		Single	✓			
	Planning	Strong	✓		Land sparing requires a strong and effective planning approach to be successful and not detrimental to wildlife.	Adams 2012
		Weak		✓		
	Governance	Strong	✓		Land sparing is difficult to implement in countries with weak governance, requires strict policy mechanisms to be effective and ensure areas farmed are restricted	Edwards et al. 2010; Hodgson et al. 2010; Adams 2012
		Weak		✓		

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[a] Typically offers homogeneous, smaller, less connected sites

[b] Generally composed of heterogeneous, larger, more connected habitat

Conclusion

As threats to biodiversity and competing demands for land increase, the effective targeting of conservation resources is increasingly urgent. While many authors have concluded that simple concrete rules for reserve design do not exist, the knowledge base is extensive. The very broadness and complexity of the literature regarding reserve design has come to represent a challenge to those adopting measures to promote landscape-scale conservation, and new threats to biodiversity conservation demand a reevaluation of classical ideas for reserve design. We have synthesised and explored existing knowledge to provide updated, generic guidance to decision makers engaged in landscape-scale conservation planning and practice in the context of levels of environmental change and biotic consequences that were not envisaged only decades ago. Ambitious global biodiversity targets are set and funding for conservation is notoriously limited. By providing an evidence-based framework that summarises the circumstances under which each strategy is best, we hope to provide increased clarity to inform urgent, cost effective modern-day conservation decision-making.

Chapter 3:

Subsistence use of papyrus is compatible with wetland bird conservation

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Updated from: Donaldson, L., Woodhead, A.J., Wilson, R.J. & Maclean, I.M.D. (2016) *Biological Conservation,* **201,** 414–422

Abstract

Conservationists have historically advocated measures that limit human disturbance. Nevertheless, natural disturbances are important components of many ecosystems and their associated species are often adapted to such regimes. In consequence, conservation managers frequently simulate natural disturbance, particularly in temperate forest systems. This practice is less widespread and seldom studied in tropical regions, where biodiversity conservation and human activities are often thought to conflict. However, many tropical systems have been subject to natural and anthropogenic disturbance over evolutionary timescales, and disturbance may therefore benefit the species they host. Determining whether this is true is especially important in tropical wetlands, where human activities are essential for sustaining local livelihoods. Here we investigate the impacts of disturbance from human resource use on habitat–specialist bird species endemic to papyrus swamps in East and Central Africa. Bird densities were estimated using point counts and related to levels of human activity using physical characteristics of wetland vegetation as a proxy for disturbance. All species were tolerant to some degree of disturbance, with particular species occurring at highest density in intensely disturbed habitat. Species were generally more tolerant to disturbance in larger swamps. Our results suggest that low-intensity use of papyrus wetlands by people is compatible with the conservation of specialist bird species, and highlight the potential benefits of traditional human activities to conserve biodiversity in the tropics.

Introduction

Habitat degradation is one of the greatest threats to biodiversity (WWF 2014) and restoring habitat is frequently the focus of conservation management (Hodgson et al. 2011a). To this end, conservationists have advocated measures that limit disturbances caused by human activity, adopting the view that the needs and actions of people often conflict with the objectives of biological conservation (Brown 2002). The classic “fences and fines” approach dominated much of the 20th century but has been criticized for its failure to account for the interests of communities by impeding the use of natural resources (Hutton, Adams & Murombedzi 2005). This is particularly problematic in developing countries (Barrett et al. 2001), where people's livelihoods are closely linked to natural resource use (Khadka & Nepal 2010). In consequence, conservation now often adopts a more community-based approach, which strengthens the link between conservation and human needs (Adams & Infield 2003). These participatory methods incorporate a variety of incentives to make conservation more favourable to local communities (Spiteri & Nepalz 2006). Nevertheless, community-based conservation schemes often restrict resource use (Lele et al. 2010), commonly with financial incentives (Barrett et al. 2001) and as such, maintain the premise that human activities are detrimental to biodiversity.

Many ecosystems have, however, been modified over very long periods of time. Thus, human disturbances potentially play a role in maintaining biodiversity (Hobbs & Huenneke 1992), with many species having evolved under natural disturbance regimes prior to the influence of humans (Lindenmayer et al. 2008). The role of disturbance is recognised and incorporated into management programmes in various temperate systems (Bengtsson et al. 2000; Seymour, White & DeMaynadier 2002). Forests, for example, were prehistorically grazed by megaherbivores, and subsequently by domestic animals following the regional extinction of large grazers (Bengtsson et al. 2000). Human-based disturbances which create early successional habitat, are used by forest managers to simulate natural forms of disturbance (Bengtsson et al. 2000; Seymour, White & DeMaynadier 2002; Lashley et al. 2014). The extent to which disturbance is important for maintaining biodiversity has seldom been studied or considered in tropical areas; home to high levels of global biodiversity (Hillebrand 2004), yet a rapidly growing human population and extreme poverty place increasing pressures on tropical societies, habitats and species (Hutton & Leader-Williams 2003; Spiteri & Nepalz 2006). Therefore, it is crucial to understand the extent to which populations of species can be sustained in human-modified landscapes and how specific land-use practices influence biodiversity (Chazdon et al. 2009).

Tropical wetland systems encapsulate the potential conflicts and synergies between human exploitation of natural resources and conservation; vital for human wellbeing (Senaratna Sellamuttu, de Silva & Nguyen-Khoa 2011) and the alleviation of poverty, as well as hosting a rich biodiversity (Russi et al. 2013). In East Africa, papyrus (*Cyperus papyrus*) swamps support the livelihoods of millions of people through the provision of ecosystem goods and services (van Dam et al. 2014) including water, food, medicinal herbs, fishing and grazing habitat for livestock (Terer, Triest & Muasya 2012). Papyrus is frequently harvested and used for roof and fence construction, and to craft items such as baskets, trays, sleeping mats and ropes, which provide basic resources and a vital source of income for rural poor communities living in close proximity to swamps (Maclean et al. 2003d). These swamps also host a unique biodiversity including a suite of generalist species of birds (Maclean et al. 2003a), alongside several species of specialist passerines (Britton 1978; Vande weghe 1981). In common with wetlands worldwide, papyrus swamps are increasingly threatened by habitat loss from drainage and encroachment for agriculture (Maclean, Wilson & Hassall 2011). As a result, population estimates of papyrus passerines suggest that they are decreasing in numbers, undergoing even greater declines than the habitat on which they depend (Maclean, Bird & Hassall 2014).

Disturbance from human activities in papyrus swamps has been considered detrimental to biodiversity and, in consequence, legislation in East Africa tends to impose restrictions on harvesting by local people (Wetlands Inspectorate Division 2001; Hartter & Ryan 2010). However, these restrictions can alienate local stakeholders and risk the success of further conservation efforts (Terer et al. 2012). Disturbance from subsistence use, including harvesting for materials and burning from smoking bees out of hives to extract honey or hunting game or fish (Maclean et al. 2006), has been ongoing for over a millennium (Terer, Triest & Muasya 2012), and papyrus swamps have been exposed to natural forms of disturbance from fire and large herbivore grazing prior to human settlement (Taylor 1990). Following the regional extinction of large herbivores, people are likely to have replaced the role of these natural forms of disturbance in maintaining a more open habitat through harvesting and burning (Maclean et al. 2006). As with forest systems, this history of disturbance could have implications for the way wetlands in sub-Saharan Africa should be managed.

Here, we investigate the effects of disturbance on a suite of habitat–specialist species as an exemplar of the potential impacts of subsistence resource use, from direct cutting and burning, by local people on biodiversity in the tropics. Specifically, we quantify the effects of varying levels of disturbance on the relative densities of specialist bird species in an area of south-west Uganda. Habitat specialists are typically more sensitive to disturbance (Devictor, Julliard & Jiguet 2008). In consequence, if the densities of these birds are not negatively affected by disturbance, resource extraction to support local livelihoods is unlikely to be detrimental to birdlife, potentially to wildlife in general, and the long-term provision of ecosystem services. We conclude by discussing the implications of our findings for the conservation management of tropical wetlands and other habitats.

Material and methods

Study site

The study was conducted between May and June 2014 at Lake Bunyonyi, south-west Uganda (01°17′S 29°55′E), to coincide with post-rainy season breeding (Britton 1978). In this area, papyrus swamps persist along the lake shore and in valley bottoms, surrounded by heavily cultivated land. This region is subject to particularly high levels of disturbance from harvesting and burning as a result of increasingly high human populations (Maclean, Wilson & Hassall 2011) and levels of poverty (Gable, Lofgren & Rodarte 2015), as well as hosting among the highest densities of papyrus endemic passerines (Maclean, Wilson & Hassall 2011). At Lake Bunyonyi, papyrus is most commonly harvested and sold in bundles to use as a source of fuel, for thatching roofs, constructing fences and occasionally creating small out-buildings (see Maclean et al. 2003d). Thin strips of papyrus are also cut and used on a smaller scale to make a variety of handcrafts used for domestic purposes, or sold locally, increasingly to tourists (Maclean et al. 2003d). Small-scale burning in this area is largely caused by fishermen in an attempt to catch eels, which are marketed locally or used to feed families (J. Ruhakana *pers. comm*). Occasionally, burning can be initiated accidently in an attempt to smoke bees out of hives while harvesting honey, often situated in the swamp interior distant from local communities (Maclean et al. 2006). These subsistence-based activities are more frequent during the dry season in Uganda, when income from crop production declines (Maclean et al. 2003d).

Study species

Research concentrated on five specialist species of passerines most closely associated with papyrus in the study area, which have global distributions centred around East and Central Africa (Maclean, Bird & Hassall 2014). White-winged swamp-warbler (*Bradypterus carpalis*), greater swamp-warbler (*Acrocephalus rufescens*) and papyrus canary (*Crithagra koliensis*) are entirely confined to papyrus, although papyrus canary often forages in adjacent cropland (Vande weghe 1981). Papyrus yellow warbler (*Calamonastides gracilirostris*) and Carruthers's cisticola (*Cisticola carruthersi*) are primarily confined to papyrus, but can inhabit wetlands dominated by other types of vegetation, namely *Typha* and *Miscanthidium* spp. (Vande weghe 1981). Carruthers's cisticola was also found to inhabit wetland recently converted to agriculture in this study. All species are currently listed as Least Concern on the International Union for Conservation of Nature (IUCN) Red List, with the exception of papyrus yellow warbler, which is classified as Vulnerable due to a small and fragmented population, suspected to be in decline owing to the exploitation of its habitat (IUCN 2015).

Point count survey

105 point count surveys were conducted by the same observer between 7 am and 11:30 am, when the birds were most vocal. Swamps surveyed ranged in size from approximately 0.01 ha to 996 ha and covered the length of the lake (~ 35.6 km) (Figure 3.1). A 1- to 2-min adjustment time was used prior to survey to

minimise disturbance caused by arrival on-site. Numbers of focal bird species were identified visually or aurally within a 15-min period and the distance of each individual from the point of survey recorded within distance bands (0–19 m, 20–49 m, 50–99 m, 100–199 m). Each point covered a circular area with a 200 m radius, the location of which was recorded on GPS in the UTM (Universal Transverse Mercator) projection system. Counts were conducted from the edge of swamps often on higher land, offering an effective vantage point of both the edge and interior. Wetlands surveyed varied in size (mean size: papyrus swamp = 6.3 ha; broad wetland = 30.8 ha), thus multiple counts were conducted at opposing sides of large wetlands (diameter > 400 m) to enhance coverage and avoid potential survey bias towards swamp edge. Given the length of survey period and variation in area of swamp surveyed, data collected per count represent a relative, not absolute, indicator of species' abundance at each point (see Maclean et al. 2011; Maclean et al. 2014, for population assessments across the region).

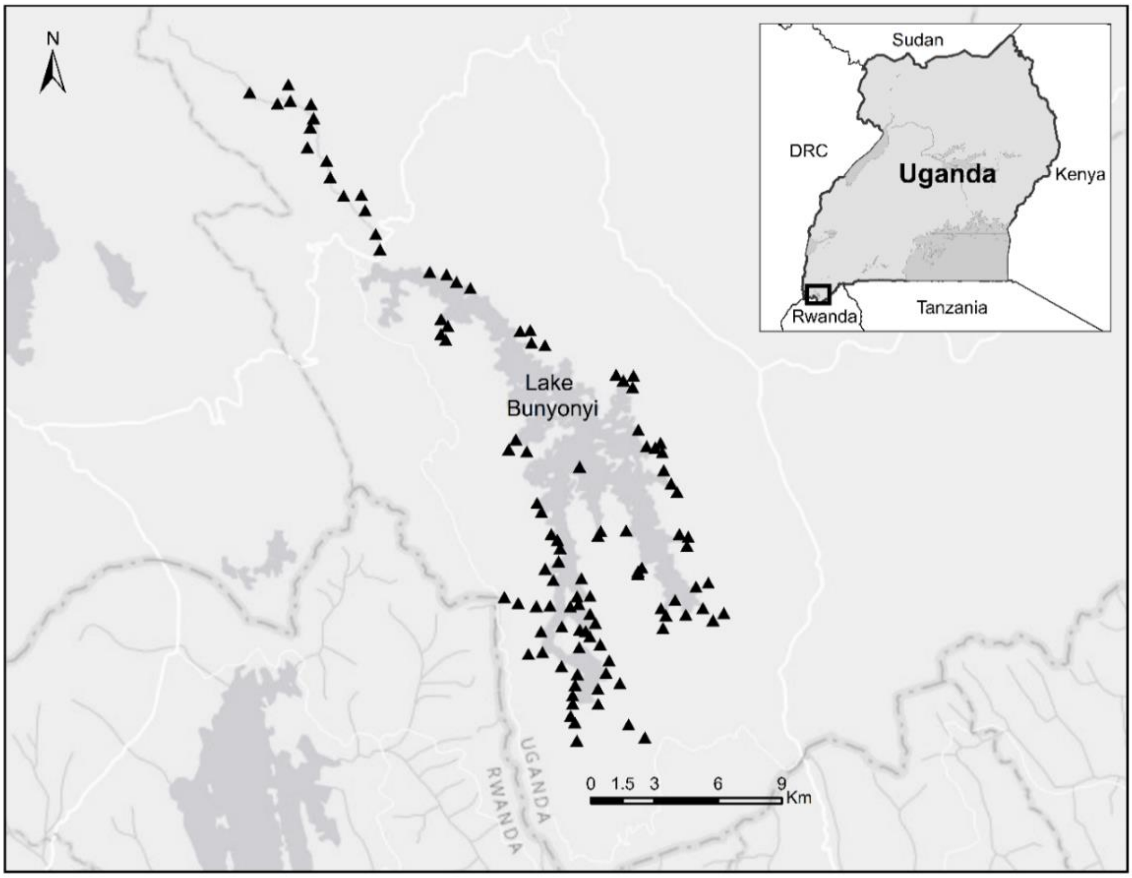

Figure 3.1. Point count locations (▲) around Lake Bunyonyi (lake shaded dark grey). Inset: location of the study site (◘) in south-west Uganda. Basemap credit:

Esri, HERE, DeLorme, MapmyIndia, © OpenStreetMap contributors, and the GIS user community.

Disturbance estimation

For the purpose of this study, we concentrate on human disturbance from recent and past harvesting of papyrus wetlands, together with occasional recent burning. As stands of papyrus first regrow following disturbance, culm width decreases and density increases (Muthuri, Jones & Imbamba 1989; Maclean et al. 2006; Terer, Triest & Muasya 2012). Thus, disturbance can be efficiently measured visually, using physical characteristics as a reliable indicator of disturbance levels. Based on this, five vegetation categories were created and used as proxies for disturbance (Table 3.1). The dominant form of disturbance in our study area was harvesting. A small amount of recent burning was also recorded (within ~ 5% of point counts), which was combined with harvesting to represent high intensity disturbance. Regeneration is similar following each of these disturbances within our study site, since the water level remains relatively stable at Lake Bunyonyi (Denny 1972) and regrowth occurs primarily from rhizomes rather than seeds (Terer, Triest & Muasya 2012). Some areas consisted of very low densities of papyrus mixed among other types of vegetation, largely due to water levels and soil conditions at particular sites (see Lind and Visser 1962; Kansiime et al. 2007). These areas were taken to represent undisturbed but suitable habitat, and allowed us to explore aspects associated with physical habitat characteristics. Sketch maps were drawn to scale on the day of survey, noting the proportion of vegetation types within the survey area. GPS readings and satellite imagery were used to record vegetation boundaries and approximate coverage of each vegetation type. Maps were later digitized in ESRI ArcGIS v 10.1 and R v 3.0.2 (R Core Team 2013) was used to calculate the proportion of each vegetation type surveyed per point count. The perimeter and area of each swamp surveyed were obtained using ArcGIS 10.1, and circularity calculated ($4\pi\text{area}/\text{perimeter}^2$) to provide an indication of patch shape.

Table 3.1. Vegetation classifications and physical characteristics used to indicate disturbance.

Vegetation category and symbol	**Description**	**History of disturbance**	**Age**	**Typical height (cm)**	**Density**	**Culm thickness**	**Senescence?**	**Intensity of disturbance**
Recently disturbed (RD)	Cleared (harvested), burnt, regrown immature papyrus[1], agricultural wetland[2]	Recent (weeks-months)	0-6 months	0-200	None/ very low	None/ very thin	No	High
Past disturbance (PD)	Mature papyrus regrown following disturbance	Past (>6 months)	>6 months-1 year	>200	High	Thin	No	Intermediate
Mature moderately disturbed (MD)	Mature papyrus previously disturbed and fully regrown to maturity	Past (1- 1.5 years)	>1 year	>200	Moderate	Thick	Some	Moderate/ low
Mature undisturbed (ND)	Mature papyrus, not likely to be disturbed, any disturbance over 1.5 years ago	None/ >1.5 years	>1.5 years	>200	Low	Thick	Yes	Low
Mixed vegetation papyrus (MP)	Mixed wetland vegetation containing >40% papyrus[1], poor growing conditions for papyrus	None	>1 year	50-200	Low	Thin	Some	Low

[1] Includes wetland dominated by other wetland types for two of the study species also found in these areas (Carruthers’s cisticola and papyrus yellow warbler) (Maclean et al. 2006)

[2] Applicable to Carruthers’s cisticola only

Data analyses

Detectability functions

Measures of abundance obtained from point count sampling depend on the detectability of species within the radius surveyed; accounted for using distance sampling techniques. As most counts were conducted from the edge of swamps, the area surveyed and distance of swamp from the observer within the circular radius differed between counts. In effect, this alters the assumption that detectability from the observer will be equal across all point counts (Thomas et al. 2010). To combat this, detectability functions for each species were calculated in Distance 6.2 (Thomas et al. 2010), using the distance of each individual recorded from the observer, and these functions used to provide weighted estimates of the swamp surveyed by each point count. Ultimately this provided a "detectability-weighted" area surveyed, which was included in subsequent analysis as a measure of sampling effort per point count.

To confirm that detection ability did not vary between vegetation types, we ensured that the distance from the observer did not differ among habitat types, then included habitat types as covariates in Distance 6.2 using the Multiple Covariate Distance Sampling (MCDS) extension (Marques & Buckland 2003). The inclusion of these effects consistently resulted in a less parsimonious model, indicating that height and density of vegetation was unimportant for the detection of the focal species, likely because most birds were recorded aurally rather than visually.

Statistical analyses

Generalized linear mixed effects models (GLMMs) were used to determine the effect of disturbance and vegetation type on species' density. Models were fitted using the "glmmADMB" package in R (Bolker et al. 2012) with a negative binomial error structure and log link function. The proportions of four distinct categories of disturbance within the survey area were included as fixed-effects; RD (recently disturbed), PD (past disturbance), ND (non-disturbed), MP (mixed papyrus/vegetation) (Table 3.1). To reduce multicollinearity (Dormann et al.

2013), MD (moderately disturbed) was removed due to correlation with ND for papyrus vegetation (Spearman coefficient = − 0.67) and broader wetland categories (Spearman coefficient = − 0.50 [PYW]; − 0.45 [CC]). As MD is intermediate between mature undisturbed papyrus and papyrus intensely disturbed in the past, removing this category enabled us to closely examine the effect of intense compared to no disturbance and explore our research aim. Prior to doing so, we ran additional models including this term, confirming that this intermediate category of disturbance was not important. Squared terms for each disturbance category were included as explanatory variables to account for the possibility of non-linear responses. Interactions of each disturbance category with the overall area of the wetland (log-transformed to improve normality) and wetland shape (circularity) were included as the study species are known to respond to patch area and edge (Maclean et al. 2006) and may, therefore, be more tolerant of disturbance in larger and/or more circular swamps. To account for the possibility of spatial autocorrelation and pseudoreplication, two random effects (region and wetland) were included in the models. A cluster analysis was performed on the location of point counts, and used to designate each point count to one of seven "regions" of the lake. All except two of the study species were found in all regions. To ensure the results obtained were not attributable to differences between regions, we repeated analysis including only those regions where the species were found. In each case, the results were qualitatively similar. Wetland ID was included as a second nested random effect, as repeated point counts were conducted in separate parts of some larger wetlands.

Effects were analysed using multi-model inference (Burnham & Anderson 2002). A global model containing the four disturbance categories, their interactions with area and circularity and squared terms as explanatory variables, was created for each species. Abundance was included as the response variable and the detectability-weighted area used as an offset in each model, allowing us to explore the effects of vegetation type on species density as opposed to abundance. All variables were zero-centred and z-score standardised prior to inclusion in models. The "MuMIn" package (Barton 2014) was used to produce all possible combinations of the global model, ranked by their Akaike Information Criterion adjusted for small sample size (AICc). A set of best models was created for each species, consisting of all those with ΔAICc ≤ 2 from the top-ranked model

(Burnham & Anderson 2002). Model averaging was used to identify key variables likely to be affecting relative abundance and account for model uncertainty (Burnham & Anderson 2002; Johnson & Omland 2004). The relative importance (RI) of each parameter was calculated as the proportion of models in the top model set with that term included. Since the interactions between patch geometry and vegetation type within the top model set may alter the strength and directional effects of terms alone, analysis was repeated with full models excluding the interactions, and confirmed that the overall qualitative conclusions held regardless of the inclusion of two-way interactions.

Results

Survey data

A total of 105 point count surveys were conducted from 80 papyrus and 57 broad wetland swamps (Table 3.2). The number of point counts in which each species was recorded ranged from 22 (21%) in 12 patches for papyrus yellow warbler, to 87 (82.9%) in 69 patches for greater swamp-warbler. Although greater swamp-warbler was the most frequently encountered species, Carruthers's cisticola was the most abundant, with a total of 198 individuals recorded. Papyrus yellow warbler was the least common, with 28 individual observations.

Table 3.2. Summary of point count data collected (n = 105). Greater swamp-warbler (GSW), white-winged swamp-warbler (WWW) and papyrus canary (PC) are entirely confined to papyrus, thus wetland patches for these species consist only of papyrus swamps. Carruthers's cisticola (CC) and papyrus yellow warbler (PYW) occupy wetlands dominated by both papyrus and other types of vegetation.

Species	Total wetland patches surveyed	Point counts with species present	Wetland patches with species present	Highest count per survey	Total individuals recorded
GSW	80	87 (82.9%)	69 (86.3%)	9	187
WWW	80	47 (44.8%)	33 (41.3%)	10	121
PC	80	25 (23.8%)	22 (27.5%)	7	69
CC	57	48 (45.7%)	19 (33.3%)	19	198
PYW	57	22 (21.0%)	12 (21.1%)	3	28

Factors affecting population density

The number of plausible models (ΔAICc ≤ 2) ranged from two for Carruthers's cisticola, to five for papyrus yellow warbler (Table A1). All species showed effects of patch geometry, habitat requirements and disturbance on population density, though the direction and magnitude of their response differed between species.

Patch geometry

Patch area was contained in the top model set for all species (Table A2). Averaging of the top model set showed that the density of all but one species was positively affected by the overall size of the wetland, with higher densities in larger patches (Figure 3.2a). Only the greater swamp-warbler was negatively influenced by area, occurring at higher densities in smaller swamps (Figure 3.2a).

Wetland shape was also important for the majority of the study species. Patch circularity was in the top model set for all species, excluding papyrus canary

(Table A2). Model averaging the top model set revealed that patch shape was most important for white-winged swamp-warbler and the broad wetland species (papyrus yellow warbler and Carruthers's cisticola), with these species occurring at higher densities in patches with a higher area: edge ratio (Figure 3.2a).

Habitat requirements

Wetland composition was an important habitat requirement for all of the study species, for which papyrus mixed with other wetland vegetation (MP) was contained in the top model set (Table A2). MP negatively affected the density of all three papyrus-restricted passerines (Figure 3.2b). This effect was non-linear for white-winged swamp-warbler for which densities were only adversely affected when swamps contained high proportions of this category. The effect of MP interacted with circularity for greater swamp-warbler, with effects reversed in more circular swamps (Figure 3.2b), and interacted with patch size for papyrus canary, where the effect was only apparent in smaller swamps (Figure 3.2b). The density of Carruthers's cisticola, a broader wetland species, was slightly higher in swamps dominated by MP, particularly in more circular swamps (Figure 3.2b). Papyrus yellow warbler was the least affected by this category, occurring at only slightly higher densities in areas with low amounts of MP (Figure 3.2b) with an RI of 0.13 (Table A2).

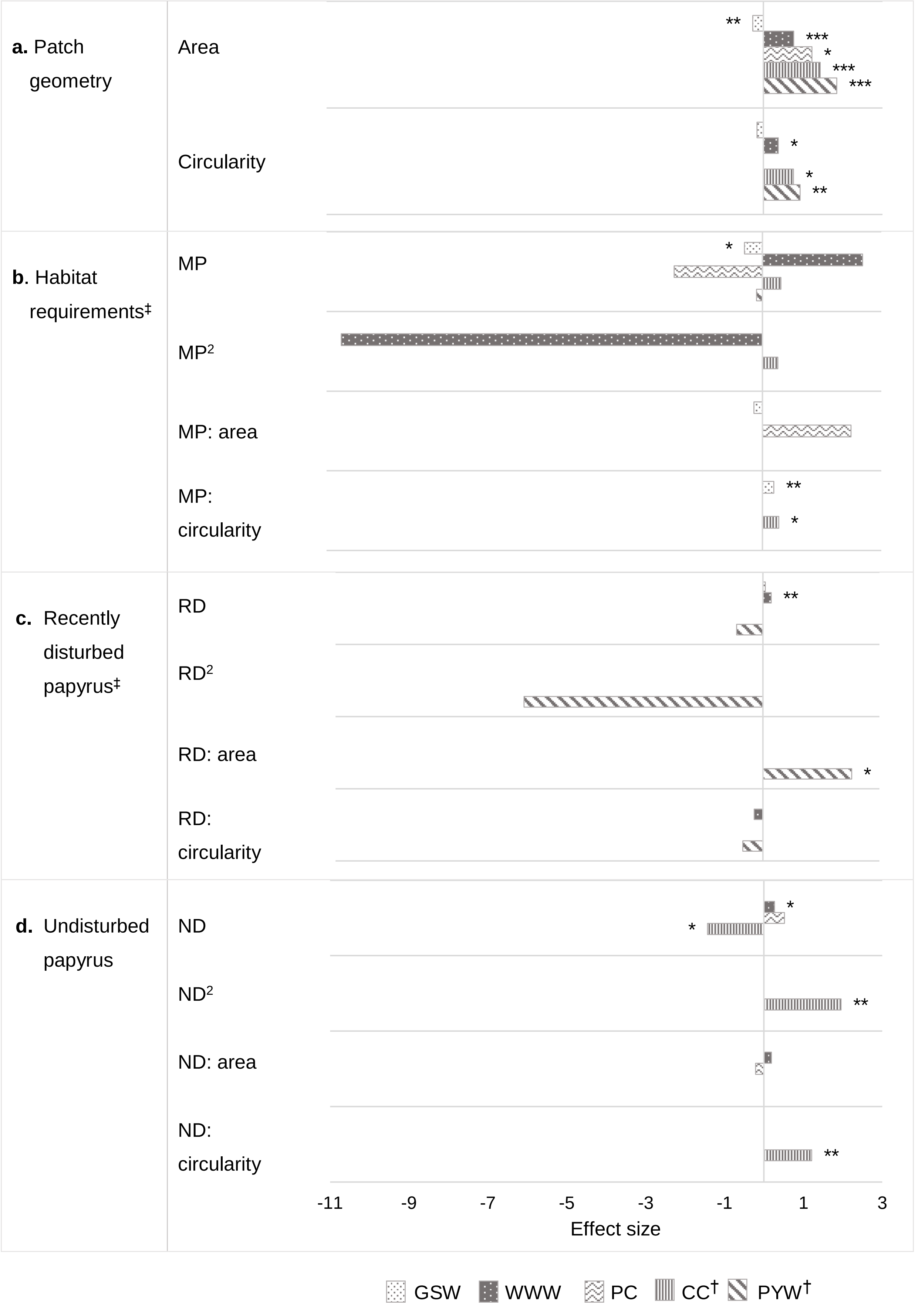

Figure 3.2. Effect sizes of model averaged coefficients (ΔAICc ≤ 2) of explanatory variables from analysis of varying vegetation types on density for each species,

displayed by category of interest: MP (mixed papyrus/vegetation), RD (recently disturbed papyrus/vegetation), ND (undisturbed papyrus); terms marked with “^{2}” represent squared term of that variable; GSW (greater swamp-warbler), WWW (white-winged swamp-warbler), PC (papyrus canary), CC (Carruthers's cisticola), PYW (papyrus yellow warbler). Bars represent the magnitude and direction of coefficients; area = log area of swamp; * significant effects where confidence intervals do not overlap with 0 ($P < 0.05, 0.01, 0.001$ represented by 1, 2 and 3 asterisks, respectively); “:” interactions with geometric variables; ‡ contains wetland dominated by other types of wetland vegetation for species which also inhabit this habitat type; † species also found in wetlands dominated by other vegetation types. See Table A2 for full model averaged output.

Effects of disturbance

Most species were positively affected by the amount of intensely disturbed habitat within the survey area and were largely unaffected by the presence of large proportions of intermediate disturbance (Figure A1). Low intensity disturbance within the survey area also did not strongly influence the density of most species, and those showing a positive relationship to undisturbed papyrus displayed a relatively weak response (Figure A1). Considering all factors together, the overall importance of disturbance differed between species, often influenced by interactions with patch geometry:

i. High intensity

The amount of recently disturbed wetland (RD) within the survey area appeared in the top model set for three of the study species (Table A2). This effect was positive for greater swamp-warbler and white-winged swamp-warbler, but with an RI of 0.24 and 1, respectively. Model-averaged results suggested that white-winged swamp-warbler occurred at significantly higher densities in areas with a high proportion of RD (Figure 3.2c). Papyrus yellow warbler showed a slight negative response to the amount of RD (Figure 3.2c). However, this effect was non-linear due to the presence of the squared term within the top model set

(Table A2), thus RD only began to negatively affect this species when there were large proportions of it within the survey area. Moreover, the direction of this effect depended on the size of the wetland (Figure 3.2c); in large swamps, large proportions of RD increased the density of papyrus yellow warbler.

ii. Intermediate intensity

The proportion of wetland disturbed in the past and regrown (PD) was the least important variable considered; only included in the top model set for papyrus yellow warbler (Table A2). Nevertheless, this term had an RI of 0.21 and was not found to be important when averaging across all models in the top model set (Table A2). As a result, all species tended to be relatively unaffected by intermediate intensities of disturbance.

iii. Low intensity

Undisturbed papyrus (ND) was in the top model set for three of the species, but unimportant for the two remaining species (Table A2). Model averaged results showed that the proportion of this category marginally influenced the number of papyrus canary (Figure 3.2d; Table A2), and had a weak positive effect on the number of white-winged swamp-warbler within the survey area (Figure 3.2d), with slightly higher densities in areas with large amounts of ND. This effect was negative for the density of Carruthers's cisticola, but as the squared term was also found to be important (Table A2), the effect was non-linear, with lower densities of this species in areas with intermediate levels of ND. Nevertheless, the direction of this effect depended on the circularity of the patch (Figure 3.2d); higher densities of Carruthers's cisticola occurred in areas with large proportions of ND in more circular patches.

Discussion

Restricting disturbance from human activities is problematic in tropical areas where people rely heavily on natural resources for their livelihoods (Hutton &

Leader-Williams 2003), and fails to consider the potential role of disturbance in maintaining biodiversity. Investigating the effects of disturbance from habitat use on papyrus-restricted avifauna, we have shown that this group of species is tolerant to some degree of disturbance and some species even benefit from it. Demonstrating that subsistence resource use can be compatible with conservation in wetland systems has the potential to increase the capacity of biodiversity conservation in tropical regions to meet the needs of both people and wildlife.

Impacts of disturbance in tropical wetlands

Habitat specialist species are thought to be the most sensitive to changes in their habitat (Ntongani & Andrew 2013), and thus papyrus-specialist passerines have been considered vulnerable to disturbance from human use (see Maclean et al. 2003a). However, the relative density of papyrus passerines within the survey area was most affected by the composition of wetland and overall size of swamps, as opposed to the level of disturbance. Should these species be adversely affected by disturbance, densities would be negatively impacted by recently disturbed and/or papyrus regrown following disturbance and positively affected by the presence of undisturbed habitat. On the contrary, papyrus disturbed in the past and regrown was not important for the density of any of the study species, highlighting that none of the species has a preference for or against papyrus that has been cut and regrown. Meanwhile, only two species (papyrus yellow warbler and white-winged swamp-warbler) responded to the amount of wetland that had been recently disturbed by cutting or burning and, consistent with occurrence data collected from large swamps across the south-west of Uganda (Maclean et al. 2006), actually appeared to benefit from cleared areas of papyrus. Given that these species are insectivorous (Britton 1978), creating open cut areas allows insects to thrive and enhances the availability of foraging for these birds. These two species also tended to prefer more circular swamps, favouring the swamp interior over the swamp edge. Open areas within the swamp could offer foraging sites that are sheltered and more secure from predators (Britton 1978). On the other hand, greater swamp-warbler preferred smaller swamps with more edge, potentially as a result of interspecific competition from the higher densities of the other species within larger swamps, and papyrus canary is known to feed on nearby crops (Britton 1971), perhaps explaining why these species appeared largely unaffected by foraging opportunities created by disturbance within swamps.

Allowing some undisturbed papyrus to remain is, however, evidently important. Papyrus yellow warbler only benefitted from intensely disturbed papyrus within larger swamps, which typically had higher proportions of undisturbed wetland, with a negative effect of intense disturbance in smaller swamps. Similarly, the density of white-winged swamp-warbler was higher in areas with large proportions of recently disturbed and undisturbed papyrus, suggesting it preferred areas with a mixture of both. The species' that appeared to benefit from the presence of large proportions of undisturbed papyrus, Carruthers's cisticola and papyrus canary, were arguably the most sensitive to disturbance. Owino and Oyugi (2008) reported that papyrus canary was sensitive to disturbance in a sample of swamps in western Kenya. Yet in the current study, each of these species were largely unaffected by both disturbed categories, suggesting that they do tolerate disturbance, providing there is some undisturbed habitat within which to nest (Britton 1978).

Species residing within papyrus swamps are likely to have evolved under a long history of disturbance and therefore, in common with temperate forest species, may have adapted to such pressures over time (Hobbs & Huenneke 1992; Bengtsson et al. 2000; O’Reilly et al. 2006). Alternatively, those most resilient to disturbance pressures remain in wetlands today (Balmford 1996). Swamps were prehistorically grazed by large herbivores such as hippopotamus (*Hippopotamus amphibious*) and exposed to natural fires (Maclean et al. 2006). Consistent with ideas from the Vera hypothesis (Vera 2000) and in common with temperate forests (see Bengtsson et al. 2000), these herbivores are likely to have maintained a more open landscape and prevented swamps from being closed, dense habitat. While the history of swamp use is undocumented in Uganda, pollen data from wetlands in the west of the country reveal evidence of human activity dating back to ca. 2200 years B.P. (Hamilton, Taylor & Vogel 1986; Taylor 1990). By creating large open cut areas of papyrus within the swamp, traditional human activities such as harvesting essentially mimic the disturbance caused by large herbivores while trampling (e.g. McCarthy, Ellery & Bloem 1998) and grazing (Boar 2006). Although most large herbivores have been lost from the region over the last 70 years, human activities ultimately replace the role of these animals in creating early successional habitat. Adopting ideas from the management of temperate systems, this has strong implications for the conservation management of wetlands in tropical East Africa.

Contrary to traditional assumptions, the results of our study suggest that the conservation of papyrus-dwelling passerines need not involve the complete restriction of natural resource use by local communities. Though our study employed proxy measures of disturbance, previous studies investigating the effects of intense forms of disturbance on papyrus birds elsewhere in East Africa also suggested levels of tolerance to low-intensity disturbance (e.g. Maclean et al. 2006; Owino and Oyugi 2008). Policy guidelines in Uganda largely recognise that papyrus extraction is a traditional activity important for the livelihoods of local people (Wetlands Inspectorate Division 2001). Yet where conservation is concerned, the principles from the “fences and fines” approach still prevail (Barrett et al. 2001), advocating that use should be restricted or prohibited (Hartter & Ryan 2010). However, providing swamps remain large and some undisturbed wetland remains, low intensity subsistence use can continue without detriment to the species dependent on it. Wetland size is often not considered within existing legislation, yet the number of interactions between vegetation category and geometry in our study highlight the need to factor wetland size or shape into policy guidelines, with evidence for greater avian tolerance to swamp structure or disturbance in larger swamps. When swamps are smaller in size, simply maintaining broad types of wetland vegetation will not suffice. Pure papyrus, as opposed to papyrus mixed among broader wetland vegetation, is important for maintaining densities of these study species, who likely require the relatively taller stands of papyrus for feeding and nesting (Owino & Oyugi 2008).

Taken together, our results support the annual rotational harvesting recommendation of Terer et al. (2012b) to maintain the biomass regeneration of papyrus following repeated destruction (Owino & Ryan 2007), ensure its availability for subsequent generations and enable sections of undisturbed papyrus to persist year-round for biodiversity. Papyrus has an exceptionally fast regeneration time, with complete regrowth within approximately 6 months of disturbance (Muthuri, Jones & Imbamba 1989). In turn, the species dependent on this habitat need only tolerate a short period of time when sections of their habitat have been cleared. Governance in Uganda has taken a decentralized approach whereby wetland management is often controlled in a hierarchy from district to village level (Maclean, Boar & Lugo 2011) which, within our study area, allows swamp users to cooperate to ensure sufficient resources remain for others nearby (Maclean et al. 2003d) and permits regrowth of alternate harvested areas between years. Application of these self-regulation methods across East Africa could be key both for continued subsistence resource use and the persistence of wetland specialist birds (Shiferaw 2006; Maclean, Boar & Lugo 2011).

Habitat loss is currently one of the main threats to papyrus in south-west Uganda (Maclean, Bird & Hassall 2014) leading to the removal of swamps, the reduced overall size of wetlands and an increased level of fragmentation across the landscape (Fahrig 2003; Owino & Ryan 2007). We have highlighted that densities of each species, with one exception, are higher within larger swamps and, in consequence, the drainage of larger swamps will have a disproportionately adverse effect on regional populations. Low intensity subsistence use of papyrus, on the other hand, results in temporary disturbance to the swamp as opposed to permanent removal following reclamation for crop production (Boar 2006). While swamp drainage for agriculture will continue to have a damaging effect on biodiversity, resource extraction is less problematic and can even be beneficial. Thus, subsistence harvesting can persist within larger swamps where species are tolerant of such disturbances, while use should be discouraged from smaller swamps where the impacts have the potential to be more detrimental. Previous work demonstrates that sustainable use of this kind can be more profitable for people, since the net present value of harvested papyrus and fish far exceeds that of crops obtained from drained swamp land (Maclean et al. 2003c).

Implications for conservation

Conservation in the tropics often views the needs of people as a trade-off with those of biodiversity. Although it is now generally accepted that conservation should involve communities, with the Convention on Biological Diversity (CBD) encouraging this approach (Berkes 2007), restrictions on natural resource use still prevail. The United Nations (UN) recognises the need to achieve a balance between poverty reduction and ecosystem conservation (Senaratna Sellamuttu, de Silva & Nguyen-Khoa 2011), yet managing systems to meet demand without detriment to biodiversity conservation is a challenge (Senaratna Sellamuttu, de Silva & Nguyen-Khoa 2011) that has been the focus of little investigation.

Using evidence from papyrus avifauna, we have shown that conservation in tropical wetlands need not require complete exclusion of human resource use. As with temperate forest systems, traditional human activities can mimic former natural forms of disturbance, creating open areas of habitat which may benefit biodiversity. Future work is needed to establish the applicability of this conclusion to other wetlands in East Africa and more widely. The productivity and regrowth of other wetland vegetation can be similar to that of papyrus (Muthuri, Jones & Imbamba 1989) and other macrophytes experience comparable forms of disturbance because of the socio-economic uses they provide (Terer, Triest & Muasya 2012). Hence, the possible effects of disturbance on both local livelihoods and conservation in other wetlands merits further research.

The long history of human activity is well-documented across Africa (Hamilton, Taylor & Vogel 1986) and other tropical regions (e.g. Heckenberger et al. 2003). Given the potential to mimic decreasing natural disturbances, conservation in the tropics, particularly of other wetlands, will benefit from acknowledging that human activities can play a role in maintaining biodiversity. Rather than promoting alternative livelihoods as a means to promote biodiversity conservation (Brown 2002), emphasis could be placed on understanding and documenting the past history of disturbance in tropical habitats and the impacts of low-intensity natural resource use on biodiversity, without the *a priori* assumption that all disturbance is detrimental. Due to the need to support rural livelihoods, “conservation through use” (Brown 2002) may in some instances prove to be of direct benefit to biodiversity, rather than a separate poverty-alleviation objective. Strong consideration for local livelihoods is also likely to lead to greater support for conservation (Spiteri & Nepalz 2006), helping to minimise conflict between people and biodiversity conservation (Senaratna Sellamuttu, de Silva & Nguyen-Khoa 2011).

Conclusion

This study highlights the potential to combine subsistence resource use and conservation management in tropical wetland systems. Using papyrus swamps as a case study, we demonstrate that specialist species can tolerate disturbance, possibly as a result of the historic disturbance of papyrus, even prior to inhabitation by humans. Striving to conserve wetlands and the biodiversity dependent on them does not necessarily involve the complete restriction of people who rely on the resources they provide. Instead, the disturbance that results from such activities may be of benefit to biodiversity and can be incorporated into the conservation management of tropical systems such as wetlands, creating a win–win situation for both wildlife and people.

Chapter 4:

Quantifying resistance and resilience to extinction for the conservation prioritisation of papyrus-endemic birds

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Abstract

Limited conservation resources and ambitious biodiversity targets necessitate effective and efficient conservation planning. Traditional approaches to this often focus on reducing the extinction risk of species at designated sites. However, with increasing levels of habitat fragmentation from land use change, and pressures from climate change and overexploitation, the surrounding landscape context will likely play a key role in encouraging the persistence of species populations. In the context of metapopulation theory, we present a framework for quantifying the resistance and resilience of populations, depending on their probability of survival (resistance) or of reestablishment (resilience) following localized extinction events. We explore the application of this framework to guide the conservation of a group of bird species endemic to papyrus (*Cyperus papyrus*) swamps in East and Central Africa, which are threatened from habitat loss and degradation and currently receive little protection. Using occupancy data collected over two years from a network of wetlands in south-west Uganda, we determine the local and landscape factors that influence local extinction and colonization for each species, and map the predicted levels of turnover across the network, in order to draw inferences about the locations which contribute most to regional resistance and resilience for all species combined. Slight variation in the factors driving extinction and colonization led to varying spatial patterns of site-level resistance and resilience between species. Despite this, locations with the highest resistance and/or resilience overlapped for multiple species in several parts of the landscape, highlighting where efforts could be focused to enhance the capacity of species to adapt and respond to future change. Overall, we emphasize the ability of this landscape-scale perspective to aid decision-making

associated with conservation planning and prioritisation for multiple species residing in overlapping, fragmented landscapes.

Introduction

Global biodiversity is declining at an unprecedented rate (Newbold et al. 2015), yet the resources available to counteract this loss are finite and insufficient to ensure that ambitious global biodiversity targets are met (McCarthy et al. 2012). Establishing protected areas, defined by the Convention of Biological Diversity (CBD) as geographic locations that are “designated or regulated and managed to achieve specific conservation objectives", is one of the main approaches for the safeguarding of biodiversity. The importance of these sites is recognised globally, with signatories to the CBD aiming to safeguard 17% of terrestrial land and inland water by 2020 as part of the Aichi Biodiversity Targets (CBD 2011). Priority sites such as Important Bird and Biodiversity Areas (IBA’s) (Fishpool & Evans 2001) and Alliance for Zero Extinction Sites (Ricketts et al. 2005), have been developed to ensure efforts are directed towards the most important locations for biodiversity. The designation and management of such areas is focused around boosting populations at individual sites to secure survival (Geldmann et al. 2013). However, landscapes are becoming increasingly fragmented as a result of changing land use practice (Newbold et al. 2015), while pressures are growing from climate change (Urban 2015) and overexploitation (Millennium Ecosystem Asessment 2005; WWF 2014). As a result, species may not remain within individual designated sites indefinitely, and the surrounding landscape context will likely play a key role for the regional persistence of species.

The theories of island biogeography and metapopulation dynamics have been influential for reserve design and management (Diamond 1975; Hanski 1994a; Akcakaya, Mills & Doncaster 2007). The principles associated with these theories state that long-term persistence is dependent on balancing the processes of local extinction and colonization within sites across the landscape (Hanski 1998a). In general, small and/or low quality sites are at risk of extinction as a result of small populations, while poorly connected sites are unlikely to be recolonized should extinction occur (MacArthur & Wilson 1967; Hanski 1999a; Thomas et al. 2001). These concepts have been pivotal for site-based design and more recently the establishment of landscape-scale conservation initiatives (see Donaldson, Wilson & Maclean 2017), though deciding which sites to invest in is complex (Hannah 2008) and remains the focus of much research (Whytock et al. 2017). Although it was originally suggested that various species respond similarly to the local and landscape effects driving the processes of extinction and colonization (Hanski 1994a), this remains untested in a variety of taxa (Whytock et al. 2017). Considering the rapid rates of habitat loss and degradation worldwide, combined with limited budgets to combat such threats, finding efficient ways to identify and protect the key sites that sustain multiple species is paramount.

In essence, the factors influencing the importance of an individual site for the regional or landscape-scale conservation of a species can be partitioned into: a) the resistance of the local population to extinction (Lawler 2009; Lake 2013), and hence the chances that the population persists through unfavourable periods or is able to act as a source for the (re)colonization of other sites; and b) the resilience of the population to disturbance (Holling 1973; Lake 2013) (also termed "recovery" [Hodgson et al. 2015]), which in the context of metapopulation dynamics, can refer to the chances that a site will be recolonized following local extinction. Quantifying resistance and resilience from this perspective could prove a useful tool for conservation planning, ensuring that sites designated for conservation are not only robust to change, but have the capacity to bounce back from change should local extinction occur (Lawler 2009; Nimmo et al. 2015). To make use of this framework and ultimately identify areas in which to invest conservation effort, an understanding of the factors that lead to resistance and resilience is required. Thus far, the extent to which the factors driving these respective site attributes differ within and between species has seldom been recognised, yet would provide valuable insight into the habitat characteristics and configuration that best ensures the regional persistence of multiple species (Nimmo et al. 2015).

We present a novel framework for determining landscape-scale resistance and resilience for a group of bird species endemic to papyrus (*Cyperus papyrus*) swamps in East and Central Africa. Papyrus is a highly fragmented habitat that has been experiencing rapid loss and degradation over recent decades, primarily from drainage and encroachment for commercial and subsistence agriculture (Maclean, Wilson & Hassall 2011; van Dam et al. 2014). This has led to the decline in populations of specialist bird species (Maclean, Bird & Hassall 2014) and the inclusion of some of these species on the IUCN Red List (IUCN 2017b). Papyrus swamps are recognised as a regional conservation priority but as yet receive little protection (Fanshawe & Bennun 1991; Kipkemboi & van Dam 2016), and evidence for where protected areas should be designated is scarce. Current approaches toward the safeguarding of biodiversity within these swamps are based on conventional methods; sites hosting high numbers of birds, for example, are regarded as priority areas for conservation (Maclean, Wilson & Hassall 2011). However, this fails to recognise either the resistance of individual sites, their resilience to unfavourable environmental extremes or changes to management, and their sensitivity to the persistence of other sites within the larger network. Papyrus swamps are exposed to frequent disturbances (Maclean et al. 2003a, 2006), seasonal drainage (Zsuffa *et al.* 2014), and will likely be subject to altered hydrology as the climate changes (Terer et al. 2012). As a result, safeguarding a network of sites, where occupied sites can act as source populations for those subject to periodic or stochastic extinction (Akcakaya, Mills & Doncaster 2007), will help ensure populations can bounce back from disturbances that lead to localized population declines or extinctions. With multiple species utilising the same landscape, an understanding of the main factors that influence the population establishment and survival of each species, and the implications of any notable differences between species, is required for the identification of important sites.

Here, we use occupancy data for five species of papyrus-endemic passerines collected from a network of swamps in south-west Uganda, to determine the local and landscape effects that influence extinction and colonization for each species. We then map the predicted probabilities of survival and colonization for each patch across the network, and use this to draw inferences about the locations and landscapes which contribute most to regional resistance and resilience for each species, and whether there is spatial congruence in these among species. We conclude by compiling this information for all the study species, to establish the potential for investing in sites that are likely to ensure resistance and resilience for specialist species in the network, and discuss the potential wider application of this framework for conservation planning and prioritisation.

Methods

Study system

Papyrus swamps host a suite of endemic passerines with distributions largely focused around parts of East and Central Africa (Maclean, Bird & Hassall 2014). This study focused on 5 papyrus species: white-winged swamp-warbler (*Bradypterus carpalis*), greater swamp-warbler (*Acrocephalus rufescens*) (race *foxi*), papyrus canary (*Crithagra koliensis*), papyrus yellow warbler (*Calamonastides gracilirostris*) and Carruthers's cisticola (*Cisticola carruthersi*). All species are primarily restricted to papyrus, although papyrus yellow warbler and Carruthers’s cisticola are also known to inhabit wetland dominated by other vegetation types, namely *Miscanthidium* and *Typha* spp., when closely associated with papyrus (Vande weghe 1981). Previous work has shown that white-winged swamp-warbler, Carruthers’s cisticola and papyrus yellow warbler preferentially inhabit the wetland interior, while the remaining two species are more often associated with swamp edge (Britton 1978; Donaldson et al. 2016). The species are also likely to differ in dispersal propensity (see below and Chapter 5).

Data collection

Data was collected over 2 consecutive years (2014-2015) across a network of papyrus swamps surrounding Lake Bunyonyi, Uganda (01°17’S 29°55’E). High densities of papyrus are found in this area, growing along deep valley bottoms and along the lake edge. The presence of some of the papyrus-specialist birds has led to the designation of an IBA at the far north of the lake (BirdLife International 2017b), while others have been proposed (Maclean, Bird & Hassall 2014). All patches of papyrus swamp within the network were located using topographical maps (Department of Land and Surveys, Entebbe), satellite imagery (Google Earth), local knowledge, and examination from motorboat and on foot. For the purpose of this study, following preliminary observations, a habitat patch was defined as wetland approximately >20 m long and >5 m wide suitable for breeding birds, separated by >10 m from other patches. Swamps dominated by other wetland types (here termed “broader wetland vegetation”) were included in the study for the two species inhabiting this habitat type. Carruthers’s cisticola was also found in areas of wetland recently converted to agriculture in this area (Donaldson et al. 2016). Shoreline fringing patches were surveyed for the presence of greater swamp-warbler and papyrus canary, as preliminary observations over the 2 years confirmed that only these species were ever located within this patch type.

Between 2014 and 2015, 232 papyrus swamps, 287 shoreline fringing papyrus patches and 177 broad wetland patches (including papyrus) were surveyed. All patches were visited at least once per year by the same observer during the main breeding season (May – August), and the presence or absence of each species recorded. Surveys were conducted between ~06.45 and ~13.45 when the birds are most vocal, using intermittent playback to aid detection. Time spent surveying varied with patch size, ranging from a minimum of 5 minutes for small, low quality shoreline fringing patches, to a maximum of 7 hours 15 minutes for large broad wetland patches (see Table B1 in Appendix B). All of the study species are highly vocal, and almost always readily detectable within short periods of visiting the site (Maclean et al. 2006). However, to provide more formal evidence of this, we examined relationships between likelihood of detection and survey effort (Appendix B), which highlight that the probability of incorrectly recording a species as absent when present during an average survey, was relatively small (Figure B1).

On the day of survey, coordinates were recorded from the edge of swamps in the UTM projection system using a handheld GPS unit (Garmin GPSMAP 64, Lenexa, KS), and sketch maps of the swamp were drawn to scale using topographical maps. Four distinct vegetation categories were assigned based on vegetation height and composition (Table 4.1, and see Muthuri et al. 1989; Maclean et al. 2006; Terer et al. 2012; Donaldson et al. 2016) and the proportion of each estimated at each site. All maps were digitized in ArcGIS v 10.1 (RGDC 2005 UTM 35S) and used to estimate patch size, circularity (defined using the formula $4\pi \text{area}/\text{perimeter}^2$) and nearest edge distances between patches.

Table 4.1. Vegetation categories defined for papyrus swamp and broad wetland[†]. See Donaldson et al. (2016) for further details.

Vegetation category	**Description**	**Age**	**Density**	**Typical height**	**Culm thickness**	**Senescence?**
Disturbed wetland	Cleared (harvested, burnt), immature and/or regrown papyrus[†], agricultural wetland[‡]	0-1 year	None (cleared)-high (regrown)	Low (0-2m) to high (> 2m)	Thin	None
Moderately disturbed wetland	Mature papyrus previously disturbed and fully regrown to maturity	>1 year	Moderate	High (>2m)	Thick	Some
Undisturbed wetland	Mature papyrus, not likely to be disturbed, any disturbance over 1.5 years ago	>1.5 years	Low	High (>2m)	Thick	Yes
Mixed vegetation wetland	Mixed wetland vegetation containing >40% papyrus[†], poor growing conditions for papyrus	>1 year	Low	Low (0-2m)	Thin	Some

[†]Includes wetland dominated by other wetland types for two species also found in these areas (Carruthers's cisticola and papyrus yellow warbler) (Maclean et al. 2006); [‡]Applicable to Carruthers's cisticola only

Analyses

Two sets of analyses were undertaken to investigate the potential drivers of patch i) colonization (determining “resilience”) and ii) survival (as a proxy for “resistance”). All analyses were performed in R version 3.3.1 (R Core Team 2016) using generalized linear models with a binomial error distribution and logit link function. The response variable was the presence or absence of each species in year 2 (2015). Models of colonization were conducted on patches in which the species was absent (0) in year 1 (2014), and either present (1) or absent (0) from those patches in year 2. Models of extinction were based on patches where the species was present (1) in year 1, and either absent (0) or present (1) in year 2.

Explanatory variables in both sets of analyses involved local and landscape factors from data collected in 2015. Relative patch size was similar between years (R^2=1.0; Table C1) and as the relative proportion of disturbed habitat per patch differed over the study period (papyrus: R^2=0.3, broad wetland: R^2=0.2; Table C1), using habitat data collected in year 2 enabled us to most accurately capture the change in occupancy that occurred over the one year examined. Local variables analysed were patch size (ha), patch circularity and the proportion of 3 distinct vegetation categories: disturbed wetland, undisturbed wetland, and mixed wetland vegetation (Table 4.1). To avoid over-fitting models, which would result if the sum of all categories is always one, moderately disturbed wetland was excluded from the analysis (see also Donaldson et al. 2016). Landscape variables comprised a measure of the functional connectivity of patch *i* as described by (Hanski 1994b):

$$Si(t) = \sum p_j exp\left(-\alpha d_{ij}\right) A_j^b \tag{1}$$

where p_j is the occupancy of patch *j* in year 1 *(t)*, *α* is a parameter that defines the dispersal kernel, d_{ij} is the nearest edge distance of the focal patch *i* to other patches *j*, A_j is the carrying capacity of patch *j,* usually approximated by area (but see below) and *b* is a scaling function for patch emigration (*i≠j*). The parameter *α* was estimated for each species using the Markov Chain Monte Carlo technique available in SPOMSIM (Moilanen 2004) (see Chapter 5 for details): greater swamp-warbler = 0.204, papyrus canary = 0.190, Carruthers's cisticola = 0.070, white-winged swamp-warbler = 0.021, papyrus yellow warbler = 0.001*.* In metapopulation models, A_j is typically defined as patch area, as a proxy for population size (Ozgul et al. 2006). However, as shown in Donaldson et al. (2016), the density of birds at each site varies depending on a variety of other factors in addition to patch size. Thus, the density of all species was predicted at each site using the model averaged coefficients obtained in Donaldson et al. (2016) from point count survey data (see Appendix A), and weighted by multiplying by patch size as an estimate of the *relative* population size for each species within each patch (A_j). The parameter b was set to 1, assuming that emigration is proportional to abundance.

Exploratory analysis was conducted to determine the importance of intermediate levels of each vegetation type. Models containing each individual vegetation category (disturbed wetland, undisturbed papyrus and mixed vegetation) as linear predictors were tested against models that also contained each predictor as a squared term. The squared terms were subsequently retained in the global model when the Akaike Information Criterion (AIC) value obtained from the model including this term was lower than without (Burnham & Anderson 2002). The MuMIN package in R (Barton 2014) was used to create all possible combinations of the global model, including any relevant squared terms for the survival and colonization datasets (Table C2). Models were ranked by AICc (AIC adjusted for small sample size) and a set of models within ΔAICc ≤ 2 of the top model created for each species (Burnham & Anderson 2002). Model averaging was performed across all models within the top ranked set to obtain parameter estimates, and the relative importance (RI) of each term within the top set was recorded (Burnham & Anderson 2002; Johnson & Omland 2004). Full model averaged coefficients were used to predict the probability of colonization and survival of each patch across the network, based on patch data collected from the 2015 survey. Semi-variograms of the residuals from the predicted vs observed values for each dataset were created using the geoR package in R (Ribeiro Jr & Diggle 2001), confirming that there was no evidence of spatial structure in our models (Figure C1).

In order to identify if each patch was most prone to experiencing colonization, extinction, or both, we categorized all patches based on their predicted levels of colonization and extinction over a period of one year. The possible space within the colonization/survival axes was divided into four quadrants for illustrative purposes (Figure 4.1). Patches with a higher probability of colonization can be classed as more “resilient” than those with a lower chance of colonization, while patches with a relatively high probability of survival represent sites with a higher level of “resistance” than those with a high chance of local extinction (Figure 4.1). At present, patches with a relatively high chance of both survival (if occupied) and recolonization (if unoccupied), can be considered “supported” by metapopulation dynamics in these systems, and both resistant and resilient to extinction. Conversely, patches with a low chance of both survival (if occupied) and recolonization (if unoccupied), can be considered “marginal” (Lawson et al. 2012) (Figure 4.1). All patches and their corresponding status were mapped across the network to recognise areas of importance for regional persistence.

Finally, the capacity to conserve multiple species was determined using overlapping maps of resistance and resilience for each species. The number of species within each of the predicted categories for a given patch was mapped across the network of papyrus patches. Since multiple papyrus patches were often located within larger broad wetland sites, the predictions for the two broad wetland species (papyrus yellow warbler and Carruthers’s cisticola) for a given wetland were allocated to those papyrus patches within that particular swamp, in order for the networks for all species to be directly comparable. Similarly, shoreline fringing patches were marked as “marginal” for the 3 species that did not utilise these patches, on the overlapping plots only.

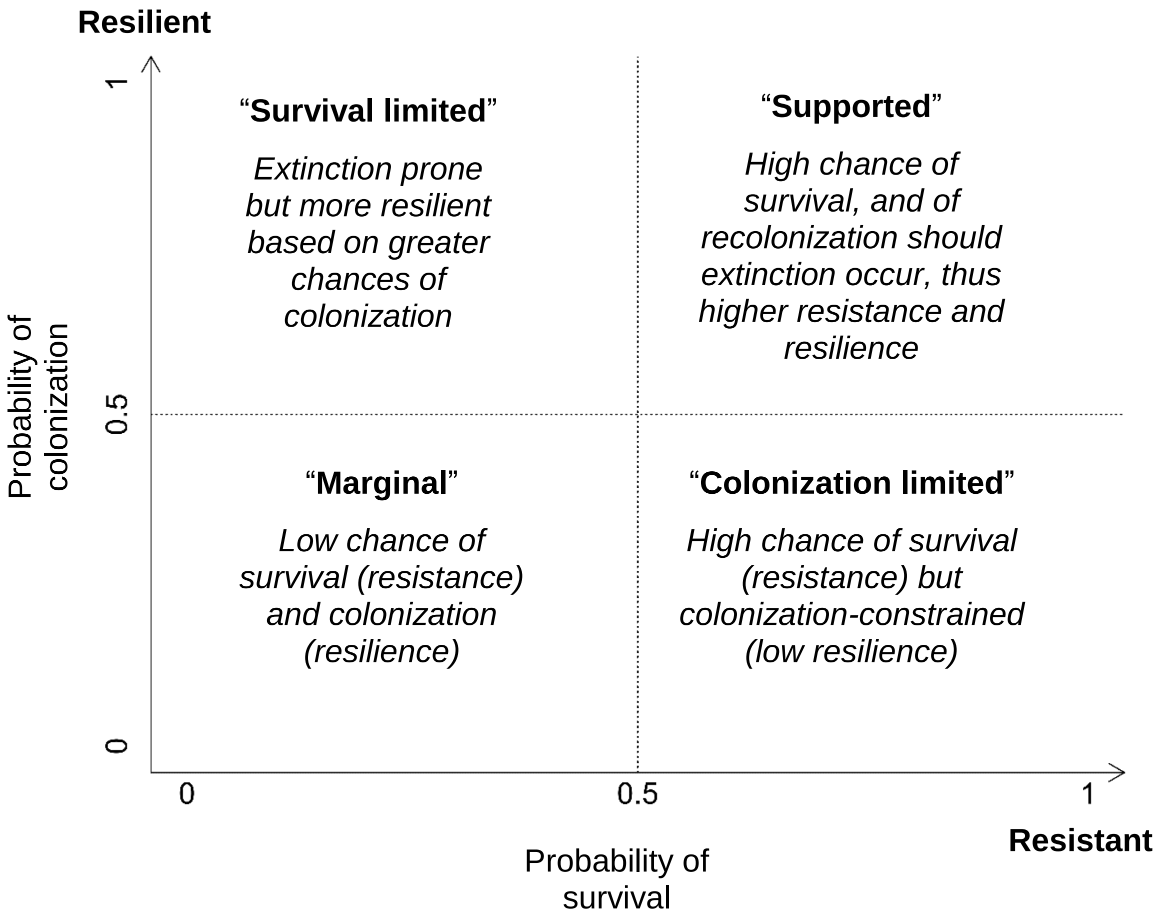

Figure 4.1. Categories based on predicted levels of colonization and extinction using 0.5 probability. Categories are shown in bold and descriptions provided in italics.

Results

Survey data

The number of colonized patches ranged from 3 for white-winged swamp-warbler to 69 for greater swamp-warbler, and the number of local extinction events ranged from 3 for papyrus yellow warbler and 4 for Carruthers’s cisticola, to 63 for greater swamp-warbler (Table 4.2; Figure C2).

Table 4.2. Presence-absence survey data for suitable patches for each species from 2014–2015: greater swamp-warbler (GSW), papyrus canary (PC), white-winged swamp-warbler (WWW), Carruthers's cisticola (CC), papyrus yellow warbler (PYW).

Species	Patches surveyed	Colonized	Survived	Extinct	Vacant
GSW	519*	69	206	63	181
PC	519*	44	40	16	419
WWW	232	3	41	12	176
CC	160†‡	8	31	4	117
PYW	177†	10	17	3	147

*Includes shoreline fringing patches; †Includes broad wetland vegetation; ‡ Includes agricultural wetland

Patch survival and colonization for papyrus endemic birds

The number of models within the top model set (ΔAICc ≤ 2) for the colonization analysis was 13 for greater swamp-warbler, 5 for white-winged swamp-warbler, 9 for papyrus canary, 3 for Carruthers's cisticola and 5 for papyrus yellow warbler. All species were more likely to colonize large swamps (RI = 1; see Table C3 for all output for colonization analyses described), though patch size was not classed as significant[1] for white-winged swamp-warbler (RI=0.34). Probability of colonization was higher within more connected patches for greater swamp-warbler (RI=1) and Carruthers's cisticola (RI=1), but this term was not found in the top model set for white-winged swamp-warbler or papyrus yellow warbler, and did not significantly influence colonization for papyrus canary (RI=0.28). More circular patches were more likely to be colonized by Carruthers's cisticola (RI=1), and white-winged swamp-warbler (RI=1), but not by papyrus canary (RI=0.71), greater swamp-warbler (RI=0.15) or papyrus yellow warbler (RI=0.12). For all species studied, patch colonization was not significantly influenced by the proportion of disturbed or undisturbed wetland. Both variables were found in a small number of models within the top set, but did not have high relative importance, with the exception of papyrus canary (undisturbed vegetation; RI=1),

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[1] 95% confidence intervals do not cross 0.

and were not found to be significant after averaging the top model set (Table C3). The probability of colonization was positively affected by the proportion of mixed papyrus vegetation for white-winged swamp-warbler only (RI=1).

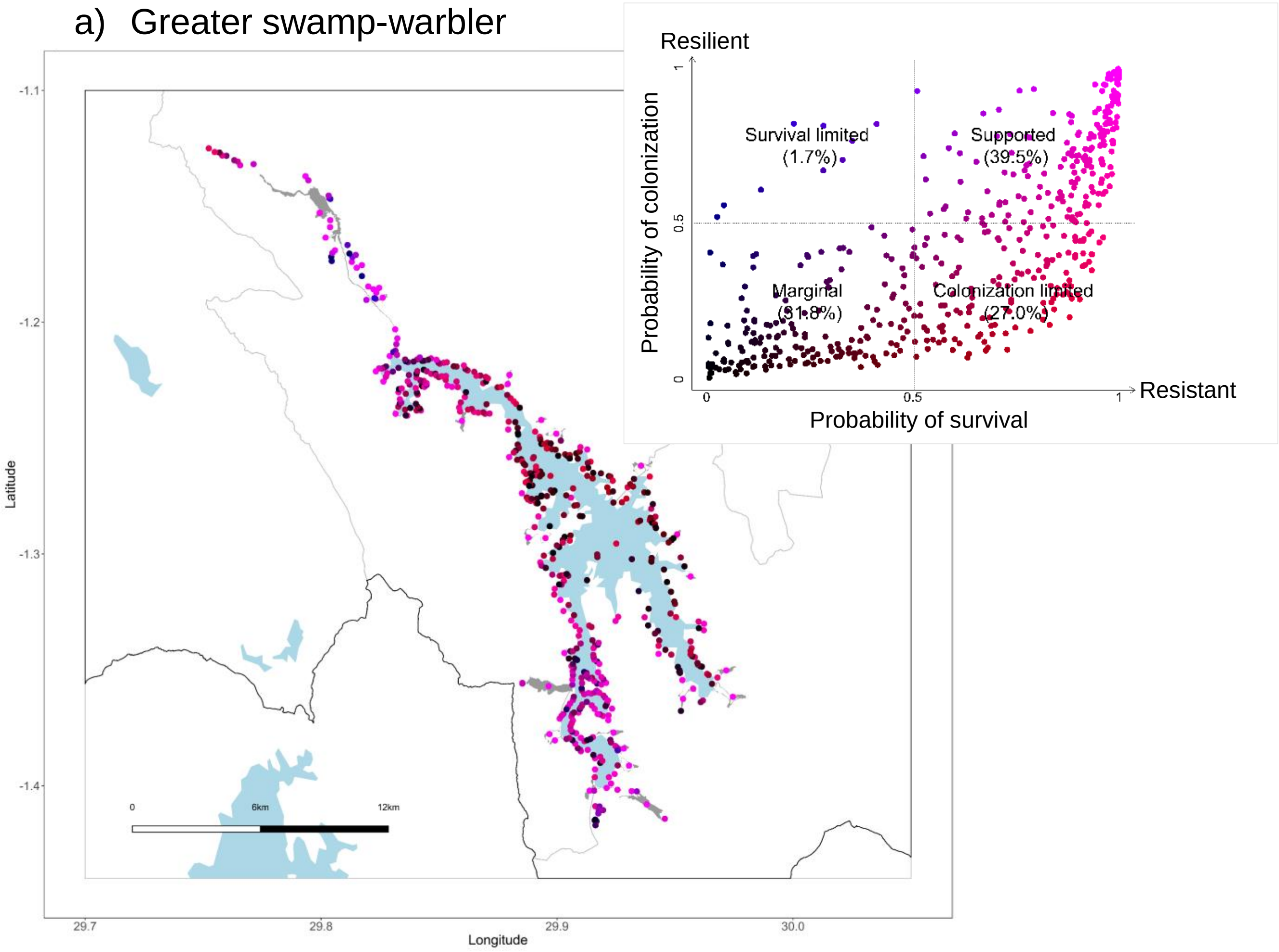
The top set for the survival analysis included 10 models for greater swamp-warbler, 4 for white-winged swamp-warbler and papyrus yellow warbler, and 2 for papyrus canary and Carruthers's cisticola. All species were more likely to survive in large patches, although this was not significant for Carruthers's cisticola (RI=1) or papyrus yellow warbler (RI=0.87; see Table C4 for all output for survival analyses described). Population survival was also more likely in less circular patches for greater swamp-warbler (RI=1), and in more circular patches for white-winged swamp-warbler (RI=1). As with colonization, the level of disturbance within the patch did not significantly impact the chance of survival for any of the species. Disturbed wetland was only in the top set for greater swamp-warbler (RI 0.42) and papyrus yellow warbler (RI = 0.28), while undisturbed wetland was in the top model set for greater swamp-warbler (RI = 0.93), white-winged swamp-warbler (RI = 0.19) and papyrus yellow warbler (RI = 0.3). The proportion of mixed papyrus within a patch negatively influenced the chance of survival for 3 of the species, shown to be marginally significant for papyrus canary (RI = 1), but not significant for greater swamp-warbler (RI = 1) or white-winged swamp-warbler (RI = 0.17). Finally, the probability of survival within a patch was not influenced by connectivity for any of the species (greater swamp-warbler: RI = 0.26; papyrus canary: RI=0.28; white-winged swamp-warbler: RI=0.22; Carruthers's cisticola: RI = 0.55).

Predicted turnover across networks

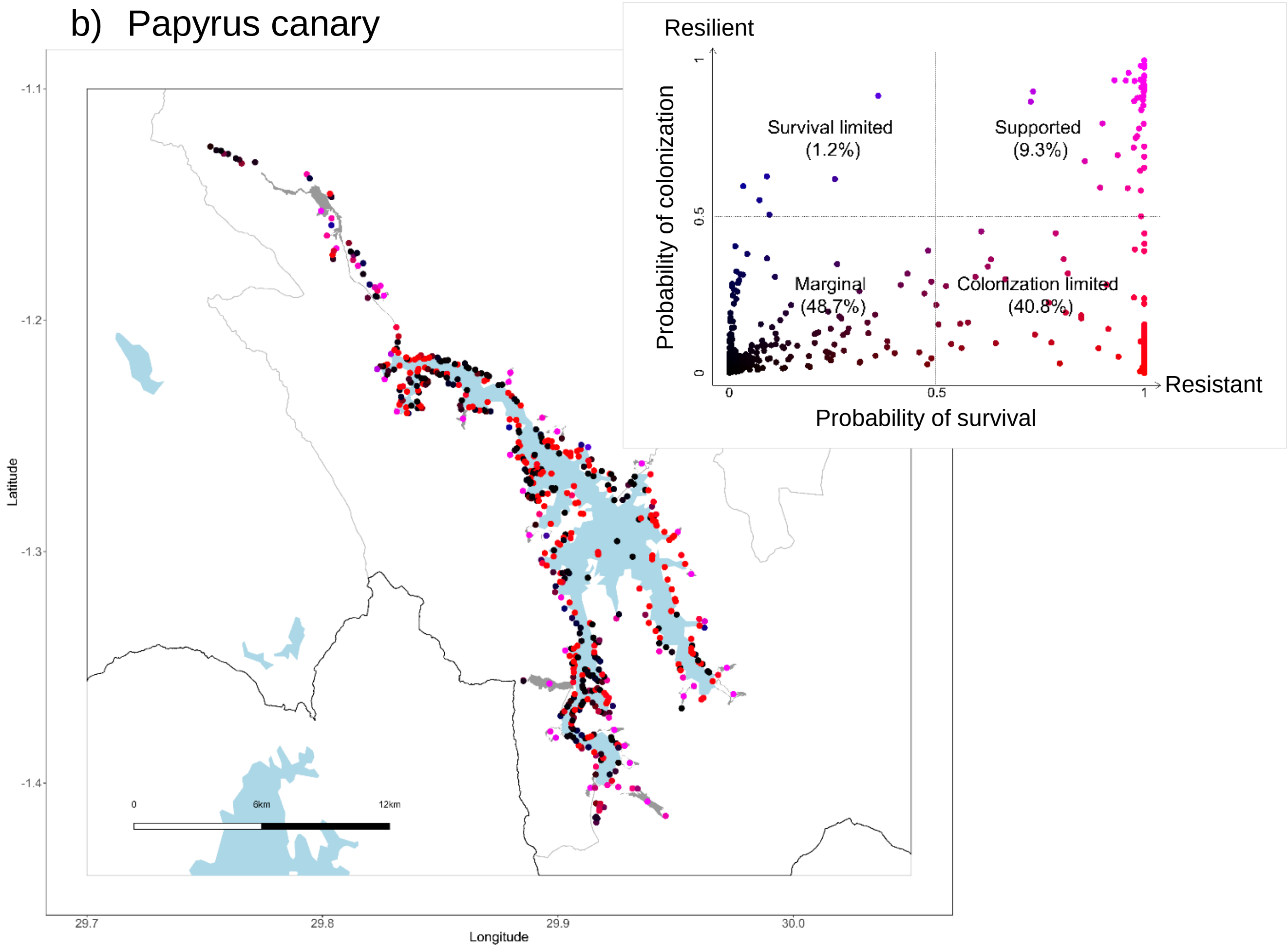
The probability of survival and colonization for each species within each patch was predicted across the swamp network, and the position of each patch in the space defined by the survival and colonization probability axes was recorded (Figure 4.2a-e). The proportion of patches in the network that exceeded 0.5 for survival and colonization, ranged from 39.5% of patches for greater swamp-warbler (Figure 4.2a), to just 0.4% for white-winged swamp-warbler (Figure 4.2c). These were distributed throughout the network for all species, though strongholds were apparent in the far north and south of the lake for greater swamp-warbler, while the only “supported” patch for white-winged swamp-warbler was located in the centre. In contrast, all species were predicted to have a very high number of “marginal” patches which had a limited probability of colonization and extinction, thus were relatively less resistant and resilient. This ranged from 31.8% of the network for greater swamp-warbler (Figure 4.2a), to 76.8% of the network for papyrus yellow warbler (Figure 4.2d). These were well spread throughout the network, most notably along the central edges of the lake.

Comparing the two limited categories, considerably more patches were limited primarily by colonization (low resilience) than survival (low resistance). No patches for white-winged swamp-warbler (Figure 4.2c) or papyrus yellow warbler (Figure 4.2d) were limited by survival, while just 0.6% of patches for Carruthers’s cisticola (Figure 4.2e), 1.2% for papyrus canary (Figure 4.2b) and 1.7% for greater swamp-warbler (Figure 4.2a) were limited by survival alone. Meanwhile, the percentage of patches limited by colonization ranged from 2.5% for Carruthers’s cisticola (Figure 4.2e) to 40.8% for papyrus canary (Figure 4.2b). Survival limited patches were often located close to supported patches for all species. Colonization limited patches, on the other hand, appeared to be focused around the centre of the network for greater swamp-warbler (Figure 4.2a) and papyrus canary (Figure 4.2b), clustered towards the north and south of the lake for papyrus yellow warbler (Figure 4.2d), and spread throughout the network for white-winged swamp-warbler (Figure 4.2c).

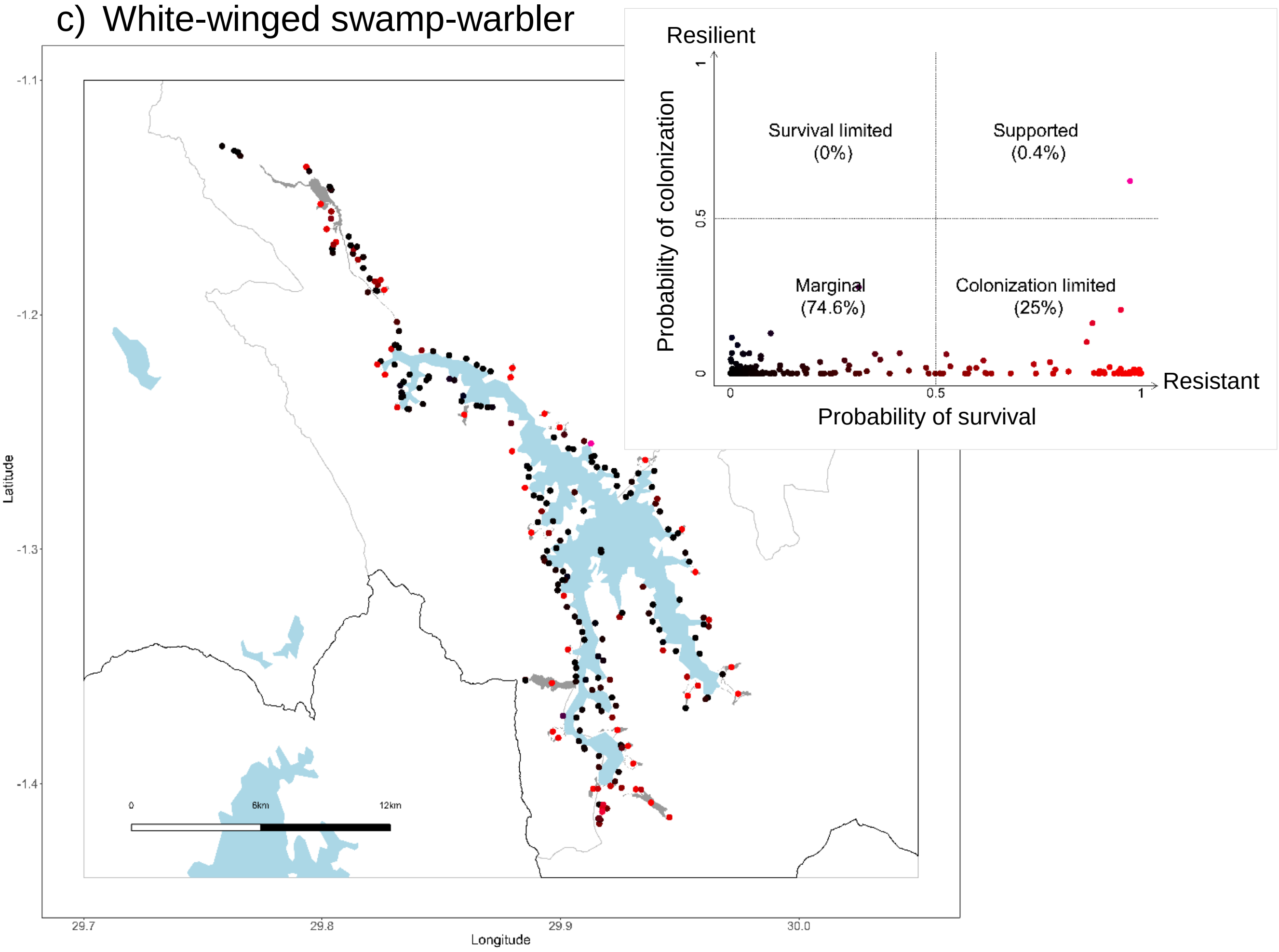
a) Greater swamp-warbler



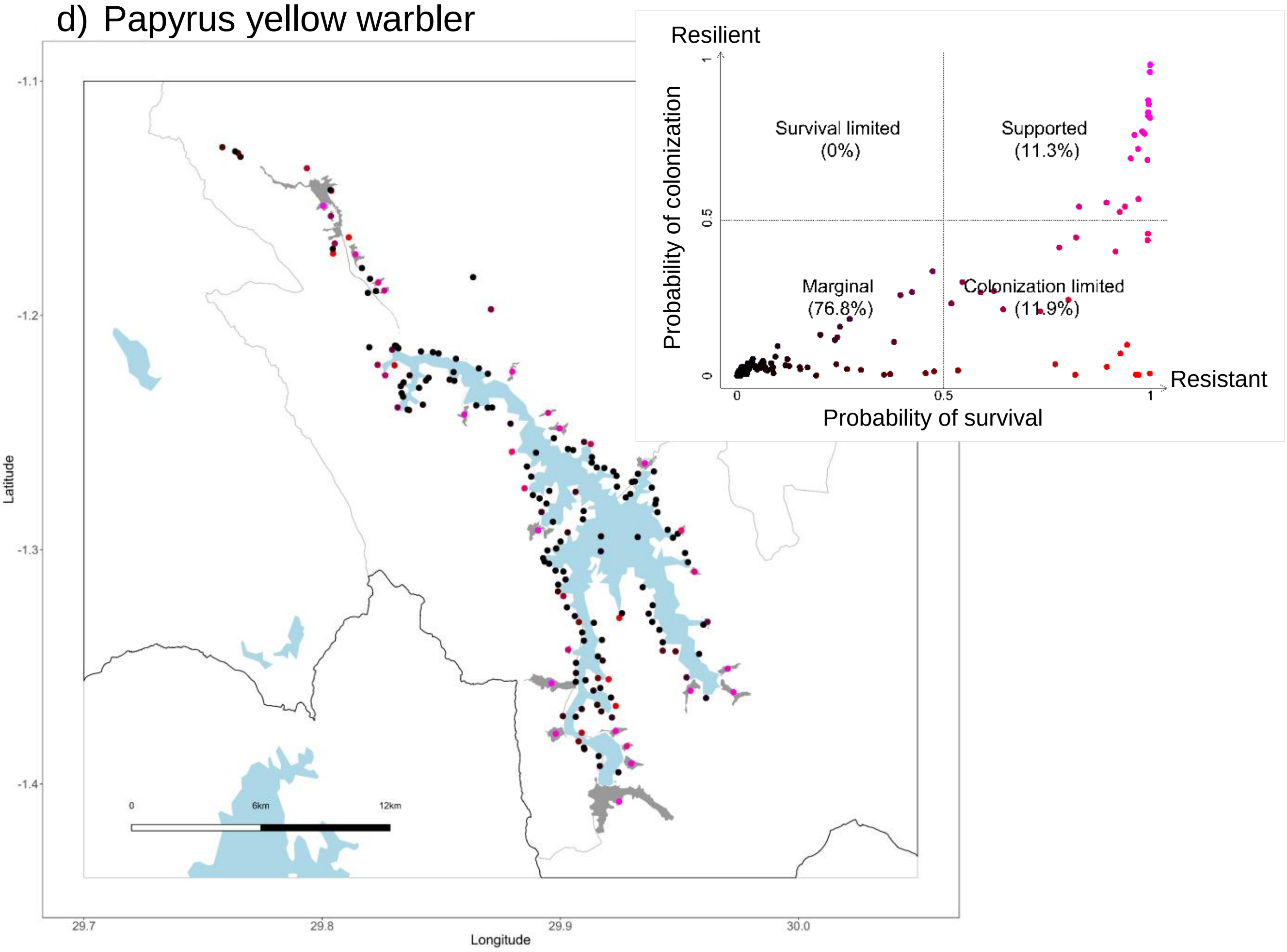
b) Papyrus canary

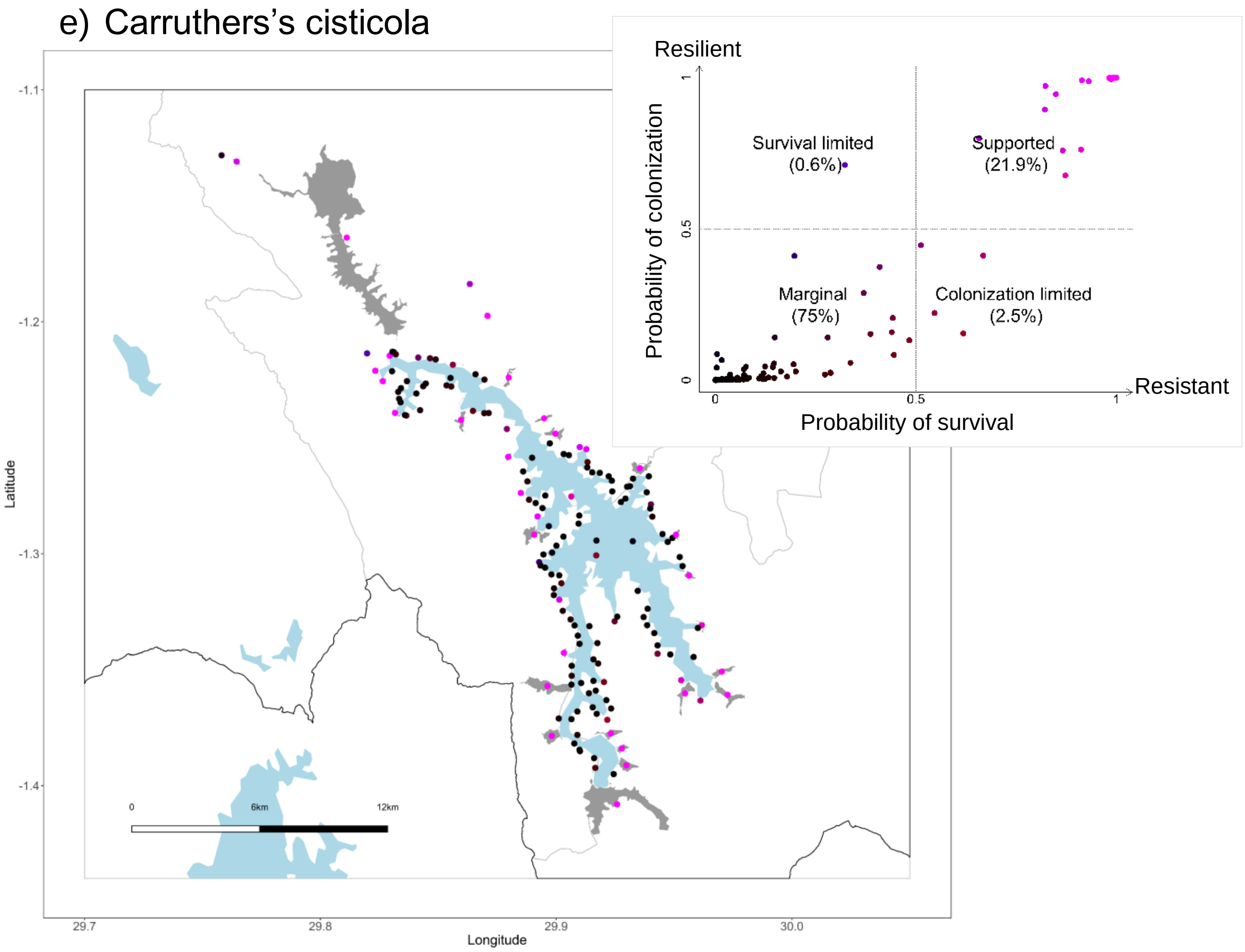


c) White-winged swamp-warbler



d) Papyrus yellow warbler





e) Carruthers's cisticola

Figure 4.2. Maps of predicted probabilities of colonization to and survival in each patch for the five study species (a-e) at Lake Bunyonyi, Uganda. Points show the centre coordinates of each patch, coloured by the strength of relationship between survival and colonization (blue = high probability of colonization, low survival; red = high probability of survival, low colonization; purple = high probability of colonization and survival; black = low probability of colonization and survival). Inset: predicted categories for each patch (% of suitable patches for that species in a given category, see Figure 4.1 for details). Suitable wetland is shown in grey. Occupancy data over 2014-2015 is displayed in Figure C2.

Overlapping priorities

Mapping the predicted categories for all species together (Figure 4.3a-f) illustrated that the most overlap between all five species existed between patches with a high probability of survival (including high and low probabilities of colonization) (Figure 4.3c), and patches with <0.5 probability of both colonization and survival (Figure 4.3b). Survival limited patches, on the other hand, intersected the least (Figure 4.3f).

9.1% of patches had a high probability of survival for all five species (Figure 4.3c), while patches with a high probability of colonization intersected for up to 4 species in 6.2% of the network (Figure 4.3e). These were situated along the length of the lake, with some clusters around the larger swamps at the north and south of the study area; corresponding closely to those sites which had a high probability of both colonization and survival for 4 of the study species (13.5% of the network) (Figure 4.3a). Patches limited by colonization only overlapped for up to 3 species (Figure 4.3d), with 0.6% patches predicted for 3 species and 16% for 2 species. Survival limited patches did not coincide for any of the study species, instead displaying that 2.9% of the patches within the network at Lake Bunyonyi were limited by survival for one species only (Figure 4.3f). 9.6% of patches had a low probability of colonization and survival for all five species (Figure 4.3b). These patches were located around the edge of the lake, consisting primarily of the fringing shoreline patches.

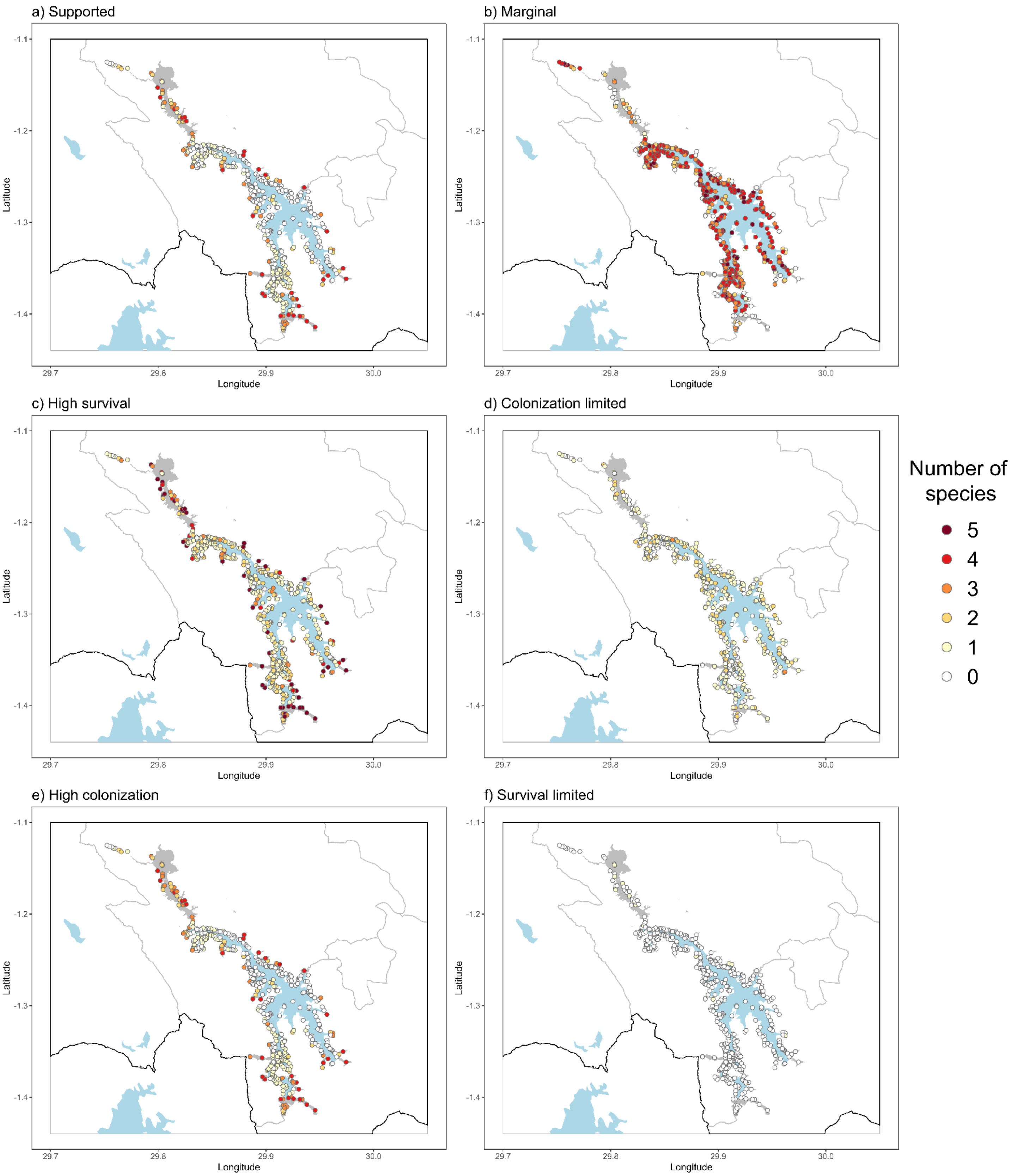


Figure 4.3. Maps displaying the predicted categories and level of overlap for all species across the network at Lake Bunyonyi, Uganda, based on 0.5 probability (see Methods): (a) supported (high survival and colonization), (b) marginal (low survival and colonization), (c) high survival (with high and low colonization), (d)

colonization limited (high survival, low colonization), (e) high colonization (with high and low survival), (f) survival limited (high colonization, low survival). Key: 0 = no species within corresponding category, 1+ = number of species within corresponding predicted category for specified patch. See Figure 4.1 for explanation of categories.

Discussion

The results of this study demonstrate that, despite variation in the local and landscape characteristics driving the processes of population survival and reestablishment between species sharing the same habitat type, several parts of the landscape are important for the resistance and resilience of all species. This is a promising result for the conservation prioritisation of papyrus-endemic birds; highlighting where efforts should be focused to assist with securing persistence across species, with consideration of the need to ensure species are able to adapt and respond to future change.

Regional persistence of multiple species

Enhancing persistence is one of the key objectives associated with the establishment of protected sites (Margules & Pressey 2000). To achieve this goal, conservation planning often focuses on ensuring population survival, yet understanding the processes that affect colonization is also important for the recovery of populations faced with extinction (Davies et al. 2005). Within fragmented landscapes, the persistence of a metapopulation is dependent on the balance of rates of extinction and colonization (Hanski & Gilpin 1991). Understanding the drivers of these processes is a significant step in conservation planning (Franzén & Nilsson 2010; Robles & Ciudad 2012), enabling the identification of the parts of the landscape which host particular species (Hodgson et al. 2011b). However, the importance of different local and landscape characteristics remain unknown for numerous species (Whytock et al. 2017), leading to uncertainty regarding the variation that exists for multiple species occupying the landscape (Hodgson et al. 2009b). Should different approaches give rise to drastically different outcomes (Brooks et al. 2006), for example, developing conservation strategies that are suitable for all in need would be considerably more challenging.

The response of population survival and establishment to habitat and landscape characteristics does vary among specialist species of passerines residing in a network of papyrus swamps. Although within the same guild, variation exists between the ecological characteristics of these species, such as habitat preferences (Vande weghe 1981) and capacity for dispersal. Local extinction is most closely linked with local variables (Lawson et al. 2012), particularly patch size and quality, because of their influence on carrying capacities and the size of source populations (Hanski 1999a; Thomas et al. 2001). In line with this, all species were less likely to become extinct in larger swamps, while aspects associated with habitat quality for these species (Chapter 3; Donaldson et al. 2016) were often found to be predictors for survival. White-winged swamp-warbler, for example, had a lower chance of extinction in more circular swamps, while greater swamp-warbler, an edge species (Britton 1978; Donaldson et al. 2016), had a higher probability of survival in swamps with a higher edge: area ratio. Further, the three species most closely associated with papyrus were less likely to occur in mixed papyrus (Donaldson et al. 2016), whereas the likelihood of occurrence of the broader wetland species was not impacted by this habitat type.

In contrast to survival, colonization is often linked with landscape variables, namely connectivity (Hanski et al. 1996), driven by the distance between patches, matrix habitat, dispersal ability and the number of potential dispersers (Dorp & Opdam 1987). Previous work by Maclean et al. (2006) found no correlation between patch occupancy and proximity to neighbouring swamps, though the range of distances examined were far greater than in the present study, and it is likely that the majority of isolated swamps lay beyond the dispersal distance of the species studied. Connectivity influenced colonization for those with relatively lower levels of dispersal (Carruthers’s cisticola and greater swamp-warbler; see Chapter 5), while in species with higher dispersal capabilities, or which are known to feed outside of swamps (e.g. papyrus canary) (Britton 1971), colonization probability was largely unaffected by levels of connectivity at the scale of this study. Enhancing connectivity is often assumed to be a fundamental element of conservation planning, without any prior investigation (Hodgson et al. 2009b). However, our results caution against simply focusing on connectivity for the benefit of all species. Over recent years, the role of area and quality in driving the process of colonization has been recognised (Franzén & Nilsson 2010; Glorvigen, Andreassen & Ims 2013; Bohenek et al. 2017). Large patches are considered more likely to be detected by the disperser (Vos, Ter Braak & Nieuwenhuizen 2000), and can be actively selected by active compared to passive dispersers (Glorvigen, Andreassen & Ims 2013), which could explain why the majority of species here were more likely to colonize larger swamps. Patch quality is also a significant influencer of habitat selection (Robles & Ciudad 2012; Glorvigen, Andreassen & Ims 2013), hence why many of the habitat factors known to influence quality (Donaldson et al. 2016) were also in the top set for colonization in this study.

Resistance vs resilience across a network

Despite developments from metapopulation theory, there is still a tendency in conservation planning to focus efforts on individual sites. Recognition of multiple sites is rarely explicitly considered (Gaston et al. 2008), yet allowing the landscape to function as a network is crucial in order to support biodiversity over the long-term (Lawton et al. 2010). In modern landscapes, where habitat fragmentation is the norm (Tilman et al. 2017), ensuring that populations are both resistant and resilient to extinction is axiomatic (Lawler 2009; Hodgson, McDonald & Hosken 2015). By recognising the mechanisms that drive these aspects, planners can identify the most important parts of the landscape (Nimmo et al. 2015), and note what is likely to be restricting the ability of a species to persist now, or how species could respond to changing land use in the future (Opdam *et al.* 1995).

Applying this resistance-resilience framework to papyrus-endemic birds, we found that the highest proportion of patches both resistant and resilient to change were predicted in species for which colonization was influenced by connectivity as well as patch size. In contrast, most of the sites within the network were limited in their ability to be colonized by all species. Specialist species are often assumed to possess poor abilities to colonize sites, compared to more generalist species (see references in Davies et al. 2005). Indeed, the species most closely associated with papyrus had more colonization-limited patches within their network than the broad wetland species, which generally had more habitat available to colonize. In turn, any future changes to the habitat of these species that cause extinction within parts of the network, such as seasonal drainage or wide-scale habitat disturbance (Maclean *et al.* 2003a; Zsuffa *et al.* 2014), could be catastrophic for their regional populations. With no flow of individuals from outside these sites, these patches effectively act as sink populations (Pulliam 1988) which may fail to exist over the long-term (Hansen & Rotella 2002). Since most species rely on large patches for colonization, as landscape fragmentation and loss continues to increase (Tilman et al. 2017), levels of resilience will continue to decline, while the need for it will simultaneously increase (Hanski & Gilpin 1991; Whytock et al. 2017). This is especially a concern for white-winged swamp-warbler, which had virtually no patches that would likely be colonized following an extinction event. The turnover data available for this species is relatively scarce; either the result of an unusually poor year for this species (and thus an underestimation of true turnover rates), or because this species disperses across the landscape only very occasionally. The scale of habitat loss may already have led to levels of habitat fragmentation that this species is struggling to deal with in this landscape (e.g. Maclean, Wilson & Hassall 2011), with the potential for “extinction debt”, where further modifications of occupied sites may lead to eventual extinction in the future (Kuussaari et al. 2009).

Prioritising conservation effort

Strategic conservation planning is vital to ensure that the limited time and money available for conservation is channelled most effectively (Brooks et al. 2006). Numerous methods have been developed to assist with this process (Margules & Pressey 2000), but the uncertainty surrounding where to invest remains (see references in Whytock et al. 2017). Alongside guaranteeing the persistence of individual species, protected sites also strive to be representative of biodiversity as a whole (Margules & Pressey 2000). Thus, not only are we faced with the challenge of ensuring sites are resistant and resilient to change, but we must apply this approach to multiple species residing in the same landscape (Darwall & Vié 2005). Further, it must be recognised that many landscapes around the world struggle to implement the strict management procedures that are often part of protected area guidelines in more developed regions. Wetlands in East Africa suffer from lack of cohesion in policy and the failure of parties to adhere to any guidance in place, while management is often determined by the actions of local communities (Kipkemboi & van Dam 2016). Therefore, placing priority on limiting habitat loss (van Dam et al. 2014) and ensuring that important sites for biodiversity are offered at least some protection, is a more achievable and realistic goal.

Mapping the probability of survival and colonization for multiple papyrus passerines at Lake Bunyonyi highlights that, as it stands, a number of swamps are relatively resistant for all species. Although high levels of resistance across the landscape for all species is reassuring, fewer sites coincidently offered resilience for all five species, due largely to the limited colonization ability of white-winged swamp-warbler. In practice, this variation emphasizes that conserving networks with multi-species resilience is a key challenge for conservation management. Despite this, most of the larger swamps surrounding the lake are both resistant and resilient for the remaining study species, indicating where conservation efforts could be focused. Sites designated for conservation purposes rarely assess if they are achieving their desired goals of species persistence and representativeness (Margules & Pressey 2000). In this case, Nyamuriro swamp IBA at the north of the lake does appear to capture a series of the most important sites for the papyrus endemic birds. Not only does it secure the intended high levels of survival of those populations residing there, but due to the inclusion of some small fragments within the designated IBA boundaries, the resilience of this site overall is high. Further proposals for an IBA have been suggested for Mugandu/Mukahungye swamp at the far south-west of the lake. Based on our framework, this designation is justified to assist with the overall persistence of papyrus-endemic birds. Similarly, there are numerous sites for which survival and establishment are low for all the study species, and therefore are unlikely to be resistant nor resilient. It is impractical to conserve all swamps for biodiversity in this region (Maclean, Bird & Hassall 2014), and given the limited resources and challenges of enforcing existing wetland policy (Kipkemboi & van

Dam 2016), such sites could potentially be regarded as lower priority for conservation (Lawson et al. 2012). However, this would necessitate observation of the consequences for the species in the network as a whole; examining the role of these neglected patches in gene flow between populations (Gibbs 2001), for example, as well as ensuring that the remaining sites are adequately managed and monitored, and maintain their levels of resilience.

The need to manage for and enhance resilience for the future persistence of systems is increasingly recognised (Hodgson, McDonald & Hosken 2015), though exactly how to implement and measure this remains a challenge (Nimmo et al. 2015). Examining the limitations of a site is useful in order to highlight how we could enhance current restrictions faced by species (Gaston et al. 2008). In comparison to sites with high survival and/or colonization probability, patches limited by each of these processes displays very little overlap between species. As a result, focusing efforts on improving either of these aspects is unlikely to yield results for all species collectively, and resources would have to be spread thinly to reverse the limitations for all. Among these species, the factors influencing both survival and colonization are reasonably consistent, such as the emphasis on patch size and shape. Thus, aiming to enhance either of these aspects is likely to improve the ability of these patches to survive and/or be colonized should extinction occur. It is commonly proposed that areas with the highest projected turnover and lowest likelihood of persistence should be targeted (Hole et al. 2009; Lawson et al. 2012). However, in systems where the drivers of these processes diverge slightly, deciding if it is best to improve any limitations (Etienne & Heesterbeek 2001; Robles & Ciudad 2012), or maintain the current status (Hodgson et al. 2009b), will largely depend on the amount of resources available for investment (Hodgson et al. 2011b), and the scope for improvement (Margules & Pressey 2000). For example, restoration is commonly proposed as a means of enhancing these processes (Bulman et al. 2007) and could assist with improving the conservation status of threatened species by 2020 (CBD 2011), though the extent to which the impacts of creating habitat relate to the loss of habitat has recently been questioned (Whytock et al. 2017). Restoring wetlands has been suggested as a mechanism to reverse the devastation caused to papyrus swamps over the past few decades (Morrison et al. 2012; Kiwango et al. 2013); enabling the continued provision of ecosystem services to local communities (van Dam et al. 2011), as well as benefiting the wildlife reliant on it. However, much of the drained land has been converted to cropland (Carswell 2002; Terer et al. 2012) and reversing this will likely impose high social and economic costs for those depending on these areas for their livelihoods. Global human population growth is expected to be highest across parts of sub-Saharan Africa (see references in Tilman et al 2017), so maintaining food security is the prime objective for the rural poor (Shiferaw 2006).

Conclusion

This chapter shows how an understanding of the mechanisms that lead to the survival and establishment of populations can be used to offer insight into the levels of resistance and resilience for multiple species residing across fragmented landscapes. Although slight differences in the response to various habitat characteristics existed between species, mapping the predicted dynamics of these species does show that there are multiple sites likely to be resistant and resilient to extinction for all species combined. Incorporating this landscape-scale resistance-resilience framework into conservation planning can help inform the allocation of valuable resources and identify the extent to which current protected sites are effective, with consideration of the growing need for biodiversity to respond and recover to future change.

Chapter 5:

Designing effective protected area networks for multiple species: a case study using endemic wetland birds in East Africa

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Abstract

For networks of protected areas to be effective at maintaining metapopulation persistence, theory emphasizes that sites should be of sufficient quality, quantity and size, and arranged in a well-connected network. But with limited conservation resources and a landscape increasingly dominated by land use change, achieving all of these is impractical, so that decisions on which strategies to adopt need to be made. Individual species are often used as surrogates for other species, assuming the community as a whole will benefit. However, the extent to which the dynamics of multiple species residing in protected area networks differ, and the implications of this for network design, is rarely considered, and remains to be explicitly tested for species with overlapping habitat requirements. We explore a range of conservation planning approaches to design networks for multiple species, using a suite of passerines endemic to papyrus swamps in East and Central Africa. We parameterise metapopulation models for 5 papyrus-specialist species that reside in an area of south-west Uganda and possess subtle ecological differences including dispersal ability, habitat preference and population carrying capacity. The optimal approach in terms of prioritising size, number, quality or connectivity of habitat to achieve metapopulation persistence differed depending on the metapopulation structure and ecological characteristics of the species in question. The rank order of strategies also varied with the overall wetland area available, and depended on the desired threshold for persistence. However, for the majority of species, an approach based on prioritising habitat quality (local population density) achieved the highest levels of persistence and overall population size for equivalent land area conserved. In contrast, connectivity showed greater overlap among species than habitat quality, thus the most effective strategy to conserve multiple species in the same network

prioritised habitat connectivity. Overall this study cautions against using the requirements of single species for the conservation of multiple species; stressing the need to consider the individual characteristics of species utilising the same habitat networks in conservation planning, but demonstrates the potential utility of prioritising protected sites based on the spatial connectivity of habitat patches, if aiming to conserve multiple species with differing or uncertain habitat requirements.

Introduction

Biodiversity is declining rapidly, with climate change, habitat loss and degradation amongst the key drivers of these declines (Butchart et al. 2010). Protected areas are often regarded as the backbone of conservation (Nagendra et al. 2013; Kukkala et al. 2016) and form part of the Aichi Biodiversity Targets to improve the status of biodiversity by 2020 (CBD 2011). Conservationists also identify priority sites for investment, such as Biodiversity Hotspots (Myers et al. 2000) and Key Biodiversity Areas (Eken et al. 2004). Despite the development of specified criteria for the designation of such sites (e.g. Fishpool and Evans 2001; Dudley 2008), the spatial configuration of habitats is not explicitly considered. Nonetheless, two prominent theories in spatial ecology, those of island biogeography and metapopulation dynamics, both indicate that the occurrence and abundance of species is related to the size and isolation of habitat patches (MacArthur & Wilson 1967; Hanski 1999a).

The principles proposed by these theories have been pivotal for the development of landscape-scale conservation over recent decades (Donaldson, Wilson & Maclean 2017), and the increasing recognition of the importance for biodiversity conservation of networks of protected areas (Butchart et al. 2012). Metapopulation theory predicts that colonization probability increases in more connected patches, while local extinction rates decrease in larger, higher quality patches (Hanski 1991, 1994b; Moilanen & Hanski 1998). Thus, protected area networks are recommended to consist of large, high quality, well connected sites (Lawton et al. 2010) to ensure long-term persistence. But with limited resources for conservation (McCarthy et al. 2012) and a landscape increasingly dominated by changing land use practice (Foley et al. 2005), achieving all of these is often impractical, and trade-offs may need to be made between site size, quality and connectivity (Donaldson, Wilson & Maclean 2017).

Metapopulation models have been fundamental for guiding conservation in fragmented landscapes (Wahlberg, Moilanen & Hanski 1996; Hanski 1999b; Hoyle & James 2005). Key to their application is the ability to highlight the most beneficial management strategy for the long-term survival of a species (Hanski et al. 1996; Gutierrez 2005; Akcakaya, Mills & Doncaster 2007), including the impact of enhancing the size, number or quality of patches for persistence (Hanski & Thomas 1994). However, empirical tests of a metapopulation approach to landscape-scale conservation often consider the effects on single species alone (Etienne 2004) rather than the influence of a given strategy on multiple species. Yet protected area networks strive to represent all species (CBD 2011), thus chosen strategies should not negatively impact co-occurring species (Gutiérrez et al. 2001) and instead balance the needs for all (Lawson et al. 2012). Importantly, species often possess different habitat requirements (Howard et al. 2000) and ecological characteristics, such as dispersal (Thomas 2000). As a result, dynamic responses to habitat availability differ between species (Glorvigen, Andreassen & Ims 2013), which must be carefully accounted for in conservation planning.

Using a suite of specialist passerines endemic to papyrus (*Cyperus papyrus*) swamps in East and Central Africa, we assess the effectiveness of five strategies for prioritising areas for conservation: protecting (1) large patches, (2) several small patches, (3) high quality patches, (4) well-connected patches, and (5) the single largest patch. Papyrus is a naturally fragmented habitat because of its limitation to wetland areas, and sites have become increasingly isolated as a result of drainage and the encroachment of intensive land-use (Hartter & Ryan 2010; Maclean, Wilson & Hassall 2011). Birds restricted to this habitat are in decline (Maclean, Bird & Hassall 2014), but the resources available for conservation in sub-Saharan Africa are severely limited (Howard et al. 2000), necessitating clear guidance to ensure efficient use. Previous work highlights the importance of habitat networks for sustaining populations of papyrus-endemic birds, at least over the short-term (see Chapter 4), and the need for a consideration of metapopulation dynamics (Chapter 4; Maclean, Wilson & Hassall 2011). But although these species have overlapping distributions, they possess different specific habitat requirements (Donaldson et al. 2016) and life history traits (Vande weghe 1981). It is not yet known how conservation recommendations differ when the needs for all species are collectively considered, which could have important implications for how resources in the region are utilised. In light of this, we parameterise metapopulation models for a suite of papyrus-endemic passerines using occupancy data collected from a network of swamps in south-west Uganda. We perform a series of simulations to estimate how each species responds to prioritizing networks based on size, quality and connectivity, and determine aspects of their ecology which could be driving their response patterns, highlighting key principles to be considered. Outcomes are compared between species to demonstrate the suitability of a single-species metapopulation method for the conservation of multiple species, and determine the feasibility of an optimal planning solution that can meet the needs of all.

Methods

Study system

Papyrus swamps dominate wetlands across Africa (Beentje 2017), but have been experiencing rapid rates of loss and degradation over the past few decades (Maclean, Wilson & Hassall 2011). At Lake Bunyonyi, Uganda (01^{o}17'S; 29^{o}55'E), high densities of papyrus grow along the lake edge and deep valley bottoms (Denny 1972). The volcanically-active nature of the region, and resulting steep topography, has led to the formation of an isolated network of swamps, where water level remains stable year-round (Denny 1972), minimising fluctuations in patch size and making it an ideal system to model metapopulation dynamics. Relatively high numbers of five species of papyrus-endemic passerines are found in this area: white-winged swamp-warbler (*Bradypterus carpalis*), greater swamp-warbler (*Acrocephalus rufescens*) (race *foxi*), papyrus canary (*Crithagra koliensis*), papyrus yellow warbler (*Calamonastides gracilirostris*) and Carruthers's cisticola (*Cisticola carruthersi*). All are primarily restricted to papyrus, though previous work has highlighted differences in various ecological characteristics, such as feeding preferences (Britton 1971) and behavioural attributes (Britton 1978), as well as variation in responses to habitat structure (Maclean et al. 2003a, 2006; Donaldson et al. 2016). Key amongst these is the preference of greater swamp-warbler and papyrus canary to occupy the edge of swamps, while the remaining three species are more commonly associated with the wetland interior (Britton 1978; Donaldson et al. 2016). Also, the specific wetland sites in which these species are found differ; papyrus yellow warbler and Carruthers's cisticola can inhabit broader wetland vegetation types, especially when associated with papyrus (Maclean et al. 2006), and Carruthers's cisticola has also been recorded in wetland recently converted to agriculture (Donaldson et al. 2016). Taken together, these species provide a useful exemplar to explore the characteristics that drive interspecific differences in dynamics, and their consequences for multi-species conservation recommendations.

Distribution survey

The study site was visited over 2 consecutive years (2014 and 2015) to allow for model parameterisation (see below). All patches of papyrus surrounding the lake were identified in 2014 using a combination of 1:50,000 topographical maps (obtained from the Department of Land and Surveys, Entebbe), satellite imagery (Google Earth), local knowledge, and close examination of shoreline and valley bottoms from motorboat and on foot (see Figure 1.5 in Chapter 1). In total, 519 discrete patches of papyrus vegetation were identified and mapped (but see *Parameter estimation* below). Papyrus yellow warbler and Carruthers's cisticola were also recorded within broader wetland vegetation (see also Maclean et al. 2006; Donaldson et al. 2016), thus these wetlands were included in the study for these species only. Shoreline fringing patches were surveyed for the presence of greater swamp-warbler and papyrus canary, since the remaining 3 species were never found to occupy this patch-type over the 2 years of survey. Following preliminary observations, a discrete patch was defined as a body of papyrus/wetland over 20 m long and 5 m wide suitable for nesting, separated from another wetland patch by approximately 10 m. As patches around Lake Bunyonyi are primarily surrounded by either cultivated farmland or the body of the lake, all habitat between patches was classed as “unsuitable” for the purpose of this study.

Presence-absence surveys were conducted between May-August over 2014 and 2015, when the birds are breeding following the rainy season (Britton 1978). Intermittent playback was used to aid with detection since the nature of this habitat results in records of these species being primarily by sound rather than sight (Maclean et al. 2006). Each patch was visited between ~06.45 and ~13.45 when birds are most vocal, and the presence or absence of each study species was noted. Swamps were surveyed from the edge of swamps, often on higher land which offers a more effective vantage point for seeing and/or hearing birds compared with the dense and largely inaccessible papyrus interior. Survey time varied by patch size, from a minimum of 5 minutes for small, low quality sites, to a maximum of 7 hours 15 minutes for large swamps (see Table B1 in Appendix B). Previous work has highlighted the rapid detection of these species upon arrival at a site (Maclean et al. 2006). However, to ensure that survey effort was sufficient to ensure low likelihood of false absences (Moilanen 2002), we conducted additional analyses to examine the relationship between the probability of detection and survey effort (see Chapter 4 and Appendix B). At the point of survey, GPS points were taken from the edge of swamps (UTM 35S using GARMIN GPSMAP 64, Lenexa, KS), and used alongside sketch maps drawn to scale with topographical maps to mark the boundary of each patch. 5 vegetation categories were created relating to the physical characteristics of swamps (see Table 3.1 in Chapter 3 [Donaldson et al. 2016] for details), and the proportion of each of these categories within each swamp was recorded. All maps were digitized in Arc GIS v 10.1 in the RGDC 2005 UTM 35S projection system, and area and perimeter calculated for each patch.

Patch quality

Estimates of patch quality were based on the relative density of each species (Hoyle & James 2005). Fifteen minute point count surveys were conducted across a subset of swamps during May-June 2014, and used alongside our vegetation categories and swamp size and shape, to determine the most important factors influencing the densities of the study species (see Donaldson et al. 2016 and Chapter 3 for details). The model average coefficients relating to patch geometry and/or the proportion of particular vegetation categories (see Appendix A), were used to predict the density of each species in each patch during 2014 and 2015, and estimate relative population sizes for each species across the study site. Densities were capped at the lowest and highest observed densities for each species (greater swamp-warbler [GSW]: 0.16/ha and 6.78/ha; papyrus canary [PC]: 0.16/ha and 21.75/ha; white-winged swamp-warbler [WWW]: 0.18/ha and 2.55/ha; Carruthers's cisticola [CC]: 0.16/ha and 2.08/ha; papyrus yellow warbler [PYW]: 0.08/ha and 0.67/ha) since predictions were made outwith the data range (Conn, Johnson & Boveng 2015), and to ensure that habitat mapped as suitable was available for colonization (Wilson et al 2009).

Metapopulation model

Stochastic Patch Occupancy Models (SPOMs) are a class of simplified metapopulation models which utilise readily available field data (Etienne et al 2004). The key feature is that local dynamics are omitted and only patch occupancy is modelled (Moilanen 2004), with the assumption that discrete habitat patches exist in a matrix of unsuitable habitat, and the probability of patch occupancy is determined by extinction and colonization events (Ozgul et al. 2006). The Incidence Function Model (IFM) described by Hanski (1994b) is the best known (Etienne, Ter Braak & Vos 2004) and most commonly used SPOM (Moilanen 2004).

Here, we use SPOMSIM software (Moilanen 2004) which is based on the IFM and specifically designed for SPOM parameter estimation and simulation. The dispersal kernel is defined as:

$$D\left(d_{ij}, \propto\right) = \exp\left(-\alpha d_{ij}\right) \quad [1]$$

where d_{ij} is the distance between patches i and j ($i \neq j$) and α defines a negative exponential distribution of dispersal distances ($1/\alpha$ = average dispersal distance)

(Hanski 1994b; Moilanen 2004). Connectivity ($S_i(t)$) defines the probability of colonization of an empty patch (Moilanen 2004), set as:

$$Si(t) = \sum p_j \exp\left(-\alpha d_{ij}\right) A_j^b$$

[2]

where p_j is the occupancy of patch *j* in year *t*, A_j is the population carrying capacity of patch *j*, usually taken as patch area (ha) but can be modified by patch quality (Hanski & Ovaskainen 2000; Thomas et al. 2001), and parameter *b* scales emigration with carrying capacity. The probability of colonization (C_i) of an empty patch *i* is:

$$C_i\,(t) = \frac{[S_i(t)]^2}{[S_i(t)]^2 + y^2}$$

[3]

where $S_i(t)$ is the connectivity of patch *i* at time *t,* and *y* is a parameter determining the relationship between colonization probability and connectivity (Wilson, Davies & Thomas 2009). The extinction probability (E_i) of an occupied patch is defined as:

$$E_i = \frac{\mu}{A_i^x}$$

[4]

where A_i is the carrying capacity of patch *i*, μ is a parameter that defines the probability of extinction of a patch and *x* defines the scaling of extinction risk with patch area (Hanski 1998b). Owing to the rescue effect lowering the extinction risk of well-connected patches (Ozgul et al. 2006), the intrinsic rate of extinction (E_i) here has been replaced by an extinction rate adjusted for this rescue effect (Moilanen 2004):

$$E_i(t) = E_i(1 - C_i(t))$$

[5]

Parameter estimation

The survey data collected over 2 years provided information on turnover, used for parameter estimation (Moilanen & Hanski 1998; Moilanen, Smith & Hanski 1998; Moilanen 1999). Using consecutive years of data close in time ensures that the habitat area has not altered considerably between years (Wilson, Davies & Thomas 2009).

In SPOMs, patch area is usually used as a substitute for population size (Hanski 1994b), primarily due to the greater availability of these data compared with population estimates (Ozgul et al. 2006). As shown in Donaldson et al. (2016) (Chapter 3), the density of papyrus passerines differs between patches, depending on patch geometry and/or vegetative composition (Appendix A). Thus, the predicted densities for each site (see *Patch quality* above), were multiplied by patch area to give an estimated relative abundance for each species per site (Hanski 1994b; Hoyle & James 2005; Bulman et al. 2007). This replaced all values of A_i described above. Given the non-circular nature of patches in this network (Donaldson et al. 2016), d_{ij} represented nearest edge distances calculated in ArcGIS.

The Markov Chain Monte Carlo (MCMC) method (Moilanen 1999) was used to estimate parameters α, y, x and e (Moilanen 2004), assuming that the 2 snapshots of data used were at a stochastic steady state (Moilanen 1999) and there was no colonization from outside the network. Though it is difficult to guarantee that patch networks are at equilibrium (Hanski et al. 1995b), there was a balance between the number of extinction and colonization events over the 2 years, consistent with a possible steady-state (Hanski 1999a; Franken & Hik 2004). Parameter b was set at 1, assuming that emigration from a patch is proportional to abundance. All patches below the minimum observed occupied patch area from the 2 years of field observations were removed, since these patches were likely too small to be occupied by that species (GSW 0.004ha; WWW 0.044ha; PC 0.01ha; PYW 0.134ha; CC 0.36ha). 19200 iterations were performed for each estimation (as specified by high effort level in SPOMSIM), repeated at least 3 times with the same starting parameters to check for convergence (Moilanen 2004). The parameter set with the lowest AIC value was selected for use in model simulations.

Model simulations

A series of metapopulation simulations were carried out in SPOMSIM to identify differences in population persistence between four distinct approaches associated with reserve design: preferentially conserving either bigger, a greater number, better (higher quality ~ population density), or more connected sites. For comparison between approaches, results are shown with respect to a given total area of habitat conserved. Metapopulation dynamics were simulated using the parameters from the most parsimonious model for each species, run for 100 iterations over 100 years, starting with the 2015 occupancy and using habitat data collected during the 2015 survey. The average probability of persistence after 100 years was recorded (the proportion of simulations where the metapopulation persisted after this time) and plotted against the total area of habitat available across the network, to enable us to directly compare persistence with an equivalent investment of resources for conservation. To approximate the minimum viable metapopulation (Hanski, Moilanen & Gyllenberg 1996), an arbitrary threshold of 95% likelihood of persistence after 100 years was used (Shaffer 1981; Shaffer & Samson 1985). The relative population size after 100 years was estimated using the average proportion of occupied area after the time period, since area within our models represented population size (see *Parameter estimation* above). The scenarios were as follows:

i. Protecting large patches

Simulations began with the 2 largest patches available in the network for each species, and patches were sequentially introduced to the network by size (largest first) until 100% persistence over 100 years was attained. In some cases, the area of the two largest patches was high compared to the minimum areas conserved in the other approaches. Thus, in order to calculate the area required for persistence at a smaller total habitat area, these were reduced in size until the metapopulation became extinct, holding density constant. Ultimately this allowed us to compare the persistence of the various approaches at equivalent levels of habitat.

ii. Protecting a large number of small patches

Patches were ordered by size (smallest first) and initial simulations were run with a network of 10% of the network's smallest patches for each species, sequentially including patches (and hence the total area) until persistence of 100% over 100 years was attained.

iii. Protecting high quality patches

To establish the importance of high quality patches, those with the highest density for that species, irrespective of patch size, were included in the network and then added in order of progressively declining quality until a persistence over 100 years was attained. Since densities were capped at the observed upper limit (see above), a set of patches with the initial highest density had equal values. As with (*i.*), to determine metapopulation persistence prior to this, this set of patches was reduced in size until the metapopulation became extinct, retaining the initial capped density values throughout.

iv. Protecting most connected patches

Connectivity values for all patches within the network were calculated based on a simplified version of the full connectivity formula used for simulations [2]:

$$Si(t) = \sum(-\alpha d_{ij}) \qquad [6]$$

This accounts for the distance between patches and the dispersal capabilities of each species, but assumes that all patches within the network are occupied and equal in size. This enabled us to establish the patches with the highest connectivity values when all patches were present, and to start our simulations with these patches. Removing the lower connectivity patches from the initial starting conditions did not alter the rank order of connectivity of patches. Hence this approach allowed us to determine the importance of connectivity during our simulation scenarios with various combinations of patches, while avoiding intractable circularity in the modelling process, which would result if there was dependence on occupancy and abundance in other patches. Patches were added into the network from most to least connected, until full metapopulation persistence was reached. Again, to calculate total wetland area required for levels of persistence prior to the two most connected patches, these remaining patches were reduced in size, keeping density levels constant (as in *i.* and *iii.* above), until persistence declined to 0.

v. Protecting single biggest patch

Metapopulation dynamics in SPOMSIM can only be modelled with a minimum of 2 patches. Thus, the probability of survival of the single biggest patch in the network was calculated manually using [4]. Population size was estimated using the initial population size (at time 0) multiplied by the survival rate after 100 years. As with (*i.)*, (*iii.) and (iv.)*, this patch was reduced in size and the simulations re-run with density held constant, to determine (and compare) the probability of persistence and estimate the population size at lower habitat amounts.

Following the simulations, the amount of wetland habitat required per strategy to reach the 95% likelihood of persistence for all five species was recorded. The amount of habitat required for each species to exceed this was first noted for each strategy, and the minimum amount of habitat required overall (across all species) was subsequently used to estimate the amount of wetland required for a given strategy to ensure all papyrus-endemics persist over the long-term. Considering that there was a degree of overlap between the optimal networks for each species within each strategy, the amount of habitat required in total to protect the individual networks was also calculated. In situations where optimal networks consisted of papyrus patches (for the papyrus-only species) and broader wetland patches (for the broad wetland species), the area including the broader wetland was used.

Regional stochasticity

Regional stochasticity refers to correlated extinctions caused by environmental events, such as disease or weather (Hanski 1991), which can strongly influence estimates of metapopulation persistence (e.g. Poos & Jackson 2012). Estimating this in metapopulations directly requires data from multiple years (Moilanen 1999), thus models were parameterized excluding this. Moderate-high levels (0.2) of regional stochasticity were subsequently introduced during model simulations (Ozgul et al. 2006; Poos & Jackson 2012); specified to be synchronous across the network for there was no evidence of differing weather patterns across the study site (Moilanen, Smith & Hanski 1998; Moilanen 2004). To test the sensitivity of our simulations to the inclusion of stochasticity, all scenarios were repeated without regional stochasticity and confirmed that all qualitative conclusions from this study, concerning the rank order of strategies and relative (approximate) areas required for persistence, still hold (Figure D1).

Results

Species-specific data

After the removal of patches below the minimum observed area for each species, the number of suitable habitat patches ranged from 77 for Carruthers’s cisticola to 518 for greater swamp-warbler (Table 5.1). Consistent with the observed capped areas (see Methods), the mean patch size available within the network was smallest for greater swamp-warbler and papyrus canary, while the suitable patches for papyrus yellow warbler and Carruthers’s cisticola were the largest in size (Table 5.1). The predicted densities across the network highlighted that papyrus yellow warbler and papyrus canary had the lowest densities at this study site, while greater swamp-warbler occurred at relatively higher densities (Table 5.1). Considering the suitable habitat available and the predicted density levels at each site, the relative carrying capacity of papyrus canary was the lowest of the five study species, followed by greater swamp-warbler and papyrus yellow warbler (Table 5.1). White-winged swamp-warbler and Carruthers’s cisticola, on the other hand, had the highest population carrying capacities across Lake Bunyonyi (Table 5.1).

Table 5.1. Survey data collected over 2014-2015 for all study species: greater swamp-warbler (GSW), papyrus canary (PC), Carruthers's cisticola (CC), white-winged swamp-warbler (WWW), papyrus yellow warbler (PYW).

Species	**Suitable patches**	**Habitat (ha)**	**Mean patch size (ha)** $^{(SD)}$	**Mean patch distance (km)** $^{(SD)}$	**Max density (per ha)**	**Relative carrying capacity**	**Occupied**		**2014-15**	
							2014	**2015**	**Ext**	**Col**
GSW	518*	550.7	1.06 $^{(8.21)}$	10.7 $^{(7.3)}$	0.042	355	269 (51.9%)	275 (53.1%)	63 (23%)	69 (25%)
PC	495*	550.6	1.11 $^{(8.4)}$	11.5 $^{(7.7)}$	0.00005	188	56 (11.3%)	84 (17.0%)	16 (29%)	44 (52%)
CC	77†‡	1829.8	23.76 $^{(119.21)}$	11.4 $^{(7.4)}$	0.00176	1320	35 (45.5%)	39 (50.6%)	4 (11%)	8 (21%)
WWW	197	537.1	2.73 $^{(13.17)}$	12.2 $^{(8.0)}$	0.0394	638	53 (26.9%)	44 (22.3%)	12 (23%)	3 (7%)
PYW	138†	1068.0	7.74 $^{(31.54)}$	10.8 $^{(6.8)}$	0.0001	330	20 (14.5%)	27 (19.6%)	3 (15%)	10 (37%)

Habitat (ha) is the total available suitable habitat across the network per species. Mean patch distance is the average distance between all occupied patches across the 2 years of survey. Max density is the maximum predicted density for each species. Relative carrying capacity represents the predicted maximum possible population size for each species, based on ∑ (patch area* patch density). The percentage of occupied patches in 2014 and 2015 (from the total number of patches), and newly extinct ("Ext") and colonized ("Col") patches in 2015 (from the total number of populations in 2014 and 2015 respectively), are shown in brackets. *Includes shoreline fringing patches; †Includes broader wetland vegetation; ‡Includes agricultural wetland.

Differences were also apparent in the proportion of swamps occupied by each species, and observed turnover between years. Papyrus canary and papyrus yellow warbler occupied the lowest proportion of patches (11.3% and 14.5% in 2014 respectively), while greater swamp-warbler and Carruthers's cisticola occupied the most wetland sites (53.1% and 50.6% in 2015 respectively) (Table 5.1). In 2015, the proportion of newly colonized swamps was the highest for papyrus canary (52%) and the lowest for white-winged swamp-warbler (7%) (Table 5.1). In comparison, the proportion of locally extinct swamps in the network since 2014 were similar between species, ranging from 11% of total patches for Carruthers's cisticola, to 29% for papyrus canary (Table 5.1).

Metapopulation parameters estimated for each species showed variation among colonization probability (y), the scaling of extinction risk with population carrying capacity (x) and dispersal (α) (Table 5.2). Papyrus canary and greater swamp-warbler had the lowest estimated dispersal abilities, Carruthers's cisticola and white-winged swamp-warbler were capable of intermediate levels of dispersal, while papyrus yellow warbler could disperse the furthest (Table 5.2). During the MCMC runs, parameters for greater swamp-warbler and papyrus canary settled at local minima (Table 5.2). Thus, estimates were calculated at least 3 times (Table D1) and confirmed similar values were obtained, although this prevented estimation of 95% confidence intervals for these species.

Table 5.2. Metapopulation parameter values (*α, y, μ, x*) for the best model (lowest AIC) for all study species: greater swamp-warbler (GSW), papyrus canary (PC), Carruthers's cisticola (CC), white-winged swamp-warbler (WWW), papyrus yellow warbler (PYW). *α* is the dispersal parameter, *y* relates to colonization probability, *μ* and *x* refer to extinction risk (see Methods for details). 95% confidence intervals shown in brackets for species where these could be calculated.

Species	***α***	***y***	***μ***	***x***	**Dispersal ability**
GSW	0.204	226.017	0.012	0.864	Low
PC	0.190	185.753	0.012	0.935	Low
CC	0.070 (0.000-0.151)	1998.430 (1164.079-5417.371)	0.061 (0.037-0.072)	0.734 (0.523-1.031)	Intermediate
WWW	0.021 (0.003-0.051)	5512.051 (3399.745-8138.029)	0.059 (0.059-0.059)	0.488 (0.361-0.509)	Intermediate
PYW	0.001 (0.000-0.021)	1446.647 (1192.023-1984.177)	0.041 (0.041-0.067)	1.340 (0.720-2.579)	High

Simulations

i. Metapopulation persistence

Levels of persistence varied depending on the network structure conserved (see *Simulations i. to v.* in Methods), and the total area of wetland available across the lake for the five study species (Figure 5.1a-e). With equivalently low amounts of habitat, focusing on the largest and/or higher quality swamps with approximately 4-8ha of wetland made it possible to achieve ≥50% probability of persistence for those with the lowest predicted carrying capacities: greater swamp-warbler, papyrus canary and papyrus yellow warbler (Figure 5.1a, 5.1b, 5.1e; Table 5.1). In comparison, levels of persistence for Carruthers's cisticola and white-winged swamp-warbler were low at equivalent habitat levels, regardless of the strategy used (Figure 5.1c; 5.1d). No species were estimated to persist within a network of smaller swamps when levels of habitat were low, while prioritising connectivity resulted in low persistence for greater swamp-warbler, papyrus canary and white-winged swamp-warbler, which were located in relatively small sites within this network (Figure 5.1a, 5.1b, 5.1d; Table 5.1).

With more wetland available across the network, investing in the highest quality patches for each species was the most consistent strategy for achieving 95% probability of persistence. Retaining a high-quality habitat network gave similar results to protecting large sites for papyrus canary (Figure 5.1b) and papyrus yellow warbler (Figure 5.1e), the species' with low population densities (Table 5.1), and was similar to conserving more connected sites for white-winged swamp-warbler (Figure 5.1d), which had the lowest observed turnover (Table 5.1). Investing in numerous smaller sites was the least favourable option for most species, requiring a large amount of habitat before 95% persistence was reached (ranging from ~82 ha for greater swamp-warbler, to ~400 ha for papyrus yellow warbler). Those with higher carrying capacities but a low population turnover, Carruthers's cisticola and white-winged swamp-warbler (Table 5.1), were an exception to this; investing in a few large sites required the most amount of habitat to ensure a 95% chance of persistence for these species (>300 ha) (Figure 5.1c; 5.1d), beyond protecting a series of smaller sites. However, investing in the single largest site for white-winged swamp-warbler never reached the 95% likelihood of persistence (Figure 5.1d), and the single largest wetland in the overall network for Carruthers's cisticola must remain intact for this species to stay beyond the 95% threshold (Figure 5.1c). Meanwhile for the most dispersive species, papyrus yellow warbler (Table 5.2), a large amount of habitat was needed before connectivity (~250 ha) or a network of small sites (~400 ha) exceeded 95% probability of persistence (Figure 5.1e).

ii. Enhancing population size

Compared with persistence, the relative population size of all species increased consistently with area for all strategies (Figure 5.1f-j). Only papyrus yellow warbler showed a reasonably steady population size for bigger and higher quality networks, before abundance started to decline more rapidly once wetland area declined below ~600 ha and ~400 ha respectively. The population size differed depending on the conservation strategy for most species (Figure 5.1g-j), with the exception of greater swamp-warbler, where all strategies generated a reasonably consistent abundance (Figure 5.1f). The greatest differences among strategies were shown for the broader wetland species which inhabit larger patches within the network (Table 5.1): Carruthers's cisticola and papyrus yellow warbler. Protecting large and high quality patches generated a higher population size than smaller and more connected sites for these species, at least until the maximum amount of wetland in the network was reached (Figure 5.1h; 5.1j). In contrast, connectivity was a beneficial strategy, alongside large and high quality networks, for achieving high populations of the least dispersive species (Table 5.2) which utilise networks of smaller patches (Table 5.1): papyrus canary and greater swamp-warbler, particularly when only a small amount of papyrus was available (Figure 5.1g; 5.1f). The optimal strategy for achieving high population size differed depending on the amount of habitat available for white-winged swamp-warbler only (Figure 5.1i). This species was predicted to reside at relatively high densities (Table 5.1), thus benefited more from high quality sites compared to the other options when a small amount of papyrus was available. However, as habitat increased, preserving a few larger sites enhanced the population size more than the other strategies.

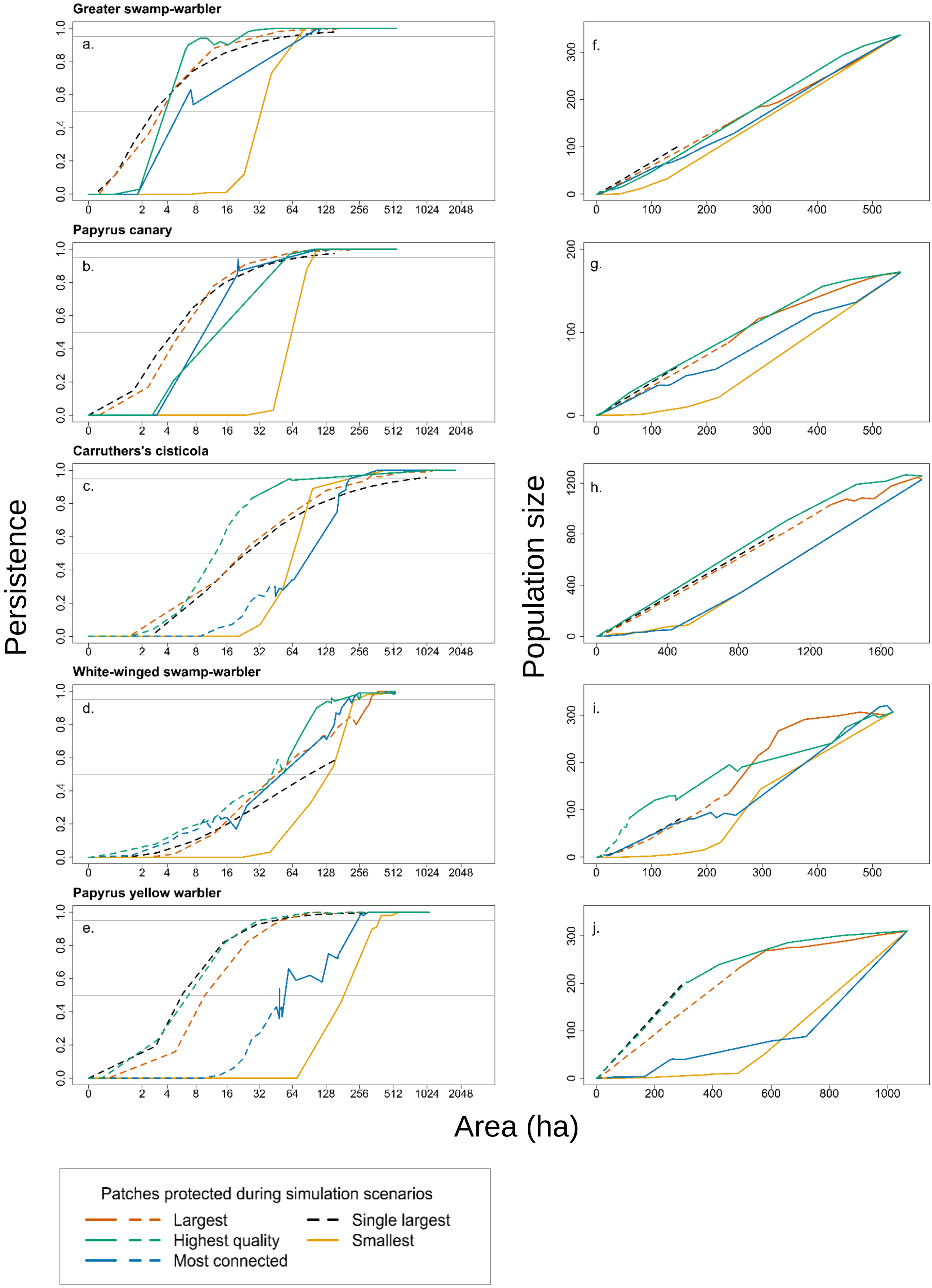

Greater swamp-warbler
Papyrus canary
Carruthers's cisticola
White-winged swamp-warbler
Papyrus yellow warbler
a.
b.
c.
d.
e.
f.
g.
h.
i.
j.
Persistence
Population size
Area (ha)
0.0
0.2
0.4
0.6
0.8
1.0
0
2
4
8
16
32
64
128
256
512
1024
2048
100
200
300
400
500
800
1200
1600
600
1000
Patches protected during simulation scenarios
Largest
Highest quality
Most connected
Single largest
Smallest

Figure 5.1. Output from metapopulation simulations for all study species: protecting the single largest, biggest (2+), smallest, most connected and highest quality patches in the current network. a-e display the mean proportion of replicates that persisted after 100 years, and f-j show the mean *relative* population size after 100 years, against the total area of suitable wetland habitat available across the network (a-e are plotted on the log+1 scale for clarity). Solid lines show simulation results from habitat configuration as it was in 2015, dashed lines represent results from scenarios modelled by reducing area to allow for a comparison between strategies at equivalent levels of habitat (see *Model simulations* in Methods for full explanation). All simulation results shown here include regional stochasticity (see Figure D1 for equivalent simulations without regional stochasticity).

iii. Achieving persistence of multiple species

The overall amount of wetland required across the network to achieve ≥95% likelihood of persistence under the optimal strategy varied between species (Figure 5.1a-e): ~25 ha for greater swamp-warbler, ~48 ha for papyrus canary, ~144 ha for white-winged swamp-warbler, ~61 ha for Carruthers's cisticola and ~31 ha for papyrus yellow warbler. Comparing the minimum required area across strategies to exceed the threshold for all species showed that conserving a network of high quality patches for each species required the least area (144 ha), followed by connectivity (255 ha) (Figure 5.2), driven by the required area for white-winged swamp-warbler and papyrus yellow warbler respectively (Figure 5.1d; 5.1e). No single sites at Lake Bunyonyi were a sufficient size to ensure 95% probability of persistence of white-winged swamp-warbler over 100 years (Figure 5.1d), and concentrating on the single biggest patch required the most amount of habitat to be suitable for the other species (Figure 5.2), due to the large amount of wetland required for a single patch to be suitable for Carruthers's cisticola (Figure 5.1c).

The optimal strategy overall changed when the total area required to conserve the optimal networks for each species were considered (Figure 5.2). The most connected sites overlapped between species to a greater extent than the other strategies, thus investing in a series of the most connected patches at Lake

Bunyonyi required the least amount of wetland overall (~299 ha) (Figure 5.2). High quality patches, on the other hand, intersected the least between species and required the conservation of approximately 528 ha of wetland overall to achieve 95% likelihood of persistence (Figure 5.2). Investing in the single largest site remained the least favourable strategy, for it could only ensure the persistence of 4 of the study species, which itself would require the protection of at least 812 ha at Lake Bunyonyi (Figure 5.2).

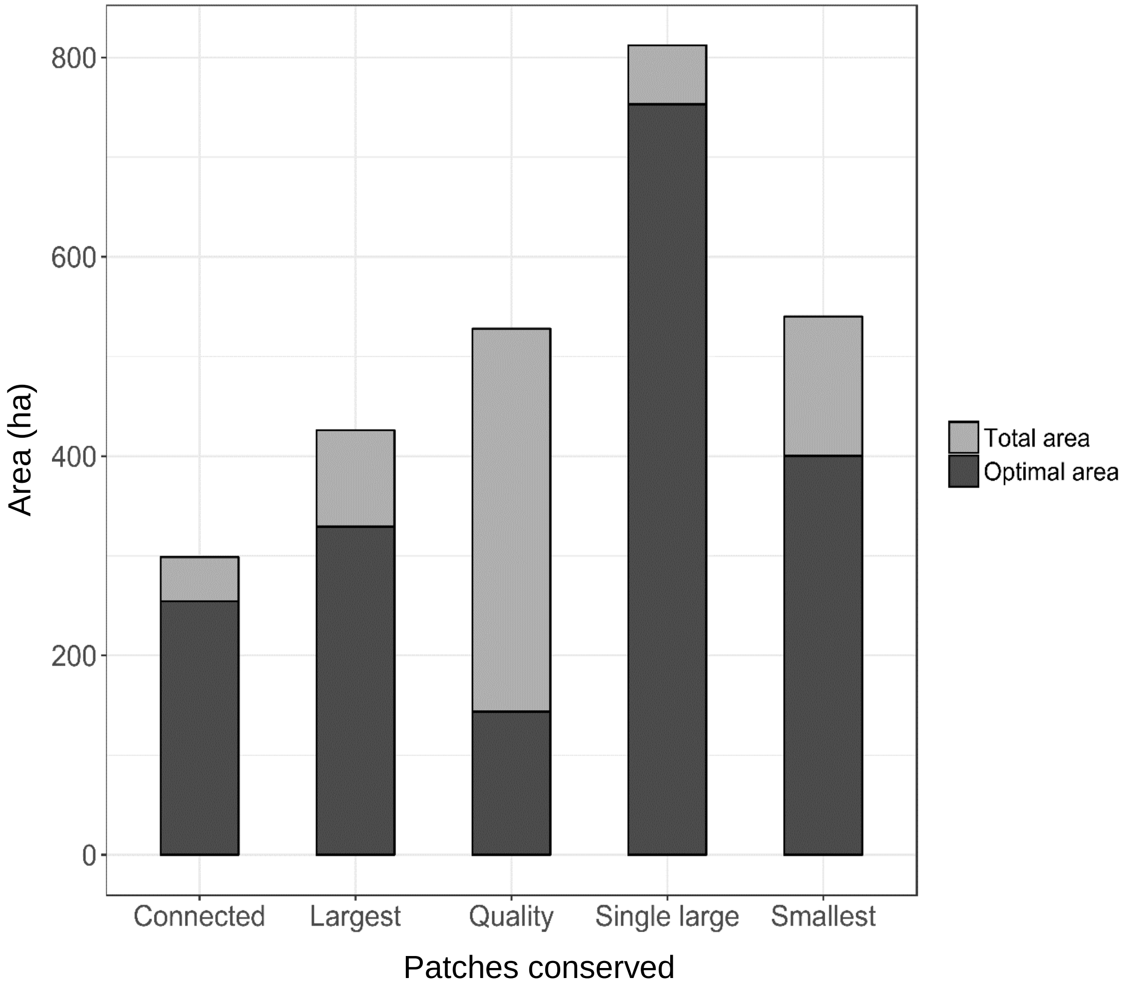


Figure 5.2. Area required for each network considered to achieve ≥95% probability of persistence over 100 years for all five species: protecting the most connected patches, 2+ largest patches, highest quality patches, single large patches* and greater number of the smallest patches across the network (see *Methods* for full explanation of scenarios). Displays the smallest area required to predict 95% chance of persistence for the most demanding species ("Optimal area") and the smallest area needed to predict 95% chance of persistence for all species combined (considering optimal patch overlap between species) ("Total

area"). [*]as it stands, no single large papyrus swamps are sufficient to ensure ≥95% probability of persistence for white-winged swamp-warbler (see text for full explanation).

Discussion

The results of this study highlight that differences in the ecology of species lead to differences in the outcomes of commonly recommended approaches to protected area designation and management, while disparity in the relative effectiveness of approaches was also evident depending on the total area available for investment. For the conservation of individual species, focusing on habitat quality is the most effective approach. In contrast, should the aim be to explicitly conserve multiple species, focusing on connectivity is the most efficient method, due to greater congruence of well-connected patches between species. Thus, designing protected networks based on one species does not necessarily guarantee the viability of all, even for those specialist species occupying the same general habitat. However, with consideration of the dispersal capabilities, carrying capacities, turnover and habitat preferences of those species residing in a network, combined with knowledge on how much habitat is available for protection, informed decisions on where to invest resources can be made.

Strategies for metapopulation persistence

Managing viable metapopulations has become more commonplace than concentrating resources on small, isolated populations (Hanski et al. 1996). Guidance for creating more effective ecological networks recommends that sites are first made better, followed by bigger, the creation of more and finally more joined sites (Lawton et al. 2010). However, variation in the ecology of species residing in population and habitat networks evidently leads to differences in the most effective network for ensuring a high probability of persistence, which must be considered when deciding which parts of the network are most important (Gutierrez 2005).

Dispersal ability is key for the response of a species to levels of isolation (Hanski 1999a). Costs are incurred by poor dispersers crossing unsuitable habitat, in terms of energy and the risk of failing to locate suitable habitat (Bonte et al. 2012), while those with high dispersal capabilities receive little benefit from connected sites for they are not restricted in their ability to reach desired areas (Bennett 2003). This study is the first to quantitatively infer relative dispersal distances for papyrus endemic birds. Although we recognise that using empirical data for metapopulation parameter estimation can cause biased estimates (Moilanen 2002), they do suggest variation in the capacity to disperse between species. In terms of probability of metapopulation persistence and overall metapopulation size, enhancing connectivity between sites was one of the least effective species-based strategies for those with the highest and lowest dispersal abilities in this study. Meanwhile, consistent with previous work (e.g. Thomas 2000), connectivity was a useful strategy to assist those capable of intermediate levels of dispersal to utilise desirable sites within the network, at least when more habitat was available. Species with comparatively higher dispersal capabilities (Carruthers's cisticola, white-winged swamp-warbler and papyrus yellow warbler) also have the freedom to choose which sites to utilise within the limits of suitable habitat available (Glorvigen, Andreassen & Ims 2013), hence why these species benefited from higher quality habitat at lower levels of area compared to the other options explored. Relative population sizes were notably higher within a network of high quality patches for these species, thus concentrating on this strategy at low levels of habitat had the capacity to protect more individuals within the available wetland, and enhance the likelihood of persistence overall (Ye, Skidmore & Wang 2013). Enhancing quality also has the potential to promote connectivity through a higher number of dispersers (Hodgson et al. 2009b), which could also be why connectivity itself made little difference to these species. Intermediate and low dispersers (greater swamp-warbler, white-winged swamp-warbler and Carruthers's cisticola) were also generally found to persist at higher densities than those with the ability to move the farthest (papyrus yellow warbler), which dispersed more frequently, potentially to ensure the densities within each patch were low, and avoid competition from others (Baguette et al. 2013). In turn, protecting high quality sites was consistently the best strategy for those living at higher densities to achieve 95% probability of persistence.

The preservation of large sites is often favoured by conservation managers for their high carrying capacity (Hanski 1999a), either because of their greater size or higher levels of heterogeneity (Thomas et al. 2001). The results here confirm that maintaining a network of bigger sites does consistently produce a higher population size than a network of smaller sites with the same total area. However, protecting larger sites is only beneficial for those with lower (regional) carrying capacities to boost population sizes (Griffen & Drake 2008) when levels of habitat are low. At equivalently low levels of habitat, for species with high regional carrying capacities such as Carruthers's cisticola and white-winged swamp-warbler, investing in high quality sites was the best option for obtaining a high population size, and therefore enhanced the likelihood of long-term persistence. Some species appeared to occupy smaller habitat patches than others in this study. However, these smaller patches alone were clearly unsuitable for persistence over the long-term when the habitat available was low, hence persistence was enhanced by the maintenance of large sites. Since these species are also capable of dispersing only short distances, smaller sites could act as useful stepping stones to reach large sites (Saura, Bodin & Fortin 2014), rather than areas that should be relied upon alone for metapopulation survival.

Finally, papyrus endemics vary in their preference to occupy the edge and interior parts of the swamp (Britton 1971; Donaldson et al. 2016). Smaller, more fragmented sites exhibit more edge than larger sites (Fahrig 2003). As expected, interior species had notably smaller population sizes when multiple smaller sites were preserved, while those residing at the edge of swamps displayed a steady increase in population regardless of smaller or bigger sites being maintained. Similarly, the threshold level of persistence for edge species differed marginally between strategies, while for papyrus yellow warbler, a species commonly located within the interior of swamps, preserving smaller sites was clearly the least favourable option.

Protected networks for multiple metapopulations

Protected area networks aim to be representative of viable populations of multiple species (Howard et al. 2000; Margules & Pressey 2000). However, making decisions beyond single species to encompass the needs of multiple species is a challenge for those involved (Opdam *et al.* 1995; Akcakaya, Mills & Doncaster 2007). To combat this, conservation managers traditionally select ‘umbrella’ species, using one species with similar needs as a surrogate for another (Opdam *et al.* 1995; Akcakaya, Mills & Doncaster 2007), assuming the community as a whole will benefit from measures specified by individual species programmes (Bennett et al. 2015). Previous studies have also demonstrated the capacity of parameters in metapopulation models to predict dynamic patterns of other related species (e.g. Wahlberg et al. 1996). However, when multiple target species occupying the same habitat exhibit varying responses to conservation efforts, using the requirements of one species to meet the needs of others is problematic.

The importance of quality for the survival of single species has increasingly been recognised (Franken & Hik 2004) and incorporated into metapopulation dynamics (Thomas et al. 2001), due to its role in providing high source populations for recolonization and preventing the network from overall extinction (Glorvigen, Andreassen & Ims 2013; Heinrichs, Bender & Schumaker 2016). Improving habitat quality through management can reduce the amount of habitat required overall to sustain viable populations of species (Lawton et al. 2010). Our evidence from papyrus avifauna supports this assumption; prioritising conservation measures on high quality (high population density) habitat patches produced the most effective results in terms of probability of persistence and estimated metapopulation size after 100 years (Figure 5.1). However, the elements that represent high quality are species-specific (Mortelliti, Amori & Boitani 2010), thus when the optimal quality networks for each species are merged, the amount of habitat required overall is higher than other planning options.

Considering the optimal networks for all species together, concentrating on a few large or the most connected sites requires comparatively less area than preserving either high quality wetlands, or investing in lots of small patches across the network. Bigger sites offer numerous benefits, such as the availability of greater habitat heterogeneity that in turn, can support a wider range of species at one site (see Chapter 2; Donaldson, Wilson & Maclean 2017). However, securing or restoring sites of a sufficient size for persistence is often not possible in modern landscapes (Doerr, Barrett & Doerr 2011). In this case, spreading resources across the network and enhancing connectivity essentially acts as a bigger site, offering the same likelihood of persistence over the long-term for multiple species, providing it is within the dispersal capabilities of those requiring more overall area. In general, the assumption is that “the bigger the reserve, the better” (Shaffer 1981), but single patches rarely persist over the long-term unless they are exceptionally large relative to the species in question (Thomas, Thomas & Warren 1992). Consistent with this, investing in a single large site was evidently the least favourable strategy to achieve a viable persistence for all species. Not only does this require a large amount of habitat to sustain populations in its own right, for those with low turnover, protecting single sites was not sufficient to maintain a high probability of persistence.

Conservation implications

It is well documented that the more habitat available, the longer a regional population can persist (Heinrichs, Bender & Schumaker 2016). Indeed, our results confirm that the persistence and population size of all species can be maintained at adequate levels regardless of the conservation strategy when the habitat across the network is plentiful. In such situations, species-specific management is not necessarily required (Tilman et al. 2017), and networks should instead be situated and designed with consideration of more practical constraints, such as ownership and finances (see references in Donaldson, Wilson & Maclean 2017). However, it is evident that the resources available for conservation worldwide are limited, in terms of both money (McCarthy et al. 2012) and space (Lawton et al. 2010). Impoverished tropical countries in particular struggle to meet demand for land, as well as maintain rich levels of biodiversity (Myers et al. 2000; Fisher & Christopher 2007), and so it is not apt or feasible to conserve all suitable space for wildlife (Maclean, Bird & Hassall 2014). Recent evidence suggests that concentrating on persistence alone could mean that we are underestimating how much habitat is required to prevent extinctions (Ceballos, Ehrlich & Dirzo 2017), and our results suggest that the area required for adequate persistence requires only a low population size. However, population declines precede extinction, thus designing protected area networks around persistence alone may not be enough to ensure populations are retained above the levels stated on the IUCN (International Union for the Conservation of Nature) Red List, and may explain why protected areas often fail to enhance or maintain populations of targeted species (Butchart et al. 2012).

In common with habitats worldwide, papyrus swamps have suffered high rates of degradation over the past few decades (Owino & Ryan 2006; van Dam et al. 2014), primarily from population growth, unsustainable levels of harvesting, lack of legal policies and weak enforcement of any restrictions in place (van Dam et al. 2014; Kipkemboi & van Dam 2016). Wetland protection across East Africa is low (Fanshawe & Bennun 1991; Pomeroy, Tushabe & Green 1999; Kipkemboi & van Dam 2016), and the protection offered to the species residing within these wetlands, such as Important Bird and Biodiversity Areas, tend to focus on large sites hosting high numbers of specific species (e.g. BirdLife International 2017b). However, focusing on large sites in isolation is not sufficient to guarantee the persistence of all species, and would require an unrealistic amount of wetland to be protected to guarantee survival in this way. Also, with high demand for land across East Africa, securing large sites alone is impractical (DeFries et al. 2007) and restoration can be expensive and time-consuming (Possingham, Bode & Klein 2015). Together with this, predicted future weather events across this region (Doherty et al. 2010; Ponce-Reyes et al. 2017) suggest that environmental stochasticity should be a consideration, and investing available resources into single sites is risky should extinction occur (Schnell et al. 2013). Instead, papyrus-specialists will benefit from a consideration of metapopulation dynamics, with investment spread across a network of appropriately sited, well-managed, large wetlands.

Since connectivity often resulted in relatively lower population sizes for each species compared to larger, higher quality sites, swamps should be carefully managed to maintain their overall linkage, through the reduction of habitat loss and permitting moderate levels of disturbance (Donaldson et al. 2016). With habitat loss occurring at a rapid rate across parts of East Africa (Maclean, Wilson & Hassall 2011), securing some of the larger sites for these species now, will be crucial to ensure persistence of papyrus-passerines over the longer-term. In practical terms, participatory approaches by those on the ground will be pivotal (Jacob et al. 2014; Kipkemboi & van Dam 2016; Tilman et al. 2017) to ensure sites are managed throughout the network. The decentralized governance already established in Uganda provides a key mechanism with which to implement this (Maclean, Boar & Lugo 2011), recognising that those living within proximity to swamps receive most benefit from appropriate management regimes (Maclean et al. 2003d).

Conclusion

Overall, this study demonstrates that differences in ecological characteristics can influence the response of species to networks prioritising bigger, higher quality, numerous smaller or more connected sites. Conservation managers must recognise these discrepancies when designing ecological networks for biodiversity in order to maintain or enhance long-term persistence and secure adequate population sizes. For single species conservation programmes, managing sites to maintain high quality is an effective approach. However, aspects that maintain quality differ between species, thus multi-species conservation programmes may gain from prioritising strategies that are more congruent between species, such as enhancing connectivity across the network. With this in mind, utilising surrogate species to predict the conservation outcomes for other species occupying the same landscape may not be sufficient, particularly when faced with differences between the habitat requirements of individual species, and the extreme habitat destruction biodiversity is faced with today. But by investing in the management of a few large sites and maintaining sufficient levels of connectivity across the landscape, the long-term persistence of multiple species can be sustained.

Chapter 6:
General discussion

Landscapes worldwide are becoming increasingly fragmented, primarily as a result of human activities (Newbold et al. 2015). Although theory has vastly enhanced our understanding of the response of populations to fragmentation (MacArthur & Wilson 1967; Hanski & Gilpin 1991; Hanski 1999a), and led to the development of conservation at the landscape-scale, many of the practical considerations paramount for conservation planning in the 21st century remain to be firmly tested and incorporated into decision making. Papyrus wetlands in East Africa have provided a useful system in which to test and apply ideas associated with the complexities of managing and conserving species in a realistic landscape context. Finances available for conservation are scarce, and conservation decisions ought to consider the reliance on this habitat by people, as well as multiple species of endemic passerines, which are declining at an even faster rate than the wetland itself (Maclean, Wilson & Hassall 2011). As is common with conservation worldwide, current conservation efforts are site-based, with little consideration of uncertainty in the future, and are situated among a landscape dominated by intense land use. In this chapter, I first review the findings from my thesis in relation to the objectives listed in Chapter 1, before drawing together the contributions of my research to the conservation of wetland birds in Africa, and the general implications for the conservation of fragmented landscapes. I conclude with suggestions for future avenues to be explored as a result of this research.

i. New perspectives on landscape-scale conservation in the face of 21st century environmental pressures

Theoretical work has undoubtedly enhanced our understanding of reserve design and landscape-scale conservation. However, the literature available on this is broad and impedes the ability of conservation practitioners and decision-makers to make informed decisions about which strategies to adopt and when. In Chapter 2, I reviewed the literature in the context of 21st century pressures including climate change, disease, pollution and invasive species (Millennium Ecosystem Assessment 2005), and highlighted the trade-offs that exist between the recommended strategies of bigger, better, more and more joined sites (Lawton et al. 2010). Although trade-offs have been examined previously (e.g. the SLOSS debate), to my knowledge, this is the first review to collectively and explicitly consider the trade-offs within and between the recommended strategies associated with reserve design. In the context of environmental change, although ongoing threats to biodiversity demand the protection of large and high quality habitats, there are rare cases when small, less-connected sites can be vital for persistence (e.g. for species threatened by disease outbreaks). Enhancing habitat quality is effective when habitat requirements are well-known and can be managed adequately, particularly in the light of climate change and environmental extremes, but evidence suggests that in fragmented landscapes, focusing on size and connectivity are likely to be more effective. I aimed to go beyond the conclusion that the optimal case-by-case solution is “context dependent”, and drew together existing evidence to provide an evidence-based framework indicating the main factors for decision-makers to consider when selecting among conservation strategies. Several factors that were not conventionally considered were incorporated, namely the configuration of the landscape, largely as a result of changing land-use practice, the balance between climate variability and vulnerability, and management practicalities, including cost and space. I demonstrated the potential application of this framework using the case-study of land spare-land share (Chapter 2); illustrating how theory associated with reserve design could help advance this intensive debate, and in my own research on papyrus-specialist birds, showed how an understanding of the key principles discussed could assist with landscape-scale conservation prioritisation within an ecological network experiencing these modern-day challenges (Chapter 5).

ii. The needs of local people are compatible with conservation planning

In Chapter 2, I emphasized the value of enhancing habitat quality for conservation planning. Managing habitat to restore or maintain quality classically involves limiting anthropogenic activity (Hodgson et al. 2009b), but this presents a challenge in areas where people rely on the resources provided by these habitats for their livelihoods. In Chapter 3, I show that specialist species of birds can tolerate disturbance caused by local people for subsistence use, and providing it takes place within large swamps with some remaining undisturbed wetland, the population density is even enhanced in the presence of disturbance. In line with our hypothesis, these species have likely evolved under a long history of disturbance, and the inhabitation of people replaced the role of natural (non-human) disturbances in maintaining a more open habitat (Maclean et al. 2006). Although these ideas have been incorporated into the management of temperate systems (Bengtsson et al. 2000; Seymour, White & DeMaynadier 2002), the principles have seldom been explored or applied in the tropics. Moreover, exploring the response of the same species to the spatial configuration of habitat in Chapter 4, suggested that disturbance was also unlikely to adversely affect the survival or colonization ability of species residing across habitat networks. Demonstrating that biodiversity can be maintained alongside the low-intensity human use of wetlands has real potential for minimising the conflict that exists between conservation management and local people.

iii. Using patch-level dynamics to assess resistance and resilience to extinction

Effective conservation planning is required to ensure that the limited resources for conservation are used wisely in the limited time available to reach ambitious global biodiversity targets. However, the conventional approaches to this focus on boosting populations at key sites (Coppolillo et al. 2004). This is problematic amid the pressures faced by ecosystems in the 21st century (Chapter 2), as species may not reside in single sites indefinitely, and the surrounding landscape plays a role in their regional persistence. In Chapter 4, I used a novel framework to prioritise sites based on their ability to resist extinction through high survival, and be resilient to extinction through high probability of colonization, to make an explicit link between metapopulation dynamics and conservation planning, and help ensure priority sites have the capacity to cope with future change. This chapter identified the importance of habitat configuration for the persistence of the focal species, highlighting the parts of the network that were likely to be most important for long-term persistence across species. In line with theoretical and empirical evidence discussed in Chapter 2, patch size and aspects of habitat quality (Chapter 3) were particularly important for the survival of most species. However, contrary to traditional assumptions (Hanski et al. 1996), connectivity was not a predictor for the colonization of all species; instead, patch size and quality were important for the likelihood of a species to (re)colonize a patch. Despite subtle differences between the patch-level dynamics of the species' using the habitat network studied here, mapping the predicted levels of resistance and resilience across the network showed that there were overlapping sites whereby all species have a high chance of survival, combined with the ability to respond and recover from change in the future.

iv. Designing effective ecological networks for the conservation of multiple species

After highlighting the key principles to be considered when deciding on the most effective strategy for landscape-scale conservation in Chapter 2, these ideas were applied to my study system in Chapter 5. Chapter 2 emphasized the importance of defining the conservation goal, and how distinguishing between multi species and individual species conservation programmes can help prioritise between bigger, better, more or more joined sites. Protected area networks aim to be representative of all species (Margules & Pressey 2000; CBD 2011), though data for particular species, such as rare or threatened species, are often scarce. In turn, the requirements of single species are often used as surrogates for wider aspects of biodiversity, thus assuming that the whole community will benefit from single species conservation (Opdam *et al.* 1995). However, as shown in Chapter 4, the patch-level dynamics of individual species can differ, but the implications of this for the long-term persistence of species has rarely been explored.

In Chapter 5, I demonstrated that differences in the ecological characteristics of species led to differences in the recommended outcomes for protected area designation and management, and the optimal outcome depended on the area of habitat that can be protected across the network. To my knowledge, this is the first study to clearly illustrate how the optimal conservation strategy for long-term persistence and population size changes with area protected, and depending on the individual species considered. Consistent with the recommendations from Chapter 2, enhancing habitat quality was the optimal approach for the conservation of individual specialist species. However, because habitat quality is species-specific (Mortelliti, Amori & Boitani 2010), a large amount of habitat was required to ensure the persistence of all species. Instead, focusing on large and well-connected swamps required the least amount of habitat to guarantee the persistence of these specialist species residing across the landscape (Chapter 2; Chapter 5). Thus, where only incomplete knowledge is available for some members of a group of species sharing the same broad habitat type, targeting conservation measures based on overall habitat connectivity may be more effective than assuming that optimal quality for one species is a reliable guide for the others.

Conservation implications

African wetland birds

Overall, the work of this PhD has enhanced the ecological knowledge of a group of endemic wetland birds that have been subject to little study to date. Wetlands have declined rapidly across sub-Saharan Africa over the past few decades (Maclean, Wilson & Hassall 2011), leading to the decline of all species of papyrus-specialist passerines, and the need for conservation protection (Maclean, Bird & Hassall 2014). Throughout this thesis, the potential consequences of the loss of wetland habitats have become clearer, and possible ways to protect these wetlands and their fauna from further environmental change have been investigated.

Ensuring swamps stay sufficiently large was important for securing high densities of most of the study species (Chapter 3), while size and overall wetland area was also important for persistence (Chapter 4; Chapter 5). Wetland shape has not been conventionally considered by legislation or existing guidelines, but given the evident role of circularity for species density (Chapter 3) and persistence (Chapter 4), consideration should be given to where and how people are draining individual swamps. Previous work concluded that the value to local people obtained from the wetlands themselves is higher than the value of draining swamps (Maclean et al. 2003c). In Chapter 3, I showed that papyrus-specialists are tolerant to disturbance from subsistence use by local people, and Chapter 4 suggested that localized disturbance did not strongly influence the ability of these species to survive in or colonize particular sites. Since habitat loss is evidently problematic for both wildlife and people, while the modest use of papyrus by people can concurrently maintain biodiversity, the most feasible solution for wetland conservation in the tropics would be to involve people, and recognise the role of disturbance in landscapes modified over thousands of years. Guidelines should, however, clearly identify the importance of retaining intact areas of habitat in larger swamps, emphasising that widespread harvesting of papyrus culms in these swamps is undesirable (Chapter 3). With comparable levels of productivity in other wetland vegetation types following similar disturbances for socio-economic gain (Muthuri, Jones & Imbamba 1989; Terer, Triest & Muasya 2012), such recommendations would likely apply across other tropical wetland systems, including *Phragmites* and *Typha* species (Chapter 3).

Few papyrus wetlands across Africa have any conservation or protections status (Kipkemboi & van Dam 2016), while efforts to conserve papyrus birds are primarily confined to the identification of Important Bird and Biodiversity Areas (IBA's) or Ramsar sites. The need to extend the current network of these sites to other areas important for these species has been recognised (Byaruhanga, Kasoma & Pomeroy 2001), but to date there has been a lack of data to support such designations. This is of particular importance across the study region; hosting high densities of papyrus, as well as being a notable stronghold for populations of papyrus-endemic passerines (Maclean, Bird & Hassall 2014). In Chapter 4, I identified several key sites at Lake Bunyonyi that are worthy of investment, that are not only expected to survive at least over the short-term, but likely have some capacity to respond to future change. Papyrus swamps are subject to seasonal drainage and intense forms of disturbance, while wetlands in general may be vulnerable to environmental change, including infrequent and more severe rainfall events (Mitchell 2013), so ensuring the ability to recover (i.e. be recolonized) following regrowth or reflooding, will be key to ensuring the survival of these species. At least at Lake Bunyonyi, achieving concurrent resilience to extinction of all species is problematic (Chapter 4), highlighting the need to protect and restore particular areas of the lake in which colonization likelihood and hence resilience, is high. Nyamuriro IBA (01°09'49.32"S; 29°48'40.32"E) at the north of the lake does appear to capture a series of the most important sites for papyrus-endemic birds but several other areas would warrant conservation status, including Mugandu/Mukahungye swamp at the far south-west (01°24'28.80"S; 29°55'32.88"E), Kaijengye at the south-east (01°21'38.88"S; 29°58'21.72"E), and Kyeni towards the north-east of Lake Bunyonyi (01°13'26.40"S; 29°52'47.64"E). Kagoma swamp at the south-west side of the lake (01°21'25.20"S; 29°53'46.68"E) has been offered some protection due the presence of sitatunga antelope (S. Katungi *pers. comm*), though the importance of this wetland for the presence and abundance of papyrus-endemic birds should also be acknowledged (Chapter 4; Chapter 5).

One problem with current approaches to wetland conservation in general is that they are largely site-based (Coppolillo et al. 2004) and despite the fragmented nature of these habitats, tend to focus on wetlands in isolation (Amezaga, Santamaría & Green 2002), with criteria for designation geared towards large sites hosting high numbers of species (Maclean, Wilson & Hassall 2011). However, in Chapter 5, I show that solely focusing on even the single largest site did not guarantee the persistence of all papyrus-specialist passerines over the long-term, and would have to remain virtually intact to help guarantee persistence for those that could survive there. Given the rate of habitat loss and degradation in the region (Maclean, Wilson & Hassall 2011), combined with threat from environmental change and climate warming (Doherty et al. 2010; Ponce-Reyes et al. 2017), sites remaining at their current state over coming years is unlikely. On the contrary, wetland-restricted species would benefit from a consideration of metapopulation dynamics, and investing in a network of habitats. In reality, it is not feasible to protect all wetland patches in a network (Maclean, Bird & Hassall 2014), so deciding where to invest to ensure the persistence of all species, depends on how much wetland you can afford (considering the economic value of conserving swamps over conversion [Maclean, Boar & Lugo 2011] and development [Schuyt 2005]) or feasibly protect, or how much wetland habitat remains (Chapter 5). Since conservation ought to consider the preservation of all papyrus-endemic passerines, conserving networks made up of the largest and/or most connected sites was evidently the most efficient method under area constraints (Chapter 5), and would offer concurrent benefits under climate change, such as the facilitation of species' range shifts (Chapter 2), and the persistence of populations over the long-term (Chapter 4). In practice, this would involve a participatory approach (Jacob et al. 2014; Tilman et al. 2017), whereby people across the lake coordinate to ensure drainage regulations are adhered to, and that they are managed sufficiently with modest resource use (Chapter 3).

Fragmented landscapes

Aside from the conservation recommendations associated with a suite of endemic African wetland birds, this thesis has advanced our understanding of conservation in fragmented landscapes more generally, and articulated and applied several considerations for those carrying out landscape-scale conservation. Chapter 2 stated the main factors to contemplate when deciding where and how to conserve ecological networks, supported by the extensive literature available on this topic. Key amongst the considerations, were the conservation goal, species' traits, landscape configuration, and the risk of future environmental extremes or climate variation.

In essence, the recommended strategies vary both at the site-level (Chapter 4), and across a network (Chapter 5). Slight variation existed between the requirements of individual species and multiple species at the site-level, but this did not significantly alter the sites prioritised for investment (Chapter 4). Meanwhile differences were also apparent between single and multi-species recommendations at the network level; emphasizing the need to carefully consider the conservation goal and needs of individual species collectively, when investing in networks of fragmented habitat (Chapter 5). Single species are often used as surrogates for other species in conservation (Opdam *et al.* 1995; Wahlberg, Moilanen & Hanski 1996). However, even specialists from the same guild and residing in the same habitat networks can possess different dynamics, which in turn led to variation in the recommended optimal networks (Chapter 5). But with an understanding of the key ecological characteristics of the species in need, and knowledge of how much area can be protected, effective habitat networks can be designed and prioritised (Chapter 5).

Throughout this thesis, the importance and desire to maintain a number of large sites for conservation is evident (Chapter 2-5), but when this is not possible, as is now the case across much of the world's landscapes, consideration of how much habitat is available overall (Chapter 5), combined with careful consideration of the goal and characteristics of species (Chapter 2; Chapter 5), can ensure other strategies are equally, or more effective. Maintaining sufficient high quality habitat is a priority, especially in the face of environmental change to promote range shift (Chapter 2), but consistent with the evidence discussed in Chapter 2, this recommendation does not hold in fragmented landscapes utilised by multiple species. In such circumstances, protecting large and well-connected sites is advisable (Chapter 5). In addition, conservation planning often assumes that enhancing connectivity is important, without *a priori* investigation (Hodgson et al. 2009b). Chapter 4 illustrates the potential pitfalls of this assumption, and highlights the need to determine the consequence before investing in this strategy, as not all species benefit from increasing connectivity.

The importance of involving and considering those who are using the landscape has also been emphasized here. Historically, people have not been considered in conservation planning (Chapter 3), but in a world dominated by land use change, methods that account for human interactions with the environment are paramount. Conservation traditionally excluded people, with protected area designation adopting the “fences and fines” approach (Brandon & Wells 1992), but this is evidently unpopular and unfeasible (Hutton, Adams & Murombedzi 2005), especially in areas where the livelihoods of people are closely dependent on natural resource use. Chapter 3 reveals the potential to minimise the conflict between humans and wildlife, by demonstrating the role that human activities can play in maintaining biodiversity.

Future directions

This thesis has greatly increased knowledge of a group of threatened bird species in East Africa, as well as contributing to our understanding of how their conservation should be prioritised. I now discuss a set of future directions that could help to develop the findings reported here, and overcome some of the potential limitations experienced.

First, it would be useful to take a region-wide approach, and test and apply some of the predictions and recommendations described to areas elsewhere in Africa. I have proposed that the subsistence use of papyrus is compatible with wetland bird conservation (Chapter 3), and I believe this would be equally likely to apply to other tropical habitats exposed to disturbances from megaherbivores, and subject to long histories of human use. However, this would merit further investigation, as would explicit tests of the influence of human activities on biodiversity, to assess the reliability of my proxy measures of disturbance (Chapter 3). I am the first to develop metapopulation models for papyrus-endemic birds (Chapter 5), but to be most useful for the conservation of these species, they ought to have the ability to be applied to other habitat networks (Hanski et al. 1996). Thus, the model predictions should be tested both at this site and elsewhere (Hanski 1994b), to ensure the validity of the parameters estimated, and assess their potential for wider application to other habitat types, for example. Advances in movement technology would also enable some of the parameter values, namely the dispersal parameter, to be quantified without reliance on modelling techniques (Moilanen 2002), and would also improve our understanding of the daily and seasonal movements of these species.

Information on the extent of wetlands across Africa is currently lacking (Davidson 2014; Kipkemboi & van Dam 2016), and up to date land cover estimates are urgently required to fully establish the degree of threat facing these systems. Specifically, investigating patterns and drivers of loss, combined with an understanding of how these patterns directly impact diversity, would be beneficial for providing potential guidelines on sustainable use. Direct and indirect effects of environmental change on papyrus swamps are recognised (Chapter 1), though the impacts of climatic variation on the distribution of papyrus wetlands, and the subsequent distribution of the papyrus-endemic bird species among protected or priority sites, particularly following extreme weather events, merits further investigation. Sustainable wetland management is a topic that has been subject to much discussion following recognition of the importance of natural resource use by people, and incorporated into various international agreements (e.g. Smart & Canters 1991; CBD 2010), but further research is required on the ecology of papyrus wetlands for sustainable utilization, as well as aspects associated with governance and socio-economics (van Dam et al. 2014). Although I explored the impacts of disturbance on biodiversity in Chapter 3, and estimated how much habitat is required across networks for persistence in Chapter 5, conclusions could not be formulated on how much papyrus may be extracted or drained before it had detrimental effects on wildlife, especially under the time-frame of this research. Restoration of papyrus has been proposed over more recent years (Morrison et al. 2012; Kiwango et al. 2013), and parts of this thesis suggest this could be a fruitful approach to assist with the conservation of wetland birds, given the advantages of larger swamps for species persistence (Chapter 4; Chapter 5) and tolerance to disturbance (Chapter 3; Chapter 4). Research is lacking on the potential for this to balance the consequences of habitat loss (e.g. Whytock et al. 2017) and the response of biodiversity and people to this, but would be a welcome advance for the future of wetland conservation in the tropics.

Finally, another element beyond the scope of this thesis, yet has a significant place in wetland conservation, is the potential to explore the social aspects of wetlands from a more interdisciplinary point of view. Moderate progress in this field has been made and has contributed to some of the ideas within this research (e.g. Maclean et al*.* 2003d; Terer et al. 2012; Zsuffa et al. 2013), but developing ways to involve people, assess the feasibility of participation across networks as well as on a local scale, and a further understanding of the driving forces that lead to intense degradation and loss, would be beneficial for the implementation of conservation strategies associated with wetlands. Understanding the adaptive capacity of people to climate change is key for wetland conservation (Mitchell 2013); monitoring the impact of environmental change on the ecosystem services provided by papyrus swamps, and how people respond to altered regimes. Related to this, wetland loss and degradation across Africa is associated with a lack of policy, failure to adhere to restrictions in place (Kipkemboi & van Dam 2016), and ill-defined property rights (Adger & Luttrell 2000). Advancing our understanding of how and why people respond to or neglect such guidelines, where to target regulations for the most success, and methods to involve people and encourage cooperation, would be a significant step forward for wetland conservation across Africa. The decentralized governance in place in Uganda has shown promise (Maclean, Boar & Lugo 2011), and would merit application elsewhere on the continent.

Concluding remarks

Landscape-scale conservation has come to the forefront of conservation planning over recent decades, primarily as a result of increasing levels of fragmentation and the need to plan and compensate for changing environmental pressures. Strategic conservation planning is now more important than ever, with limited resources available to meet ambitious global biodiversity targets and combat rapid biodiversity declines before it’s too late. Clear recommendations accounting for what is practically achievable are lacking, while criteria for conservation planning and prioritisation still often fail to explicitly consider the importance of ecological networks at the required scale. In this thesis, I have synthesized the key concepts associated with reserve design to provide a framework for those involved in landscape-scale conservation amid 21st century pressures, and used a suite of endemic wetland bird species in East Africa to test some of these approaches to conservation. This work has made several important advances to both the conservation of the study system, as well as approaches for prioritising efforts across fragmented landscapes more generally. In the context of modern-day pressures, trade-offs were apparent between the four axes of reserve design (site area, quality, number and connectivity), but with careful consideration of the situation at hand, informed decisions can be made. Contrary to traditional assumption, conservation planning does not need to exclude people, particularly in landscapes subject to disturbances over historic periods of time. Finally, criteria for designating important areas for conservation ought to consider the role of networks in sustaining populations over the long-term. In practical terms, my research has aimed to demonstrate methods to increase the efficiency of site protection when there is a limited area available to be protected, particularly when multiple dependent species occupy the landscape and are in need of conservation protection. Overall, this work has contributed to the conservation planning process; assisting those responsible for making critical conservation decisions for fragmented systems, including African wetlands, to make informed choices on where and how to invest. With this in mind, I hope that conservation resources can be managed and utilised most effectively, in a bid to control the impending threat from habitat destruction, and ultimately help combat global biodiversity declines.

Appendix A: Chapter 3

Table A1. Top-ranking models (ΔAICc ≤ 2) for point counts of all five species.

	Formula	df	logLik	AICc	ΔAICc	Weight	Overall weight	R^2
	Greater swamp-warbler							
1	Circularity:MP - circularity - area - MP	8	-168.29	354.08	0	0.53	0.05	0.05
2	Circularity:MP - area:MP - circularity - area - MP	9	-167.89	355.68	1.6	0.24	0.02	0.06
3	Circularity:MP - circularity - area - MP + RD	9	-167.9	355.69	1.61	0.24	0.02	0.06
	White-winged swamp-warbler							
1	Circularity + area + MP + ND + RD - MP^2 - circularity:RD	11	-96.98	218.8	0	0.32	0.02	0.19
2	Circularity + area + MP + ND + RD - MP^2	10	-98.31	218.95	0.15	0.3	0.02	0.18
3	Circularity + area + ND + RD	8	-101.15	219.8	1	0.2	0.01	0.15
4	Circularity + area + MP + ND + RD - MP^2 + area:ND	11	-97.53	219.91	1.1	0.19	0.01	0.18
	Papyrus canary							
1	Area - MP + ND	7	-99.8	214.75	0	0.41	0.04	0.08
2	Area - MP	6	-101.51	215.88	1.13	0.23	0.02	0.07
3	Area - MP + ND + area:MP	8	-99.38	216.26	1.51	0.19	0.02	0.09
4	Area - MP + ND - area:ND	8	-99.52	216.54	1.79	0.17	0.01	0.09
	Carruthers's cisticola[†]							
1	Circularity + area + MP - ND + ND^2 + circularity:MP + circularity:ND	11	-132.22	289.28	0	0.71	0.06	0.17
2	Circularity + area + MP + MP^2 - ND + ND^2 + circularity:MP + circularity:ND	12	-131.86	291.12	1.84	0.29	0.02	0.18
	Papyrus yellow warbler[†]							
1	Circularity + area - RD - RD^2 + area:RD	9	-51.6	123.09	0	0.33	0.03	0.19
2	Circularity + area - PD + RD - RD^2 + area:RD	10	-50.85	124.04	0.94	0.21	0.02	0.21
3	Circularity + area - RD + area:RD	8	-53.27	124.05	0.96	0.21	0.02	0.16
4	Circularity + area - MP - RD - RD^2 + area:RD	10	-51.29	124.92	1.83	0.13	0.01	0.2
5	Circularity + area - RD - circularity:RD + area:RD	9	-52.57	125.04	1.94	0.13	0.01	0.18

Formula indicates the terms included in the model and the direction of their effect (±); Df=degrees of freedom; logLik= Log likelihood; AICc = Akaike Information Criterion corrected for small sample size; ΔAICc = difference in AIC between current and top model; Weight = weight of model within ΔAIC_c 2; Overall weight = weight of model within full model set; R^2 = the proportion of deviance explained by the fixed effects in the model by comparing to the deviance of the null model (intercept only model including nested random effects and offset) $(deviance_{null}-deviance_{model})/deviance_{null})$. †species also found in wetlands dominated by other vegetation types; Area = Log (patch area) (m^2); Circularity = circularity index of patch; Vegetation characteristics refer to proportion of each category within the survey area: MP (mixed papyrus/vegetation), RD (recently disturbed papyrus/mixed vegetation), PD (past disturbed papyrus), ND (undisturbed papyrus); terms marked with “^{2}” represent squared term of that variable; “:” indicates interactions between terms.

Table A2. Full model averaged output for models (ΔAICc ≤ 2) for point counts of all five species.

Variable	Estimate	Std. Error	Adjusted SE	z value	Lower CI (2.5%)	Upper CI (97.5%)	Pr(>|z|)	RI
Greater swamp-warbler								
(Intercept)	-9.599	0.089	0.090	106.296	-9.776	-9.422	< 2e-16	
Circularity	-0.158	0.098	0.099	1.594	-0.353	0.036	0.111	1
Area	-0.269	0.093	0.095	2.844	-0.454	-0.084	0.004	1
MP	-0.452	0.196	0.198	2.277	-0.840	-0.063	0.023	1
Circularity: MP	0.291	0.110	0.112	2.604	0.072	0.510	0.009	1
Area:MP	-0.212	0.215	0.217	0.976	-0.638	0.214	0.329	0.24
RD	0.063	0.070	0.071	0.890	-0.076	0.203	0.373	0.24
White-winged swamp-warbler								
(Intercept)	-12.004	1.579	1.595	7.526	-15.130	-8.878	< 2e-16	
Circularity	0.378	0.157	0.159	2.381	0.067	0.689	0.017	1
Area	0.763	0.142	0.144	5.311	0.481	1.044	0.000	1
MP	2.528	1.845	1.868	1.354	-1.133	6.189	0.176	0.8
ND	0.269	0.116	0.117	2.291	0.039	0.499	0.022	1
RD	0.216	0.081	0.082	2.646	0.056	0.376	0.008	1
MP^2	-10.624	8.282	8.388	1.267	-27.064	5.815	0.205	0.8
Circularity: RD	-0.225	0.128	0.130	1.733	-0.479	0.029	0.083	0.32
Area:ND	0.189	0.149	0.151	1.251	-0.107	0.486	0.211	0.19
Papyrus canary								
(Intercept)	-11.716	0.994	1.006	11.645	-13.687	-9.744	<2e-16	
Area	1.222	0.579	0.585	2.088	0.075	2.368	0.037	1
MP	-2.225	1.441	1.457	1.527	-5.081	0.631	0.127	1
ND	0.522	0.284	0.287	1.816	-0.041	1.085	0.069	0.77
Area:MP	2.239	2.719	2.753	0.813	-3.157	7.635	0.416	0.19
Area:ND	-0.212	0.283	0.287	0.741	-0.774	0.349	0.459	0.17
Carruthers's cisticola[†]								
(Intercept)	-10.999	0.316	0.320	34.340	-11.626	-10.371	< 2e-16	
Circularity	0.759	0.304	0.308	2.466	0.156	1.362	0.014	1
Area	1.433	0.364	0.369	3.885	0.710	2.156	0.000	1
MP[‡]	0.468	0.326	0.329	1.423	-0.177	1.113	0.155	1
ND	-1.428	0.612	0.620	2.305	-2.643	-0.214	0.021	1
ND^2	1.958	0.592	0.600	3.264	0.782	3.134	0.001	1
Circularity: MP[‡]	0.415	0.193	0.196	2.117	0.031	0.798	0.034	1

Variable	**Estimate**	**Std. Error**	**Adjusted SE**	**z value**	**Lower CI (2.5%)**	**Upper CI (97.5%)**	**Pr(>|z|)**	**RI**
Circularity: ND	1.214	0.445	0.451	2.691	0.330	2.099	0.007	1
$MP^{2‡}$	0.392	0.462	0.468	0.839	-0.525	1.309	0.402	0.29
Papyrus yellow warbler[†]								
(Intercept)	-13.329	0.621	0.628	21.226	-14.559	-12.098	< 2e-16	
Circularity	0.925	0.344	0.348	2.657	0.243	1.607	0.008	1
Area	1.850	0.537	0.543	3.406	0.786	2.915	0.001	1
RD[‡]	-0.674	1.341	1.354	0.498	-3.328	1.981	0.619	1
$RD^{2‡}$	-6.146	3.486	3.530	1.741	-13.066	0.773	0.082	0.67
Area:RD[‡]	2.286	1.050	1.062	2.152	0.204	4.368	0.031	1
PD	-0.969	1.249	1.265	0.766	-3.448	1.509	0.443	0.21
MP[‡]	-0.145	0.185	0.187	0.773	-0.511	0.222	0.440	0.13
Circularity: RD[‡]	-0.515	0.432	0.437	1.177	-1.372	0.342	0.239	0.13

Area = Log (patch area) (m^2); Circularity = circularity index of patch; Vegetation characteristics refer to proportion of each category within the survey area: MP (mixed papyrus/vegetation), RD (recently disturbed papyrus/vegetation), PD (past disturbed papyrus), ND (undisturbed papyrus); terms marked with "^{2}" represent squared term of that variable; ":" indicates interactions between terms; CI= Confidence Intervals; RI = Relative Importance (proportion of models within the set with this term included); [†]Species also found in wetlands dominated by other vegetation types. [‡]Includes wetland dominated by other types of wetland vegetation.

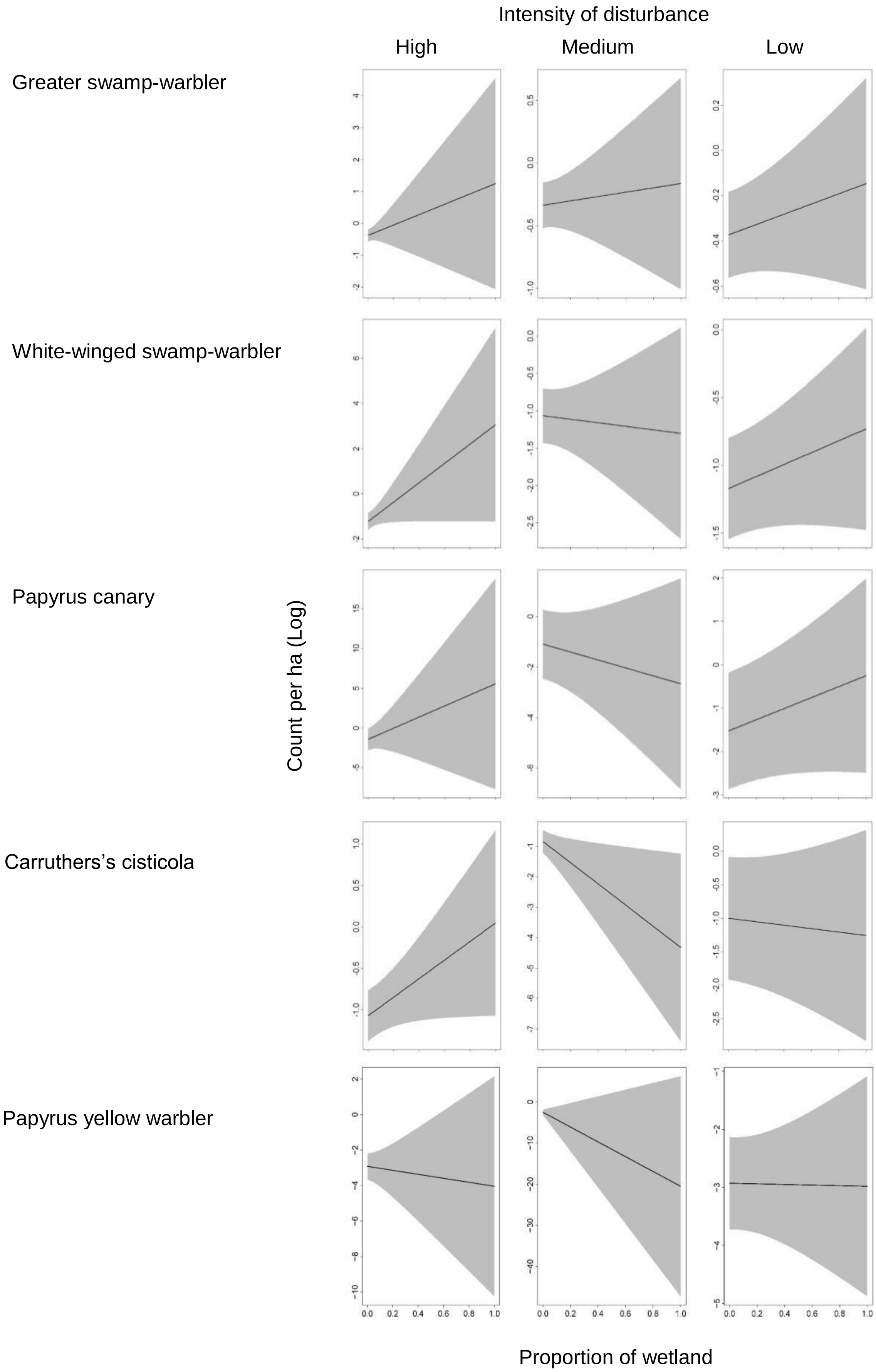

Intensity of disturbance
High
Medium
Low
Greater swamp-warbler
White-winged swamp-warbler
Papyrus canary
Carruthers's cisticola
Papyrus yellow warbler
Count per ha (Log)
Proportion of wetland
0.0
0.2
0.4
0.6
0.8
1.0

Figure A1. Effect of proportion of high (recently disturbed papyrus/vegetation), medium (past disturbed papyrus) and low (undisturbed papyrus) intensity disturbance, from left to right respectively, on the density of all five study species. Derived predictions from single term models (with offset and random effects) to illustrate overall effects of disturbance. ±95% confidence intervals are shown in grey. See main text (Chapter 3) for more detailed explanations.

Appendix B: Likelihood of detection of papyrus-specialist birds

In order to highlight the probability of detecting each of the five study species during an average presence-absence survey (see Chapters 4 and 5), additional data was collected on the frequency of detection within a subset of swamps surrounding Lake Bunyonyi. Given the need to quantify habitat associations and distributions across all sites within the breeding season, it was not feasible to conduct multiple visits across all sites during this research (e.g. Mackenzie et al. 2002; Royle et al. 2005). Alternatively, the amount of time spent at each patch during each presence-absence survey over the two years was recorded, and the probability of detection was modelled over time in a subset of sites. In turn, the probability of detection could be quantified:

Methods

Detection survey

Patches known to be occupied by at least one of the study species were visited between 07:00 – 13:30; within the survey period used for data collection (see Methods in Chapters 4 and 5). The number of observations per minute for each species (visual and/or by sound) were recorded over a period ranging from 30 to 146 minutes, from 1 - 6 randomly selected locations at a subset of swamps. Each observation was treated as a separate encounter, regardless of the number of individuals recorded (see below). Playback was used intermittently throughout, representing a typical survey. In total, over 29 hours of this detectability data was collected from 23 different points across 11 papyrus (0.08 ha~54.5 ha) and 6 broad wetland patches (2.03 ha~311.5 ha).

Analysis

Total length of survey during the presence-absence data collection varied depending on the size of the patch. Thus, data collected for the detectability survey was separated into small (<2.1 ha) and large (>2.1 ha) patches, based on the typical time spent surveying patches of these sizes. The datasets collected per species during each individual survey were analysed separately. To account for the temporal autocorrelation arising as a result of the tendency of birds to sing regularly for a few minutes before becoming silent again, data were analysed using generalized estimating equations (GEEs) with a binomial error structure in R package geepack (Halekoh, Højsgaard & Yan 2006). Using this approach, clusters of temporally-autocorrelated data points can be incorporated into the framework to estimate the mean probability of a bird being detected per minute. In turn, using standard probability propagation formulae, the likelihood of detection over any time interval can be estimated as follows:

$$P_t = 1 - (1 - P_1)^t$$

where P_t is the probability of detecting the bird during time t and P_1, the mean probability of detecting the bird per minute. In effect this offers a conservative approach to calculate detectability, since some of the delayed detections are likely to be “new” detections (i.e. a bird did newly arrive in that area of swamp) and detections are clustered into one minute periods, regardless of the number of detections within that minute. Clusters were identified using the R package mclust (Fraley et al. 2012), which automatically specifies the optimal number of clusters and assigns each data point to a cluster using a Bayesian model comparison. No prior was assumed. The cumulative probability was subsequently estimated over 120 minutes for small and large patches. The probabilities of detection were then plotted separately for the individual surveys for each species against time, and compared with the average presence-absence survey time for which a species was recorded as absent.

Results

Presence-absence survey data

Over the 2 years of data collection, presence-absence surveys were conducted for an average of 20 minutes for small papyrus patches, and up to an average of 164 minutes for large broad wetland swamps (Table B1). In small swamps, a species was recorded as absent following a mean of 14 minutes at patches for greater swamp-warbler, and a mean of up to 34 minutes for papyrus yellow warbler and Carruthers's cisticola. Meanwhile, large swamps were surveyed for a period of ~67 minutes for Carruthers's cisticola before marked as absent, and up to a mean of 98 minutes for papyrus yellow warbler. Greater swamp-warbler was not recorded as absent at any of the larger swamps over the 2 years of survey (Table B1).

Table B1. Mean survey time (minutes) spent at suitable small (<2.1 ha) and large (>2.1 ha) patches for all species during 2014-2015 presence-absence data collection. 'All patches' represents the mean time spent surveying all suitable patches for that species; 'Absent patches' shows the mean time spent at patches before that species was recorded as absent. Standard deviations are shown in brackets. n = total number of suitable patches surveyed within small and large categories.

Species	**Small patches (mins)**			**Large patches (mins)**		
	n	**All patches**	**Absent patches**	**n**	**All patches**	**Absent patches**
Greater swamp-warbler	487	20 $^{(15)}$	14 $^{(9)}$	32	130 $^{(81)}$	N/A
Papyrus canary	487	20 $^{(15)}$	18 $^{(13)}$	32	130 $^{(81)}$	86 $^{(39)}$
White-winged swamp-warbler	200	29 $^{(19)}$	27 $^{(17)}$	32	130 $^{(81)}$	77 $^{(26)}$
Papyrus yellow warbler	141	34 $^{(24)}$	34 $^{(24)}$	36	150 $^{(91)}$	98 $^{(43)}$
Carruthers's cisticola	130	35 $^{(25)}$	34 $^{(25)}$	30	164 $^{(95)}$	67 $^{(9)}$

Probability of detection

Results suggest that most species had >95% probability of detection within the average time spent surveying a patch before it was marked as absent (Figure B1). Within smaller swamps, Carruthers's cisticola and white-winged swamp-warbler had the highest chance of detection within the mean survey time, while papyrus canary had the lowest probability of being detected during the time spent surveying (Figure B1a). This is likely due to the low densities of these species in smaller patches, being relatively less vocal, and the fact they have been known to occasionally forage outside of swamps (Vande weghe 1981). Detectability within large swamps was notably higher, particularly within the longer time periods spent at these sites (Figure B1b; Table B1). The results show that the detectability of Carruthers’s cisticola was slightly lower in two (13%) of the surveys for larger swamps (Figure B1b), due to the fact that densities in these patches were relatively lower than some of the other sites surveyed here.

Overall, these results confirm the high likelihood of detection of the study species within the average presence-absence survey time. We recognise that there is a chance of false absences for some swamps within the network, particularly in smaller patches where species may move through more frequently. However, the analysis performed here is a conservative approach, and combined with previous research which demonstrated that surveying for more extensive periods made little difference to the records of these species (Maclean et al. 2006), we can be confident that the chances of missing a bird in a given patch during our surveys was relatively low.

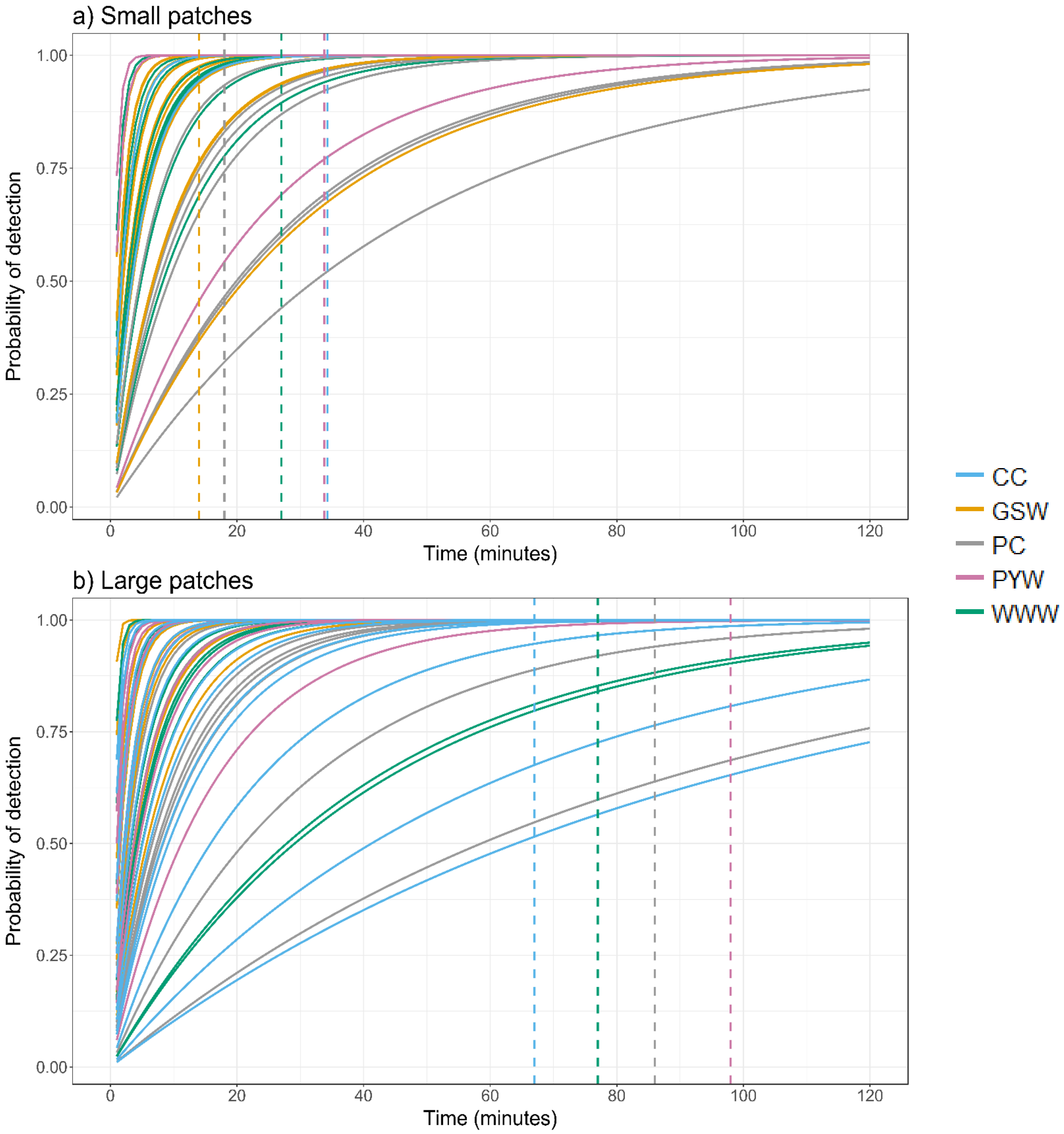


Figure B1. Probability of detection for each species within a) small patches (<2.1 ha) and b) large patches (>2.1 ha) over 120 minutes. Solid coloured lines represent the probability of detection for each species during each of the detection surveys (n = number of *detection* surveys in wetland areas containing that species): CC = Carruthers's cisticola (a: n=3, b: n=15), GSW= greater swamp-warbler (a: n=11, b: n=10), PC = papyrus canary (a: n=9, b: n=10), PYW = papyrus yellow warbler (a: n=3, b: n=8), WWW = white-winged swamp-warbler (a: n=8, b: n=11). Dashed coloured lines indicate the mean presence-absence survey time for patches where that species was recorded as absent over the 2 years of survey (see also Table B1).

Appendix C: Chapter 4

Table C1. Mean patch size (ha) and proportion of disturbed habitat in 2014 and 2015 for all wetland patches surveyed across the study site.

Wetland type	**Patch area (ha)**		**Proportion of disturbed wetland**	
	2014	**2015**	**2014**	**2015**
Papyrus	1.22	1.06	0.23	0.17
Broad wetland (Papyrus yellow warbler)	3.75	3.19	0.14	0.11
Broad wetland (Carruthers's cisticola)[†]	6.58	5.73	0.14	0.10

[†] Includes agricultural wetland

Table C2. Global models for colonization and survival analysis for all species: greater swamp-warbler (GSW), papyrus canary (PC), white-winged swamp-warbler (WWW), Carruthers's cisticola (CC), papyrus yellow warbler (PYW)

Species	Colonization	Survival
GSW	log(area) + connectivity + circularity + disturbed + undisturbed + mixed veg + disturbed^2 + mixed veg^2 + undisturbed^2	log(area) + connectivity + circularity + disturbed + mixed veg + undisturbed + disturbed^2 + mixed veg^2 + undisturbed^2
PC	log(area) + connectivity + circularity + disturbed + undisturbed + mixed veg + undisturbed^2	log(area) + connectivity + circularity + disturbed + mixed veg + undisturbed + disturbed^2 + mixed veg^2
WWW	log(area) + connectivity + circularity + disturbed + undisturbed + mixed veg + disturbed^2 + mixed veg^2	log(area) + connectivity + circularity + disturbed + mixed veg + undisturbed + disturbed^2
CC	log(area) + connectivity + circularity + disturbed + undisturbed + mixed veg + mixed veg^2	log(area) + connectivity + circularity + mixed veg + undisturbed + disturbed
PYW	log(area) + connectivity + circularity + disturbed + undisturbed + mixed veg	log(area) + connectivity + circularity + disturbed + mixed veg + undisturbed

Table C3. Full model averaged output (ΔAICc ≤ 2) for colonization analysis (2014-15).

Species	Variable	Estimate	Std. Error	Lower CI	Upper CI	Significance	RI
GSW	(Intercept)	-1.047	0.974	-2.966	0.872		
	area (log)	**0.732**	**0.179**	**0.380**	**1.083**	*******	**1**
	connectivity	**0.044**	**0.010**	**0.025**	**0.062**	*******	**1**
	mixed papyrus	-0.985	0.871	-2.696	0.727		0.78
	disturbed	-1.152	1.097	-3.307	1.004		0.73
	undisturbed	0.288	1.355	-2.375	2.950		0.59
	mixed papyrus ^{2}	-0.409	0.837	-2.052	1.234		0.29
	disturbed^2	-0.472	1.100	-2.632	1.688		0.26
	undisturbed^2	-0.682	1.597	-3.817	2.454		0.23
	circularity	-0.002	0.005	-0.012	0.009		0.15
WWW	(Intercept)	-10.681	4.863	-20.300	-1.093	*	
	circularity	**0.099**	**0.054**	**-0.008**	**0.206**	**•**	**1**
	mixed papyrus	**105.624**	**61.976**	**-16.700**	**227.901**	**•**	**1**
	mixed papyrus^2	-455.681	335.511	-1120.000	206.371		1
	undisturbed	1.439	2.266	-3.020	5.896		0.46
	area (log)	0.248	0.541	-0.817	1.313		0.34
	disturbed	-0.395	2.102	-4.540	3.747		0.12
PC	(Intercept)	0.300	1.003	-1.668	2.269		
	area (log)	**1.186**	**0.179**	**0.833**	**1.538**	*******	**1**
	undisturbed	2.949	2.562	-2.082	7.980		1
	undisturbed^2	-4.798	2.985	-10.660	1.063		0.91
	mixed papyrus	-1.420	1.047	-3.476	0.635		0.83
	circularity	0.013	0.012	-0.010	0.037		0.71
	disturbed	-0.387	0.835	-2.025	1.252		0.31
	connectivity	0.006	0.013	-0.021	0.032		0.28
CC	(Intercept)	-10.422	4.556	-19.436	-1.408	*	
	area (log)	**4.248**	**1.417**	**1.443**	**7.052**	******	**1**
	connectivity	**0.013**	**0.006**	**0.001**	**0.024**	*****	**1**
	circularity	**0.098**	**0.047**	**0.004**	**0.191**	*****	**1**
	disturbed	1.835	4.131	-6.307	9.976		0.3
	undisturbed	-0.272	1.399	-3.038	2.493		0.19
PYW	(Intercept)	-2.268	0.912	-4.065	-0.472	*	
	area (log)	**1.230**	**0.285**	**0.666**	**1.793**	*******	**1**
	mixed papyrus	-0.767	1.369	-3.461	1.927		0.39
	undisturbed	0.249	0.938	-1.598	2.097		0.16
	disturbed	-0.484	2.257	-4.931	3.963		0.13
	circularity	0.001	0.010	-0.018	0.021		0.12

Species: GSW = greater swamp-warbler; WWW = white-winged swamp-warbler; PC = papyrus canary; CC = Carruthers’s cisticola; PYW = papyrus yellow warbler. CI = Confidence Intervals. Variables; RI = Relative Importance (proportion of models including this term); Levels of significance: *** p = 0.001, ** p = 0.01, * p =0.05, • p = marginal. ^{2}indicates squared term.

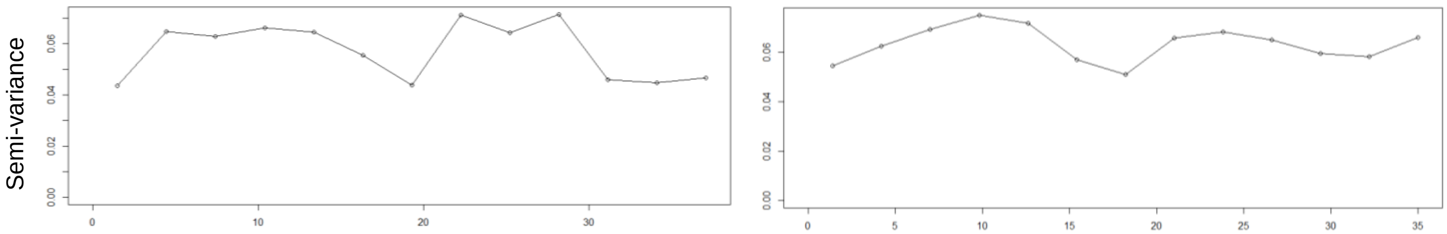
Table C4. Full model averaged output (ΔAICc ≤ 2) for survival analysis (2014-15).

Species	**Variable**	**Estimate**	**Std. Error**	**Lower CI**	**Upper CI**	**Significance**	**RI**
GSW	(Intercept)	4.935	1.075	2.821	7.049	***	
	area (log)	**0.843**	**0.207**	**0.436**	**1.250**	*******	**1**
	circularity	**-0.045**	**0.011**	**-0.066**	**-0.024**	*******	**1**
	mixed papyrus	-3.143	2.161	-7.387	1.102		1
	undisturbed	3.848	2.551	-1.166	8.861		0.93
	undisturbed^2	-4.439	2.806	-9.953	1.075		0.87
	disturbed^2	-3.098	2.632	-8.267	2.071		0.71
	disturbed	-1.048	1.901	-4.780	2.683		0.42
	mixed papyrus^2	1.210	2.186	-3.083	5.504		0.36
	connectivity	0.003	0.007	-0.011	0.016		0.26
WWW	(Intercept)	-2.288	5.012	-12.255	7.678		
	area (log)	**2.056**	**0.665**	**0.721**	**3.391**	******	**1**
	circularity	**0.062**	**0.034**	**-0.006**	**0.131**	**•**	**1**
	connectivity	0.003	0.010	-0.016	0.023		0.22
	undisturbed	-0.231	0.787	-1.799	1.337		0.19
	mixed papyrus	-0.340	1.398	-3.129	2.449		0.17
PC	(Intercept)	2.957	2.616	-2.268	8.181		
	area (log)	**2.174**	**0.704**	**0.761**	**3.587**	******	**1**
	mixed papyrus	**-89.115**	**50.256**	**-189.931**	**11.701**	**•**	**1**
	mixed papyrus^2	339.036	239.775	-141.995	820.066		1
	connectivity	0.016	0.049	-0.081	0.113		0.28
CC	(Intercept)	-3.527	5.522	-14.602	7.549		
	area (log)	2.650	1.583	-0.559	5.858		1
	connectivity	0.006	0.008	-0.010	0.021		0.55
PYW	(Intercept)	-3.619	3.212	-10.275	3.037		
	area (log)	2.050	1.633	-1.324	5.425		0.87
	undisturbed	2.860	6.942	-11.391	17.111		0.3
	disturbed	14.506	35.648	-58.098	87.110		0.28
	circularity	0.010	0.043	-0.079	0.099		0.12

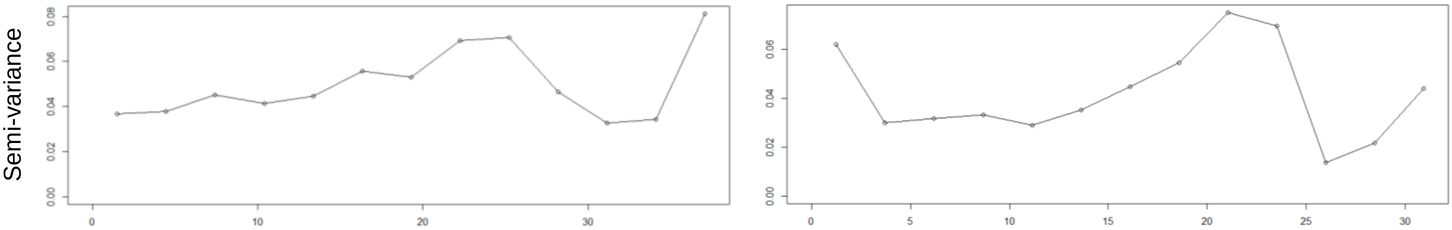
Species: GSW = greater swamp-warbler; WWW = white-winged swamp-warbler; PC = papyrus canary; CC = Carruthers's cisticola; PYW = papyrus yellow warbler. CI = Confidence Intervals. Variables; RI = Relative Importance (proportion of models including this term): Levels of significance: *** p = 0.001, ** p = 0.01, * p =0.05, • p = marginal. ^{2}indicates squared term.

Colonization data **Extinction data**

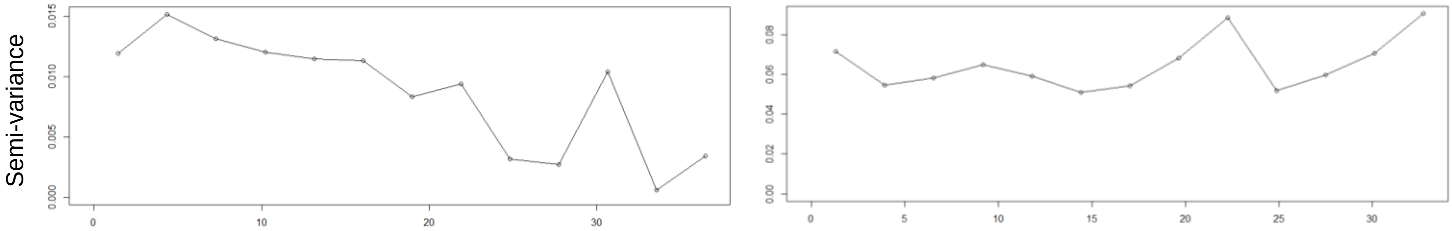
Greater swamp-warbler



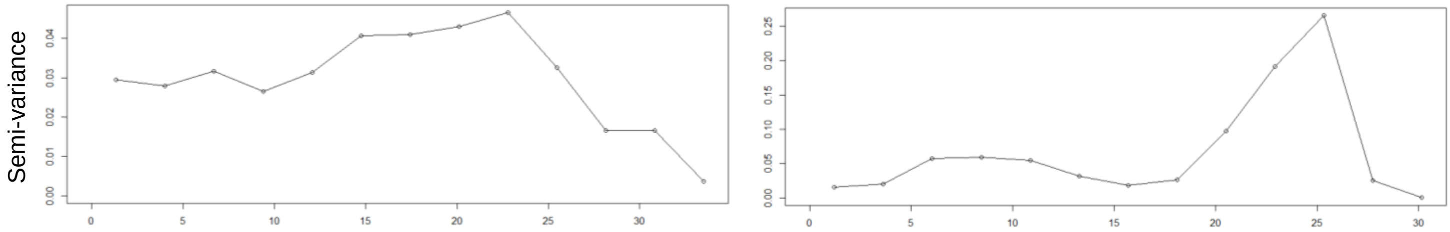
Papyrus canary



White-winged swamp-warbler



Papyrus yellow warbler



Carruthers's cisticola

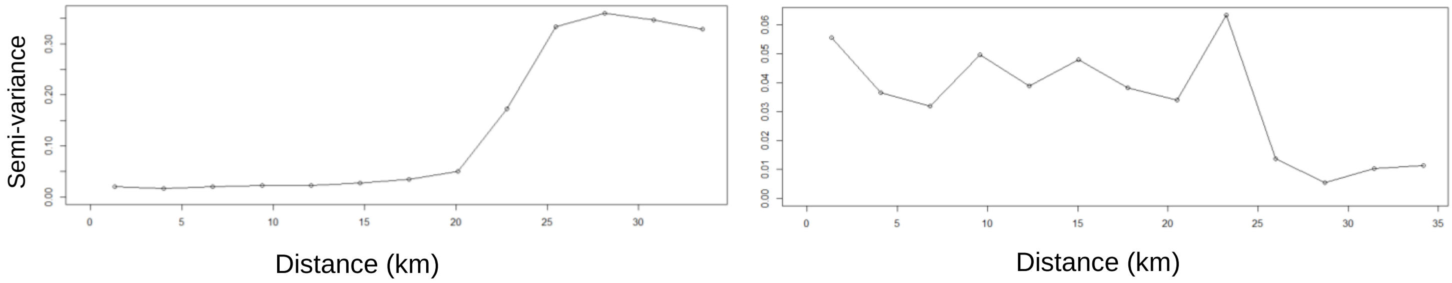


Figure C1. Semi-variogram plots of the residuals from the predicted vs observed values for colonization (left) and extinction (right) data sets for all species.

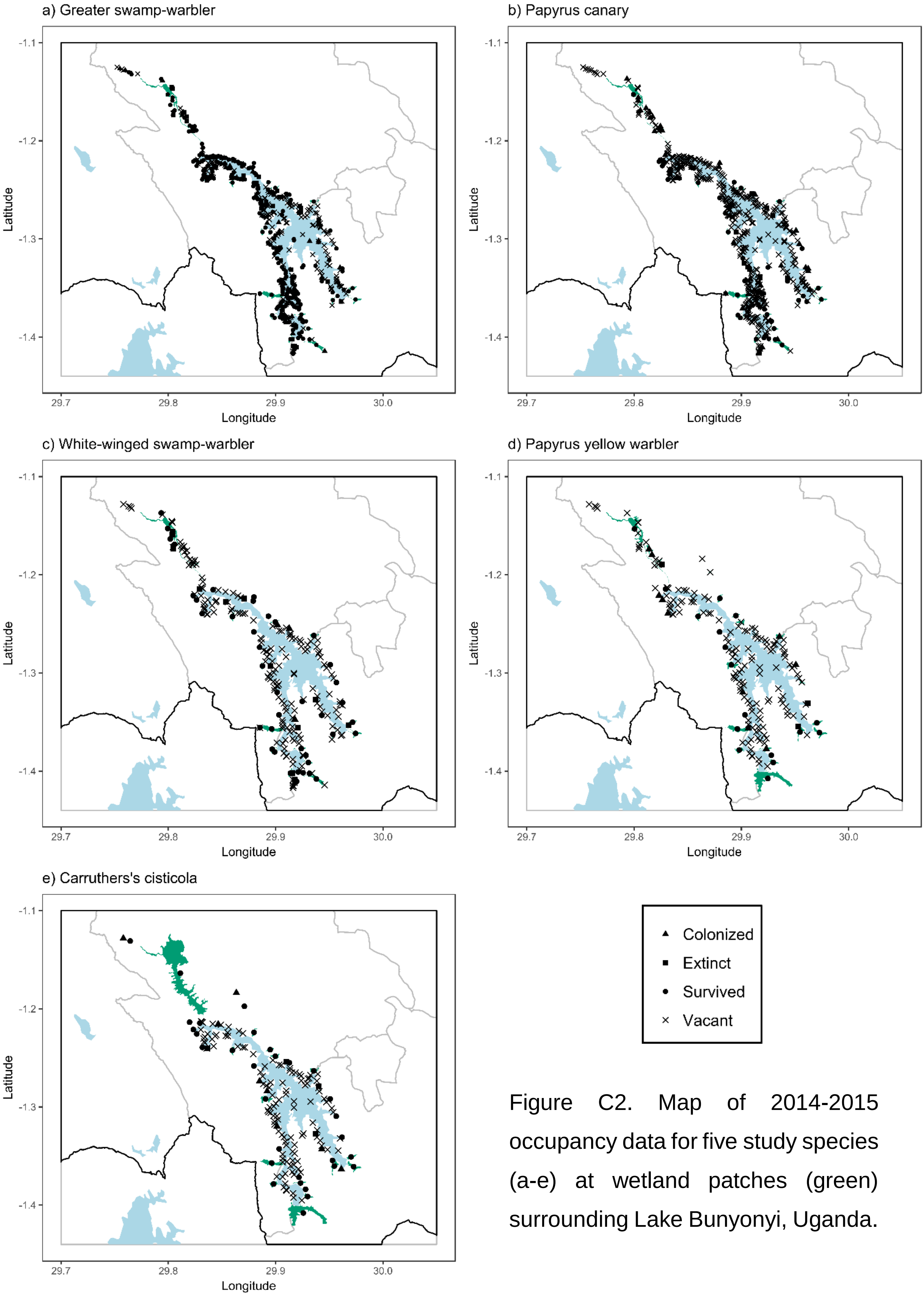


Figure C2. Map of 2014-2015 occupancy data for five study species (a-e) at wetland patches (green) surrounding Lake Bunyonyi, Uganda.

Appendix D: Chapter 5

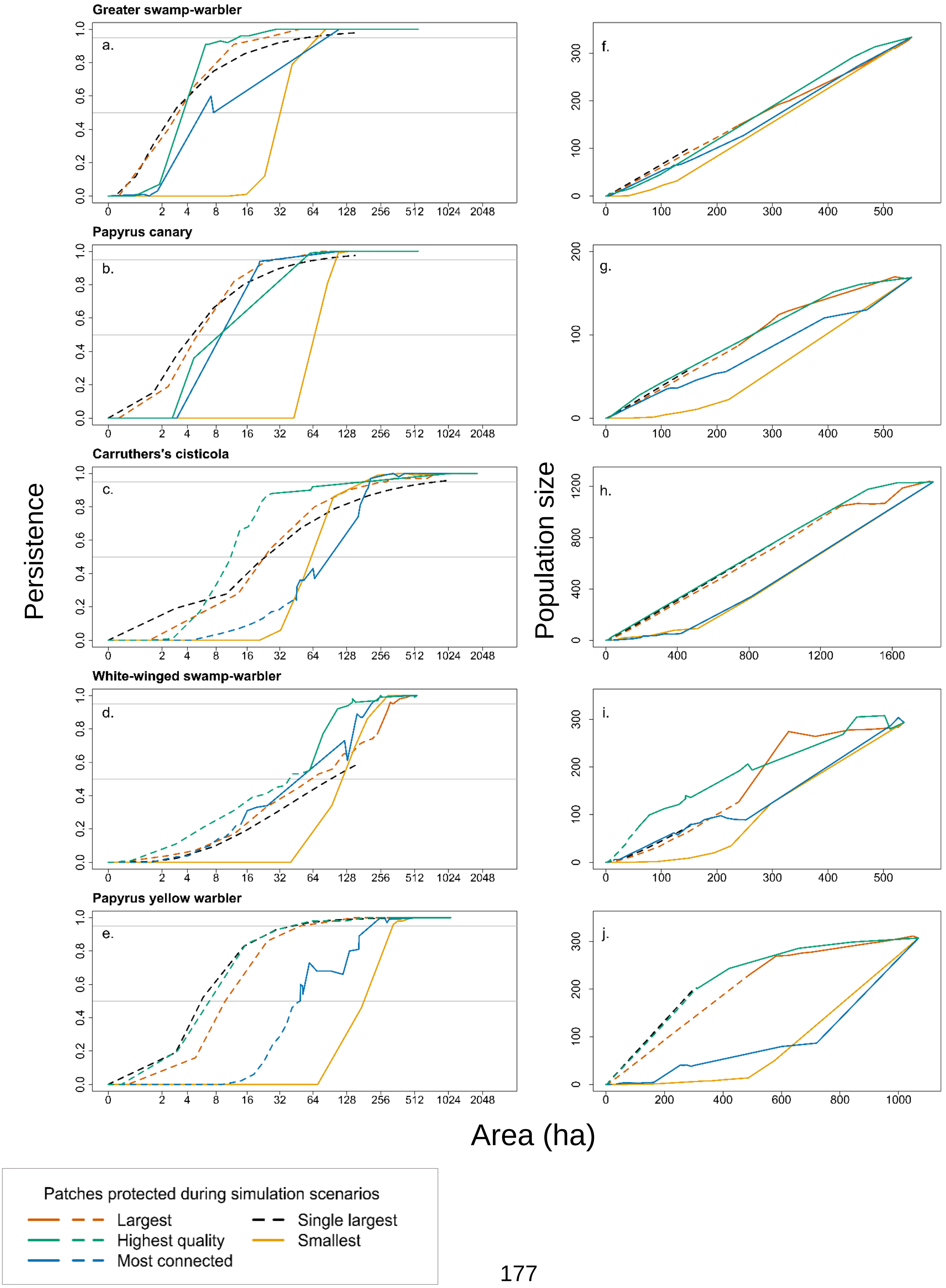


Figure D1. Output from metapopulation simulations for all study species without regional stochasticity: protecting the single largest, biggest (2+), smallest, most connected and highest quality patches in the current network. a-e display the mean proportion of replicates that persisted after 100 years, and f-j show the mean *relative* population size after 100 years, against the total area of suitable wetland habitat available across the network (a-e are plotted on the log+1 scale for clarity). Solid lines show simulation results from habitat configuration as it was in 2015, dashed lines represent results from scenarios modelled by reducing area to allow for a comparison between strategies at equivalent levels of habitat (full explanation provided in *Model simulations* in Methods). See Figure 5.1 (Chapter 5) for equivalent figure with regional stochasticity.

Table D1. Parameter estimates and lower and upper (95%) confidence intervals following repeat runs with same starting parameters for five species: greater swamp-warbler (GSW), papyrus canary (PC), Carruthers's cisticola (CC), white-winged swamp-warbler (WWW), papyrus yellow warbler (PYW). The parameters with the lowest AIC selected for use in subsequent simulations are shown in bold.

Species	**Run**	**Parameters**												**AIC**
		α			y			μ			x			
		value	lower	upper	value	lower	upper	value	lower	upper	value	lower	upper	
GSW	1	0.257	0.257	0.259	168.010	168.010	168.010	0.028	0.028	0.028	0.500	0.500	0.500	864.1
	2	**0.204**	**0.204**	**0.204**	**226.017**	**226.017**	**226.017**	**0.012**	**0.012**	**0.012**	**0.864**	**0.864**	**0.864**	**852**
	3	0.236	0.179	0.236	212.909	197.884	290.399	0.016	0.016	0.016	0.615	0.615	0.694	873.7
	4	0.124	0.100	0.131	354.309	354.309	449.176	0.025	0.025	0.032	0.439	0.439	0.500	891.6
PC	1	0.125	0.125	0.172	278.859	226.851	278.859	0.006	0.005	0.006	1.177	1.126	1.177	465.1
	2	**0.190**	**0.190**	**0.190**	**185.753**	**185.753**	**185.753**	**0.012**	**0.012**	**0.012**	**0.935**	**0.935**	**0.935**	**457.6**
	3	0.187	0.187	0.187	197.122	197.122	197.122	0.004	0.004	0.004	1.083	1.032	1.129	464.8
CC	**1**	**0.070**	**0.000**	**0.151**	**1998.430**	**1164.079**	**5417.371**	**0.061**	**0.037**	**0.072**	**0.734**	**0.523**	**1.031**	**104.3**
	2	0.084	0.000	0.164	1770.502	1062.212	4837.755	0.038	0.022	0.056	0.691	0.438	1.155	105.2
	3	0.086	0.001	0.160	1780.592	1148.651	5375.216	0.034	0.034	0.043	0.726	0.270	1.180	105.6
WWW	1	0.018	0.006	0.052	5131.224	3639.992	8106.736	0.065	0.064	0.065	0.471	0.338	0.638	124.5
	2	**0.021**	**0.003**	**0.051**	**5512.051**	**3399.745**	**8138.029**	**0.059**	**0.059**	**0.059**	**0.488**	**0.361**	**0.509**	**123.9**
	3	0.008	0.005	0.060	5413.138	3242.185	8501.896	0.065	0.045	0.065	0.514	0.333	0.585	124.4
PYW	1	0.001	0.000	0.026	1440.835	1131.181	1978.382	0.054	0.040	0.055	1.513	0.651	2.768	123.5
	2	**0.001**	**0.000**	**0.021**	**1446.647**	**1192.023**	**1984.177**	**0.041**	**0.041**	**0.067**	**1.340**	**0.720**	**2.579**	**123.3**
	3	0.000	0.000	0.008	1358.071	1231.682	2050.646	0.029	0.029	0.034	1.722	0.934	2.475	123.3

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