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Research Paper

Testing the effectiveness of surrogate species for conservation planning in the Greater Virunga Landscape, Africa

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HIGHLIGHTS

- We present the first test of the landscape species approach.
- We test whether landscape species are effective surrogates for biodiversity.
- Landscape species are the worst surrogates of all species groups tested.
- Prioritising for randomly selected species gives better surrogacy performance.
- Landscape species approach should be used with more robust planning approaches.

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ABSTRACT

Given the limited funds available, spatial prioritisation is necessary to help decide when and where to undertake conservation. One method for setting local scale priorities for conservation action is the landscape species approach which aims to identify priorities based on the needs of a small number of wide ranging species with large environmental impacts. Despite being used for the past decade by conservation organisations such as Wildlife Conservation Society, the effectiveness of the approach for representing a more comprehensive range of biodiversity has never been evaluated. Here we compare conservation priorities identified using a suite of landscape species ($n = 13$) against those using many alternative sets of threatened or endemic species ($n = 7–88$) to assess the applicability and suitability of the landscape species approach in a biologically diverse landscape (Greater Virunga Landscape, Uganda, Rwanda, and Democratic Republic of Congo, Africa). We defined the minimum area needed to conserve each species on the basis of the species' range size. We found that prioritising for landscape species adequately conserves only 31 (35%) species, whereas prioritising for an equal number of endemic species, threatened species, or randomly sampled species adequately conserves 74%, 69% and 42% of species, respectively. We also found that prioritising for one taxonomic group (birds or plants) alone resulted in better surrogacy performance than the Landscape Species. These results question the underlying assumption of the landscape species approach, that managing threats to Landscape Species will also manage threats to all other species, as it is applied in the Greater Virunga Landscape.

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1. Introduction

Biodiversity is currently in rapid decline, with extinction rates 100–1000 times background levels (Butchart et al., 2010; Pimm, Russell, Gittleman, & Brooks, 1995; Vié, Hilton-Taylor, & Stuart, 2009). The impacts of losing biodiversity are widespread, as biodiversity influences ecosystem processes upon which humanity is dependent for goods and services (Cardinale, 2012; Cardinale et al., 2012; Stachowicz, Bruno, & Duffy, 2007). For example, increasing biodiversity generally leads to increased productivity of ecosystems, a fundamental supporting ecosystem service that underpins the provision of services such as food or wood (Balvanera et al., 2006). Conservation action is vital if we are to preserve ecosystem function, and associated ecosystem services (Balmford et al., 2002; Nelson et al., 2009). Conservation practitioners have a range of potential conservation actions available for use (Driscoll et al., 2010; Hobbs & Humphries, 1995; Hobbs & Norton, 1996; Richards, Possingham, & Tizard, 1999), and different combinations of actions must be planned for in each specific conservation landscape (Levin et al., 2013).

Conservation planning, the organised process of identifying conservation priorities and developing a group of actions to meet conservation goals (Groves et al., 2002; Knight, Cowling, & Campbell, 2006), is considered vital for conservation actions to be effectively implemented (Sarkar et al., 2006; Sewall et al., 2011). Numerous approaches for conservation planning have been developed by various governmental and non-governmental organisations (NGO's) (Early & Thomas, 2007; Manne & Williams, 2003; Moilanen & Cabeza, 2002; Moilanen, Wilson, & Possingham, 2009; Watts et al., 2009). The landscapes species approach (LSA) (Didier, Glennon, et al., 2009; Sanderson, Redford, Vedder, Coppolillo, & Ward, 2002) was developed to plan conservation actions at the landscape scale and is currently used by the Wildlife Conservation Society (WCS) and other international bodies such as the U.S. Fish and Wildlife Service, Melbourne Water, and the Kenya Wildlife Authority (Didier, Wilkie, et al., 2009; Hamer, Ainley, & Hipler, 2010; U.S. Fish and Wildlife Service, 2012). For the purposes of the LSA, a landscape is defined by the sum of all areas required to support a population of landscape species (LS) (Sanderson et al., 2002). Within the LSA, and indeed within most conservation planning approaches, spatial priorities for conservation must be identified (Moilanen et al., 2009).

Spatial prioritisation requires spatial information about the distribution of species and ecosystems, but our knowledge of the earth's biodiversity is remarkably limited, and much of the diversity we do know about is yet to be catalogued and described (Bini, Diniz-Filho, Rangel, Bastos, & Pinto, 2006; Whittaker et al., 2005). Thus, conservation planning is often based upon surrogates for biodiversity. Surrogacy, in a conservation planning context, is defined as the extent to which conservation planning based on a particular set of biodiversity features (surrogates) effectively represents another set of species (Caro & O'Doherty, 1999; Rodrigues & Brooks, 2007). Surrogates usually fall into two categories: coarse-filter surrogates, which represent broad features (e.g., habitat types, well known taxa), and fine-filter surrogates, which represent more specific features (e.g., threatened species) (Larsen, Bladt, & Rahbek, 2007; Rodrigues & Brooks, 2007). The use of certain groups of species as surrogates for the total biodiversity of an area has garnered significant attention in recent times, mostly due to its potential for greatly simplifying data requirements for conservation planning (Gladstone, 2002; Larsen, Bladt, & Rahbek, 2009; Leal, Bieber, Tabarelli, & Andersen, 2010; Moritz et al., 2001). Numerous conservation approaches are based around suites of surrogate species, such as focal species, umbrella species and flagship species, as well as landscape species (Andelman & Fagan, 2000; Didier, Glennon, et al., 2009; Lamberck, 1997) Although the use of surrogates presents many advantages for conservation practitioners, there is considerable debate around the effectiveness of surrogates at representing biodiversity; that is how well conservation planning based around surrogate species also acts to conserve other species (Grantham, Pressey, Wells, & Beattie, 2010; Larsen et al., 2009).

The LSA focuses on identifying areas of conservation intervention using a suite of LS at a landscape scale to ensure that their long-term conservation requirements are met. While not described as a conservation prioritisation process for species per se, there is an assumption that the approach will 'capture' or act as a surrogate for other biodiversity (Didier, Glennon, et al., 2009). The assumption behind the approach is that if threats facing the LS are effectively managed, threats to all other species will also be effectively managed (Didier, Glennon, et al., 2009). To choose a suite of LS, candidate species are scored based on five categories: (1) area: whether the size of the home range of the species, where large home ranges score higher, (2) heterogeneity: whether species need more than one habitat type in their life cycle, and the proportion of each habitat type needed, (3) vulnerability: whether species to threats from human activities, (4) functionality: whether the effect of a species on the structure and function of natural ecosystems, and (5) socioeconomic significance: whether a species has positive or negative cultural value, whether it is a flagship species (Coppolillo, Gomez, Maisels, & Wallace, 2004). Usually a group of experts score a suite of candidate species and from these a suite of LS is selected, where the highest scoring species is selected first, and then the most complementary species is chosen from the next 5 highest scored species. Complementarity is defined as minimum overlap in habitat requirements, distributions, and distinctiveness of threats encountered. This process is continued until the needs of the next species to be added are already met by the current suite of species (Coppolillo et al., 2004). Because each LS is chosen to form part of a suite of species, each species is not required to have all of these characteristics, but the suite as a whole should.

Despite the use of the LSA by WCS and other organisations, the underlying assumption that LS are suitable surrogates to identify conservation priorities has never been tested, although other surrogacy approaches have been frequently tested (Andelman & Fagan, 2000; Che-Castaldo & Neel, 2012; Grantham et al., 2010; Larsen, Bladt, Balmford, & Rahbek, 2012; Leal et al., 2010; Nicholson, Lindenmayer, Frank, & Possingham, 2013). Therefore, it is unknown how well spatial conservation prioritisation using LS works to comprehensively represent other aspects of biodiversity across a landscape (Margules & Pressey, 2000). The assumptions underlying the LSA may have never been tested because it has been mostly used in areas where there are few data on other biodiversity. This makes it difficult to determine whether LS are suitable surrogates for identifying conservation priorities. The Greater Virunga Landscape in Africa presents the first opportunity to test the assumptions of the LSA, as a suite of LS have been identified, widely studied, and existent extensive data are available. Here, we identified priorities for conservation management in the Greater Virunga Landscape by targeting only LS, and evaluated how well other aspects of biodiversity were represented. Further, we investigated the effectiveness of various combinations of species, other than LS, at representing other biodiversity to further inform surrogacy selection.

2. Methods

2.1. Study area

The Greater Virunga Landscape (GVL), in Africa, straddles the borders of 3 countries: Uganda, Rwanda, and the Democratic Republic of the Congo in Africa (Appendix A). The GVL is one of the most biodiverse regions in the world, containing three world heritage sites, one Ramsar site, and one UNESCO biosphere reserve

(Plumptre, Kujirakwinja, Treves, Owiunji, & Rainer, 2007). This area contains a variety of habitats due to its wide elevation gradient, ranging from 600 to 5100 m above sea level as in the Rwenzori mountains (Plumptre et al., 2007). Although 88% of the GVL lies within 13 protected areas (Plumptre et al., 2007), the level of enforcement of the law does not prevent many illegal activities taking place in these areas (Rainer et al., 2003). As a result there is a need to focus conservation efforts within the GVL and prioritise where to take conservation action (Plumptre et al., 2014). A new conservation plan is needed to conserve the 1409 terrestrial vertebrate and 3755 plant species (Plumptre et al., 2011). We divided the GVL into 16,268 planning units with an area of 1 km^2, each of which could be selected or not selected as a priority conservation area in the spatial prioritisation analysis. We chose these planning units to be consistent with the scale of the species distribution maps that have been created in this landscape.

2.2. Species selection

A large amount of data on animal and plant species has been collected in the GVL. The data includes thousands of observations from a variety of sources described in Plumptre et al. (2011), and include: ranger based monitoring data (point data on species occurrence), WCS and Uganda Wildlife Authority aerial surveys of large mammals, and surveys of birds, plants, and mammals collected through transects and reconnaissance walks in forests by WCS. A LS assessment for the GVL was made in 2004, attended by scientists and protected area managers from across landscape, and using methods detailed in Coppolillo et al. (2004). The chosen species were: buffalo (*Syncerus caffer*), chimpanzee (*Pan troglodytes*), elephant (*Loxodonta africana*), giant forest hog (*Hylochoerus meinertzhageni*), gorilla (*Gorilla beringei*), hippopotamus (*Hippopotamus amphibius*), spotted hyaena (*Crocuta crocuta*), leopard (*Panthera pardus*), lion (*Panthera leo*), okapi (*Okapia johnstoni)*, Rwenzori duiker (*Cephalophus rubidus)*, topi (*Damaliscus lunatus*), and white-backed vulture (*Gyps africanus*). WCS has also collected data for 26 bird species and 49 plant species that are endemic to the Albertine Rift or threatened on the IUCN Redlist and that occur in the GVL.

2.3. Species data and modelling

Distribution models for all species, except the Rwenzori duiker, were created using the computer program MAXENT (Phillips & Dudík, 2008), as it is known to be one of the best distribution modelling software packages for presence only data (Elith et al., 2006, 2011). These models were not analogous to biological landscapes as defined in Sanderson et al. (2002), and the modelling methods are described in Plumptre et al. (2011). The MAXENT prediction layers (all with a resolution of 250 m) included land cover, rainfall, elevation, land slope, aspect, soil type, fire frequency and distance from roads, settlements, rivers, and patrol posts. As input data on species presence were biased (ranger based data has more observation near patrol posts, and surveys made by WCS were not evenly distributed across the GVL because of insecurity in some areas), bias layers were used in MAXENT in order to account for it (Plumptre et al., 2011). The area under curve (AUC) values (a measure of the proportion of variation explained by the model) for each model was significant and had low standard deviation (Plumptre et al., 2011).

As there is a lack of point location information available for the Rwenzori duiker, we modelled its distribution based on where it is known to occur, which is in the Ruwenzori Mountains between Uganda and the Democratic Republic of Congo (Kingdon, 1997). As density data are not available, we assumed that its densities are similar to the black fronted duiker in a montane environment (Plumptre & Harris, 1995), but at a higher altitude. Thus, we estimated that the Ruwenzori duiker occurred at a density of 7.1 individuals/km^2 at 3000 m asl, and was normally distributed around this value, with density decreasing to 1 and 0.5 individuals/km^2 at 4800 and 1400 m asl, respectively.

2.4. Prioritising areas for conservation

As our goal was to design conservation areas for a suite of species that achieved target representation for species while minimising cost, we used the conservation planning software Marxan (Ball et al., 2009; Watts et al., 2009). Marxan is a widely used decision support tool that selects areas for management so that a target amount of each species is included in those areas for management action, while minimising the total cost of those actions. Marxan uses a simulated annealing algorithm to minimise the objective function score, which is the sum of the protected area system total cost, along with any penalties allocated to the protected area system for not fulfilling targets prescribed by the operator (Kirkpatrick et al., 1983). By doing this Marxan creates a group of near optimal solutions based on customised input settings. The best solution is the one with the lowest objective function score, which is determined by meeting representation targets for the lowest cost.

We aimed to test the LSA in two ways: (1) by prioritising for LS and other groups of species, to determine the effectiveness of LS and other species as surrogates; and (2) by conducting a species accumulation analysis to determine how the number of species in four groups: landscape, range limited, threatened and randomly selected species, affected the surrogacy performance and cost of conservation areas. The purpose of the first analysis was to identify priorities for conservation management in the GVL by targeting only LS, and evaluate how well other aspects of biodiversity were represented. We then identified priorities based around other sets of species, to compare their surrogacy performance against the suite of LS. The purpose of the second analysis was to prioritise for four equally sized suites of species, and examine how the number of species in each group affects surrogacy performance, and how each group compared to LS. This analysis also allowed us to examine the contribution of each target species to the surrogacy performance of a suite of species. Finally, we conducted two sensitivity analyses to examine how sensitive our results were to our cost layer and the methods we used to set conservation targets, and thus see if our conservation priorities would change with different cost and target-setting methods (Carwardine et al., 2010).

We did not intend to use the full methodology of the LSA as outlined in Didier, Glennon, et al. (2009), but simply to design conservation areas for LS and assess the effectiveness of these areas for protecting other species in the GVL. Cost was calculated based on the distance of planning units from ranger patrol posts, incorporating the effort required for park rangers to travel to each planning unit and combat the threats facing species in that planning unit (Plumptre et al., 2014). Ranger patrols are the primary method that is used to tackle threats in this landscape. These threats include armed poaching, snaring, illegal timber harvesting, charcoal production, fuel wood collection, and livestock grazing. Armed poaching and snaring are the main threats to LS, while habitat destruction from other threats may affect all species in the GVL.

2.5. Species conservation targets for Marxan

There is considerable debate about how much of a species range or population proportion needs to be conserved in order to ensure the persistence of that species (Carwardine et al., 2009; Pressey et al., 2007; Rodrigues et al., 2004). Given this debate around appropriate target-setting methods, we conducted three spatial prioritisation analyses using different target-setting approaches. For the LS, we identified targets based on population-size (within

Table 1
Landscape species for the Greater Virunga Landscape and amount of each species targeted for inclusion in a conservation area. We identified conservation areas for three different scenarios, each with a different amount of each species distribution targeted based on population sizes, range sizes, and an arbitrary target of 30%.

Common name (graph reference)	Population based target – number of individuals (% of population)	30% target – number of individuals	Range-size target – % of population
Buffalo (1)	1000 (10.7)	2791	20
Chimpanzee (2)	2000 (54.5)	1100	20
Elephant (3)	1000 (29.9)	1002	20
Giant forest hog (4)	1000 (15.5)	1931	20
Gorilla (5)	400 (75.3)	159	100
Hippopotamus (6)	1000 (16.1)	1862	20
Spotted hyaena (7)	300 (25.2)	356	20
Leopard (8)	300 (40.6)	221	20
Lion (9)	300 (48.6)	184	20
Okapi (10)	500 (78.9)	190	32
Rwenzori duiker (11)	1000 (14.2)	2098	100
Topi (12)	500 (83.4)	179	100
White-backed vulture (13)	200 (61.6)	97	29

the GVL), range-size (within the GVL), and an arbitrary flat 30% target (Table 1). For scenarios that targeted species other than LS, we used range-size based targets, as population size based targets were unavailable. We used population size based targets for LS that were calculated in Plumptre et al. (2011), where large mammal survey data was used to convert modelled species distributions to density (number of animals per planning unit). For each species, this survey data was used to estimate the total number of individuals in the GVL, which was divided by the sum of all probability values (MAXENT output) for the GVL. Finally, this value was multiplied by the probability of species occurrence value for each individual planning unit, to estimate the number of individuals in each planning unit. These targets were based on the number of individuals of each species in the GVL, and were generally set at 1000 individuals, or near the maximum number of the population if it was less than 1000.

For large scale conservation plans with many species, the most widely applied target setting method is to develop targets for species ranges that changes as a function of species geographic range size (Carwardine et al., 2008; Rodrigues et al., 2004). As such, to determine range-size based targets we used methods outlined in Rodrigues et al. (2004), and built upon by Watson et al. (2011) using the following guidelines: (1) for species with a geographic range of <5000 km^2 within the GVL we set a target of 100% inclusion in the GVL; (2) for species with a geographic range of >15,000 km^2 we set a target of 20% inclusion in the GVL; (3) for species with ranges between 5000 and 15,000 km^2, we used a log-linear relationship between these two values to scale our targets to range, so that the target percentage of a species range decreased as the range of the species increased. We conducted multiple scenarios where we targeted different combinations of species (Table 2). Because most of the GVL is contained within protected areas, and the current threats within these areas are impacting species, we did not assign weightings to whether a site was currently a protected area or not. To determine the sensitivity of our results to the use of different percentage targets, we also conducted analyses using a flat 30% protection target for all species. If the results were similar using both groups of targets, this suggests that our results were not sensitive to the target setting method used, and that our results would not change significantly if using other targets.

2.6. Marxan analysis

For each group of species (Table 2) we generated 100 different networks of conservation areas that achieve our objective. Using the ten solutions with the lowest objective function score (the ten most efficient solutions), we calculated the amount of each species range that was represented in a conservation area and the percentage of species that were adequately represented. A species was considered to be adequately represented if the range captured in conservation areas was equal to or greater than its target (targets were set either using range size, population or flat targets).

Further, we used the mean percentage gap (Sutcliffe, 2013) to compare solutions, which is advantageous as the performance of a solution can be simply represented with a single number. This method uses adequacy levels, which are the levels of representation at which we consider species to be adequately represented in a conservation network, to summarise the shortfall of achieving the desired representation (i.e. the adequacy level) across all species:

$$\text{Mean percentage gap} = \sum_{1\ldots N}^{i} \frac{(P_i/t)}{N},$$

where P_i is the amount that species i is less than the adequacy level t, and N is the total number of species.

We assessed performance against two adequacy levels for each species, either a flat 30% level, or a range-size based level the same as described in Section 2.4. For example, if we were using a flat 30% adequacy level, the percentage below the adequacy level was calculated for all species. This would range from 0 if ≥30% of a species range was captured to 100 if 0% of a species range was captured, and was calculated for each species separately (Fig. 2D shows percentage gap as grey shading). This value for each species was summed and then divided by the total number of species. This gives a number between 0 and 100, where a scenario in which all species are adequately represented has a mean percentage gap of

Table 2
Species used to identify conservation areas for each spatial prioritisation scenario. The first column shows the groups of species for which Marxan prioritisation was undertaken, while the second column shows the number of species contained in each group. The results of these analyses are shown in Figs. 4 and 5.

Species in each scenario (graph reference)	Number of species
Landscape species (1)	13
All species (2)	88
All plants (3)	49
Endemic plants (4)	32
Endemic birds (5)	22
Threatened plants (6)	17
Landscape species + endemic birds (7)	35
Landscape species + endemic plants (8)	45
Landscape species + threatened plants (9)	30
Threatened species + large mammals (10)	28
Range limited species (11)	13
Most threatened species (12)	13
Random species (13)	13

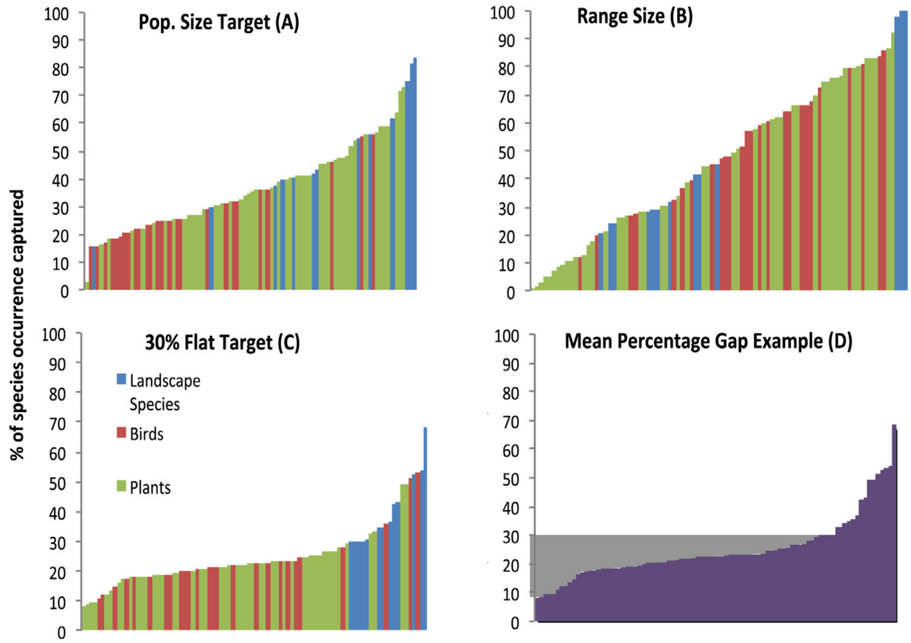

Fig. 1. Percentage of species (n = 88) occurrence captured when prioritising for landscape species (n = 13) using three target setting methods: population-size (A), range-size (B), and 30% flat (C) targets. (D) A graph for calculation of mean percentage gap. *X-axis contains 88 species, ordered from lowest to highest percentage occurrence captured. Landscape species are shown in blue, birds in red, and plants in green. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

0, and a scenario in which no species range is captured has a mean percentage gap of 100. A value of 20 for example, could mean that 20% of species had no occurrence captured, or 40% of species had half of the amount required to meet their adequacy level captured. When comparing the effectiveness of different suites of surrogate species, the mean percentage gap was used because it gives a good indication of the degree of under-representation, for species that did not meet their adequacy level.

We also conducted a species accumulation curve to determine how the number of species in a surrogacy suite (e.g., LS) affected surrogacy performance and cost. This analysis allowed us to examine how each species individually affected surrogacy performance and cost, and also how each species affected the performance of the group. For this analysis we developed four groups of 13 species: LS, range limited species, threatened species and randomly selected species. We chose range limited and threatened species as they are commonly targeted for conservation, and we chose random species to provide a baseline surrogacy scenario. Each group contained 13 species, as this is the number of LS. Species accumulation analysis was conducted by using Marxan to prioritise for the first species in each group alone (e.g., the most threatened species); then prioritise for the first and second species; then the first, second, and third species, and so on. LS were those selected in Plumptre et al. (2011). Range limited species were those with the smallest ranges in the GVL, even if there are other populations outside the GVL. Threatened species were those most threatened (according to IUCN threat classifications), where if species shared the same threat classification, those with smaller ranges in the GVL were considered more threatened. Random species were a group of species selected using the RAND function in Microsoft Excel, where all species were allocated a random value between 0 and 1, and the 13 species with the lowest values were chosen. This was done 10 separate times, to develop 10 groups of 13 random species. We then performed species accumulation analyses for each group of 13 species, calculating the minimum, maximum and average values for cost and surrogacy performance. Range-size based targets were used for species accumulation analysis.

Table 3
Percentage of species meeting their respective targets and mean percentage gap, using 3 target setting methods for landscape species (rows) and two different methods for assessing adequate representation of other species (columns). A low mean percentage gap indicates that species are under-represented by a small amount and vice versa.

	Percentage of adequately represented species (mean percentage gap) – using flat 30% adequacy level	Percentage of adequately represented species (mean percentage gap) – using range-size based adequacy level
Pop.-size target	64.8 (10.1)	31.8 (36.1)
Range-size target	72.7 (14.3)	35.2 (26.8)
30% flat target	22.7 (24.3)	17.0 (53.2)

2.7. Cost sensitivity analysis

In order to determine how sensitive our analysis was to our cost layer, and to assess whether priority areas would change if we used different cost values, we conducted a cost-sensitivity analysis using an approach similar to that of Carwardine et al. (2010). Our cost layer was based on the effort required for park rangers to travel to each planning unit and combat the threats facing species in that planning unit, where planning units that require more effort have a higher cost. To conduct our cost sensitivity analysis we ran Marxan 4 times using LS as targets, while varying the cost of planning units. One scenario was run as a baseline, where cost was unchanged from the original values. In the other 3 scenarios we randomly selected one third of the total planning units, and increased their cost by 100%, 150% or 200%. We used the Fleiss' Kappa statistic to analyse the results, by summarising the difference in selection frequency across all planning units. This gives a value between 0 and 1, where 1 indicates that the combination of planning units selected

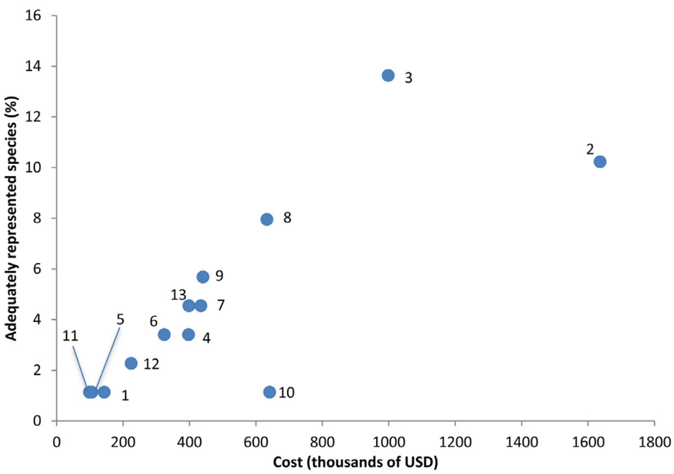

Fig. 2. Percentage of species adequately represented and cost, prioritising for each landscape species on its own (with population-size based targets), using range-size based adequacy levels. Cost was calculated based on the distance of planning units from ranger patrol posts, incorporating the effort required for park rangers to travel to each planning unit and combat the threats facing species in that planning unit. Refer to Table 1 for graph reference numbers.

in each scenario is identical, and 0 indicates that there is no overlap between the planning units selected in each scenario.

3. Results

3.1. Adequacy of landscape species as surrogates for other aspects of biodiversity

Regardless of targets used for LS, they did not adequately represent the full range of species for which data are available in the GVL. In all scenarios there were large numbers of birds and plants that were not adequately represented, with the percentage of species being adequately represented ranging from 22.7% to 72.7% (Table 3). Prioritising for LS using range-sized based targets resulted in the highest percentage of other species being adequately represented (72.7%, Table 3), but there were a large number of plants that were extremely under-represented (Fig. 1). When prioritising for each LS by itself, the percentage of species that were adequately represented varied from 0% to 21% (Fig. 2).

The lowest mean percentage gap (10.1) was found when prioritising for LS using population-size based targets and evaluating species representation against a 30% adequacy level. The relative performance of the other scenarios was consistent with the percentage of species adequately represented (Table 3), with values ranging from 14.3 to 53.2, where higher mean percentage gaps were found in scenarios that have low percentages of species adequately represented. Prioritising for LS using a 30% flat target had poorer performance than population-size and range-size based targets (i.e., higher mean percentage gap) for both adequacy levels (Table 3). When prioritising for LS using population-size based targets, plants are generally represented at high levels, with birds forming the majority of species that have <30% of their occurrence captured (Fig. 1A). This scenario also had the lowest number of species that had less than 10% of their occurrence captured (Fig. 1).

Our results had low sensitivity to cost. When comparing across all 4 cost scenarios, the Fleiss' Kappa statistic was 0.8, indicating that there was a high level of agreement between all 4 cost scenarios (a value of 1 indicates that all scenarios are exactly the same, and 0 indicates all scenarios are distinct), and that the vast majority of planning units selected in each scenario were the same (Appendix D).

3.2. Effectiveness of other species combinations as surrogates for biodiversity

Prioritising for the 13 range limited species, the 13 most threatened species, or 13 random species (on average) resulted in a greater number of species being adequately represented than when prioritising for the 13 LS (Fig. 3A). The 13 range limited and the 13 most threatened species were similarly effective as surrogates, adequately representing 65 and 61 species, respectively. A group of 13 randomly selected species adequately represented 37 species on average. LS were the least effective surrogate, adequately representing only 31 species (Fig. 3A). However, the total cost for range limited, threatened or random species groups was also much greater than for LS (Fig. 3B). Prioritising for only the 4 most threatened species resulted in better surrogate performance than the entire suite of 13 LS. Prioritising for the 8 most range limited species also resulted in better surrogate performance and a lower cost than prioritising for the entire LS suite (Fig. 3). Prioritising for LS results in a protected area network concentrated in three main areas (Appendix A). Prioritising for the three other scenarios results in protected area networks that are more spread across the GVL (Appendix A) and cover more area in total (Appendix B).

We found that prioritising for endemic birds, endemic plants, or threatened plants resulted in a higher percentage of species being adequately represented than when prioritising for LS (Fig. 4). Cost was higher when prioritising for endemic or threatened plants than when prioritising for LS, but endemic birds had a lower cost than LS (Fig. 4). Endemic plants were the best surrogates of any species group alone, with 81.8% of species adequately represented, followed by endemic birds (65.9%) and threatened plants (56.8%). The mean percentage gap was low for both endemic (9.0) and threatened plants (12.2) (Fig. 5), suggesting for species that were not adequately represented, the amount by which they were under-represented was low. In contrast, endemic birds had a high mean percentage gap (23.6), indicating that it was under-representing many species. In general, mean percentage gap reflected the percentage of species that were adequately represented (i.e., scenarios with high percentages of species adequately represented had low mean percentage gaps, and vice versa).

Scenarios which combined LS and endemic birds, endemic plants or threatened plants always resulted in a greater percentage of species being adequately represented, and also a greater cost, than when prioritising for those groups without LS (Fig. 4). The mean percentage gap for each scenario decreased with the addition of LS (Fig. 5). LS and endemic plants were one of the best surrogate groups, adequately representing 87.5% of species, with a mean percentage gap of 5.2. LS and threatened plants, along with LS and endemic birds were slightly less effective surrogate groups, with 77.2% and 72.7% of species being adequately represented, respectively.

The percentages of species that were adequately represented did not vary greatly between target setting methods (Appendix C). Scenarios using range-size based targets had higher costs, because the majority of range-size based targets are higher than 30%, and thus require more area to be selected, but the general trends were similar.

4. Discussion

4.1. Landscape species as surrogates for threats to biodiversity

LS do not adequately represent other elements of biodiversity when planning for conservation areas for threat management, in the GVL. Depending on the targets used, and the adequacy levels used to evaluate each scenario, the percentage of species that were adequately represented varied from 22.7% to 72.2% (Table 1).

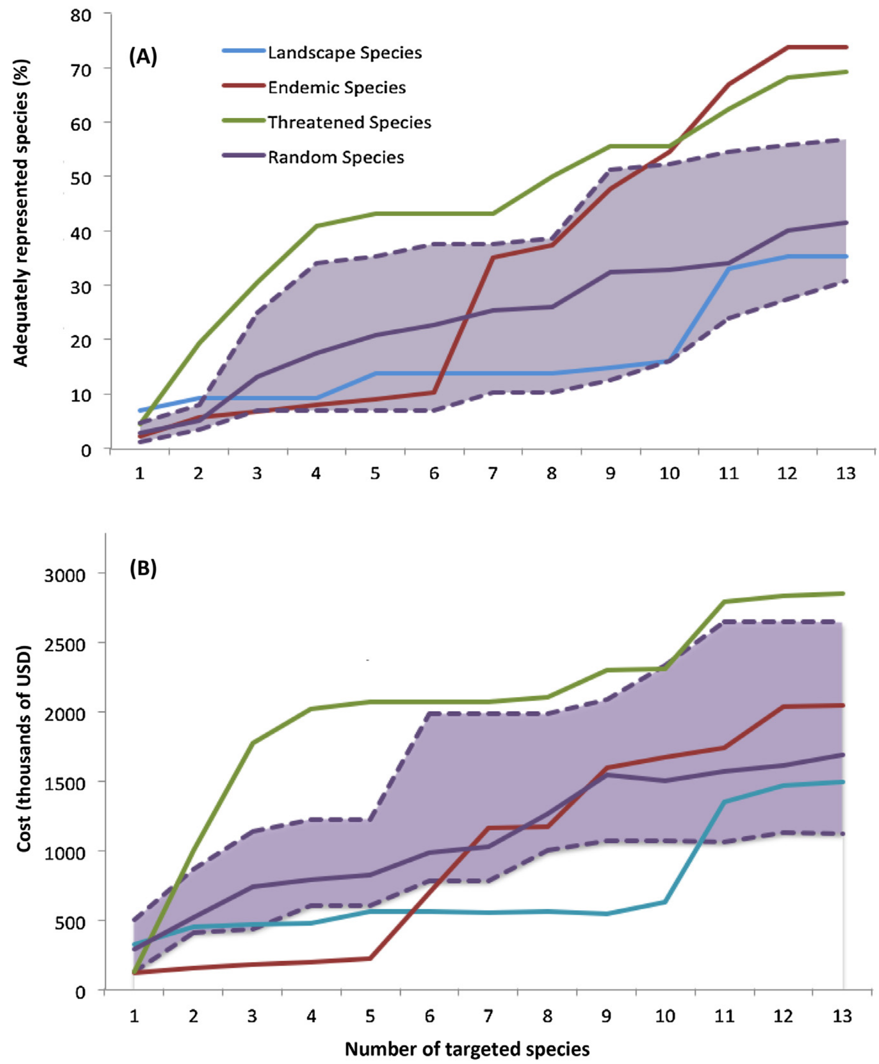

Fig. 3. (A) Percentage of species adequately represented and number of species targeted, for 4 groups of target species. (B) Cost and number of species targeted, for 4 groups of target species. The *x*-axis represents the number of species targeted in prioritisation. For example, the 1st point on the *x*-axis represents prioritisation targeting only the most range limited or most threatened species. The 2nd point represents prioritising for the 2 most range limited or 2 most threatened species, and so on. The dashed purple lines represent the minimum and maximum values from analyses using 10 different groups of random species, while the solid purple line represents the average of all 10 groups. Total area contained in each scenario is shown in Appendix B. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

These scenarios had high mean percentage gaps that suggest many species were under-represented by a large amount (Table 1).

One of the basic assumptions of the LSA is that managing threats to LS will also manage threats to all other species (or at least a large percentage of species) in the GVL (Didier, Glennon, et al., 2009; Sanderson et al., 2002). We have shown this assumption to be incorrect in the Greater Virunga Landscape. Conservation areas selected when prioritising for LS do not adequately capture other biodiversity elements, regardless of how (and the level at which) conservation targets for biodiversity are set. These results are similar to other planning exercises using surrogate species, where it has been found that even among one group of species (e.g., plants), there are no species groups for which threat management of that group would also result in threat management for other species (Che-Castaldo & Neel, 2012).

The unreliability of LS to spatially represent threats to other biodiversity may be due to the fact that there is often little spatial overlap between different taxa (Jaarsveld et al., 1998; Prendergast et al., 1993). Another factor that probably contributes to the poor surrogacy performance of LS is that one of the selection criteria for LS is that they use several habitats. Thus, LS may be chosen and conserved in only a portion of the available habitats without necessarily conserving all of the habitats. It is logical, and indeed widely recognised, that suites of species are generally more effective surrogates for biodiversity than individual species (Mouillot et al., 2013; Williams et al., 2000). The LSA attempts to select a suite of species to act as surrogates for the threats facing a landscape, but there are no requirements or guidelines to ensure that a broad range of taxa are included in the suite. The LS suite used in this study was chosen following methods detailed in Coppolillo et al. (2004) and contains 12 mammals and one bird (Table 1). It has often been found that using one taxonomic group as a surrogate for the richness of all groups can be extremely unreliable (Hess et al., 2006; Lawton et al., 1998). Including a wider variety of taxa that are dependent on different habitats in the LS group may improve surrogacy performance, but this would entail changing the selection criteria.

The LSA is heavily reliant on the untested assumption that protecting LS will also protect other biodiversity in a landscape. We have shown this assumption to be untrue in our study. We found that prioritising for a random 13 species from the GVL resulted

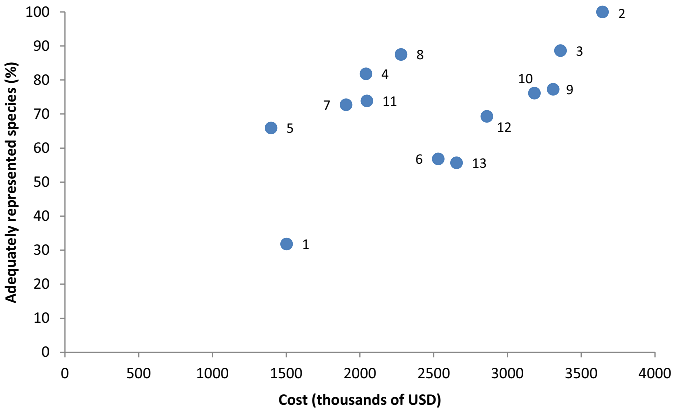

Fig. 4. Percentage of species adequately represented and cost, for different combinations of species using range-size based targets. Cost was calculated based on the distance of planning units from ranger patrol posts, incorporating the effort required for park rangers to travel to each planning unit and combat the threats facing species in that planning unit. Refer to Table 2 for graph reference numbers.

in significantly better surrogacy performance than prioritising for LS (Fig. 3). Similar results have been found for other surrogacy approaches, such as flagship, focal, and umbrella species. Andelman and Fagan (2000) studied the aforementioned species types, also finding that none performed significantly better than the same number of species selected randomly from their study area. Indeed, surrogacy approaches such as the focal species approach have been heavily criticised for relying on similar assumptions to the LSA (Lindenmayer et al., 2002).

Despite these criticisms, surrogacy based conservation planning approaches have been shown to work, with surrogates accurately representing other biodiversity. Nicholson et al. (2013) found that reserve systems which minimise expected loss for focal species also minimise expected loss for other species. However, such success may have been due a small set of target species (10), with most species able to use all habitat types. When species distribution and habitat requirements are diverse among target species the focal species approach may be less effective, and much of the criticism directed at the focal species approach can apply to the LSA.

We recognise that the LSA is different to other threat-based surrogacy approaches (e.g., focal species; Lamberck, 1997), in that it considers the influence of human activities, as well as the potential

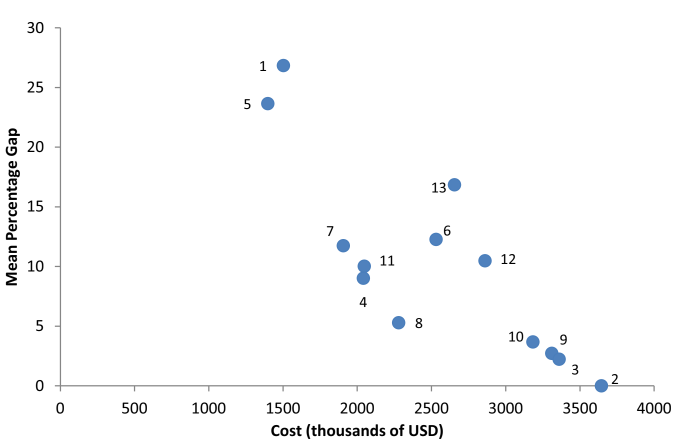

Fig. 5. Mean percentage gap values and cost, for different combinations of species, using range-size based targets. Cost was calculated based on the distance of planning units from ranger patrol posts, incorporating the effort required for park rangers to travel to each planning unit and combat the threats facing species in that planning unit A scenario in which all species are adequately represented will have a mean percentage gap of 0, and a scenario in which no species range is captured will have a mean percentage gap of 100. Refer to Table 2 for graph reference numbers.

impacts of conservation actions and the future attainable habitat capacity for LS (Didier, Glennon, et al., 2009). The LSA incorporates both vulnerability of biodiversity, and possible recovery. The approach is useful as a way of planning for the conservation and management of these large species, which are often most affected by anthropogenic activities, and assessing their needs within a landscape. It is also a useful method for defining how large a landscape needs to be considered as it will be the requirements of the LS that are likely to need the largest areas. However, given that we have shown that prioritising for a random selection of species gives better surrogacy performance than LS on average, the LSA should be supplemented by other, more robust conservation planning approaches. Because the LSA is currently being used by WCS and other organisations such as the U.S. Fish and Wildlife Service, the Kenya Wildlife Authority, and Melbourne Water (Didier, Wilkie, et al., 2009; Hamer et al., 2010; U.S. Fish and Wildlife Service, 2012), it is crucial that more tests of the LSA are carried out to provide knowledge on the utility of the LSA in different study areas, and to show if similar results are found outside the GVL.

It is also important to consider the limitations concerning the cost layer used in this analysis. The cost layer we used in the Marxan analyses was an estimate of the cost to patrol each cell in the GVL at least once per month from existing patrol post locations (Plumptre et al., 2014). It therefore reflects the reality of the conservation costs to manage the GVL and assumes that a visit once per month is sufficient deterrence to ensure the conservation of species in each cell. Illegal activities that occur in the GVL, such as poaching, are dynamic processes that will vary spatially depending on where ranger patrolling is concentrated. However, financial resources are not sufficient to patrol the entire landscape effectively, so patrolling should focus on areas of maximum conservation impact (i.e., maximum threat reduction), and this is the approach we have taken. If more frequent patrolling is needed to effectively combat threats to biodiversity, then we expect our results would be similar, as this would increase the total cost of each planning unit, but not the cost of planning units relative to each other. However, if certain aspects of biodiversity require more frequent patrolling than others (e.g., elephants which are heavily poached for ivory), then a cost layer that better incorporates the dynamic nature of threats to biodiversity could have improved our results. There are also other types of conservation actions that could be used in this area, such as lobbying district officials, strengthening penalties for crimes, or establishing community based conservation initiatives, but these are very difficult to incorporate into a spatial analysis, and so we feel that we have used the best cost layer available. Regardless, as our results had low-sensitivity to cost (Appendix D), we can assume that this would not have changed our results importantly.

4.2. Developing accurate surrogates for biodiversity

Irrespective of the profile-raising value or other appeal of surrogate species, to be biologically useful they must co-occur spatially with a large proportion of the biodiversity of an area, and should also have a high probability of persistence (Mouillot et al., 2013; Simberloff, 1998). As threats to species vary in space, surrogate species must also effectively represent those threats. However, it is difficult to identify a group of species that is small enough to be effectively managed, while still having high sensitivity to all threats in the GVL. As such, conservation planners are faced with a trade-off between sensitivity to threat, and keeping surrogate groups small enough to be effectively managed.

The criteria used to select a suite of LS focus on selecting species with large home ranges (along with other criteria), because conserving intact habitats large enough for these species will generally have benefits for species with smaller ranges (Coppolillo et al., 2004; Manne & Williams, 2003). However, this does not ensure that the LS will co-occur spatially with a large proportion of the biodiversity of a landscape, which face threatening processes that vary over space and time. Indeed, our results have shown that this is the case for the GVL.

Prioritising for birds or plants alone resulted in a higher percentage of species being adequately represented than prioritising for LS, and thus these groups are superior surrogates for biodiversity than LS. However, the total costs for the conservation plan for many of these groups, with the exception of endemic birds, were also higher than for LS (Fig. 4). Interestingly, the cost increase was not always proportionate to the increase in species representation. For example, targeting endemic plants had a slight higher cost than LS, but more than double the percentage of species that are adequately represented, and thus could be considered a superior surrogate. Combining these plant or bird groups with LS further increased the cost and percentage of species adequately represented. These results are similar to those reported by Larsen et al. (2012), who found that birds alone act as satisfactory surrogates for overall species diversity, but the effectiveness of the surrogate suite can be improved by supplementing birds with other taxa. However, these groups also had higher numbers of species than the original LS suite. It has been shown in numerous studies that the number of species in surrogate groups strongly influences their surrogacy performance (Larsen et al., 2007; Manne & Williams, 2003). Therefore, it is difficult to determine whether the surrogacy performance of these groups was related to the biology of species in those groups, or is simply an artefact of the greater number of species involved.

When considering surrogate groups of the same size as the LS suite, we found that prioritising for the 13 most threatened or 13 range limited species resulted in far better surrogacy performance than prioritising for LS. However, the total cost and area of these scenarios was also much greater than for LS (Appendix B). Prioritising only for the eight most range limited species results in better surrogacy performance and lower cost than prioritising for the entire LS suite. The use of range limited species may then be a more efficient way to plan conservation action in the GVL. Both the threatened and range limited surrogate groups contained a variety of birds, plants and mammals, whereas the LS suite contains 12 mammals and 1 bird. The poor surrogacy performance of LS, and the superior surrogacy performance of range limited species, may be because species-rich areas do not often coincide for different taxa (Prendergast et al., 1993). High levels of biodiversity are contained in areas of the GVL not selected when prioritising for LS, as shown by the superior surrogacy performance of scenarios that did conserve these areas (Appendix A).

5. Conclusions

The LSA is currently being used by many organisations to make conservation decisions in the field. These decisions determine how, where, and when limited conservation resources will be allocated. This is the first study to test an underlying assumption of the LSA: that LS accurately represent other biodiversity in a landscape. The results of this study show that this assumption is poor for the GVL, and suggest that the assumption may not be accurate for all study areas and species. Although we recognise that all conservation efforts will be of some benefit, the results of this study show that implementation of the LSA is not the most efficient way to use limited conservation resources. It may be a worthwhile approach to managing viable population of these large species, that require large areas for their conservation; however, this study shows that it should not be the sole approach used in a landscape. Another option would be to revise the LS selection criteria in order to include a greater variety of taxonomic groups, which may lead to more effective surrogacy using LS.

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Appendix A.

Selection frequency maps for 4 groups of 13 species used in species accumulation analysis: (A) range limited species, (B) landscape species, (C) threatened species, and (D) random species. Selection frequency ranges from areas selected in every Marxan run in dark red, to areas not selected in any Marxan runs in pale yellow. Current protected areas are outlined in black.

Appendix B.

Cost and area for 4 combinations of 13 species used in species accumulation analysis.

	Range limited species	Landscape species	Threatened species	Random species
Cost (000s of dollars)	2047.0	1501.6	2860.3	2654.7
Area (number of planning units)	6072	4212.8	6904.4	6999.4

Appendix C.

Percentage of species adequately represented and cost, for different combinations of species, using flat 30% targets (red) and range-size based targets (blue). *In scenarios prioritising for 30% flat targets, we used population-size based targets for landscape species and 30% flat targets for all other species (Fig. A1).

Appendix D.

Fleiss' kappa values comparing areas selected when prioritising for landscape species using original cost layer, and when prioritising for landscape species in scenarios with increased costs. The

Fig. A1.

"All" column compares the original landscape species result against all cost-increased scenarios.

Percentage cost increase			
100%	150%	200%	All
0.8	0.8	0.8	0.8

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