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RESEARCH ARTICLE



Spatial characteristics of species distributions as drivers in conservation prioritization

Heini Kujala^{1,2}  | Atte Moilanen³ | Ascelin Gordon^{2,4}

¹School of BioSciences, The University of Melbourne, Melbourne, Vic., Australia

²National Environmental Science Program (NESP) Threatened Species Recovery Hub, Melbourne, Vic., Australia

³Department of Biosciences, University of Helsinki, Helsinki, Finland

⁴School of Global, Urban and Social Studies, RMIT University, Melbourne, Vic., Australia

Correspondence

Heini Kujala

Email: heini.kujala@unimelb.edu.au**Funding information**

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Abstract

1. Spatial prioritization, based on the biogeographical identification of priority areas for conservation actions, is an important aspect of conservation planning. Although the influence of factors such as costs, threats or use of surrogates on the resulting priorities has been studied extensively, relatively little is known about how the spatial characteristics of species distributions drive the spatial pattern of priorities in multi-species conservation plans.
2. Using datasets from Australia and Finland, we explore how excluding or including a given species changes spatial priorities in a multi-species prioritization. We develop three metrics to quantify changes in priorities, and explore how these changes depend on the total number of species used in the prioritization, the spatial characteristics of the given species distribution, and how species share their space with other species used in the prioritization. We randomly selected 12 set of 10 species from each dataset, and explore the influence of each of these species in prioritizations done for a total of 10, 20, 50 or 100 species.
3. We show that spatial priorities become increasingly stable as the number of species is increased, and that the stability of highest and lowest priority areas behave differently. When less than 50 species were used in a prioritization, intermediately rare species that occupy mostly species-poor habitats tend to have the greatest influence on priorities, whereas very rare and common species that co-occur with many other species tend to have a small influence.
4. Our results present a systematic method to explore the stability of spatial priorities to changes in the species pool used for a conservation plan. Although the analysed two datasets differed in data type, location, scale and species composition, they both showed how using a small number of species leads to unstable spatial solutions, where the choice to include or exclude an individual species can strongly influence the conservation outcome. Our results also show that conservation planners should carefully assess the use of spatial prioritizations for identifying least important areas (e.g. for development) as these can be particularly unstable when the prioritization is based on a small number of species.

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KEYWORDS

conservation trade-offs, spatial conservation prioritization, spatial prioritization, species characteristics, species distribution, systematic conservation planning, uncertainty, ZONATION

1 | INTRODUCTION

The aim of conservation is to preserve all biodiversity as efficiently as possible, given limited resources. Part of this challenge requires determining where and when to apply different types of conservation interventions in the land- or seascape. Recent decades have seen a rapid development in a range of methods to support decision-making on efficiently allocating conservation interventions, loosely formulated under the framework referred to as “systematic conservation planning” (Kukkala & Moilanen, 2013; Margules & Pressey, 2000). Initially prioritizing areas for protection based only on data capturing biodiversity features (Kirkpatrick, 1983), these methods were further developed to incorporate, costs (Bode et al., 2008), threats (Wilson, Cabeza, & Klein, 2009), socio-political factors (Knight, Cowling, Difford, & Campbell, 2010; Whitehead et al., 2014), and most recently a broader range of conservation actions such as restoration or mitigating threats (Watts et al., 2009).

A fundamental step in this framework is the biogeographical identification of areas important for conservation, commonly referred as “spatial prioritization” (Kukkala & Moilanen, 2013). The utility of spatial prioritization is in balancing or trading-off the multiple factors that determine the importance of an area for conservation interventions. These include ecological factors (such as habitat or species distribution maps, or habitat condition), ecological processes (e.g. connectivity), and socio-political factors (costs, threats, existing reserves or administrative boundaries). Related to these are factors aggregated across sets of features such as species richness and rarity, and the complementarity or irreplaceability of given locations (Margules & Pressey, 2000).

In reality, all biodiversity features are rarely thought to be equally important and the choice of which to include in a prioritization is of critical significance, as these decisions may change areas identified as important by the analysis. In many cases, data limitations determine which features can even be considered for inclusion, and often data on species of conservation concern comprise the only features that are used (or surrogate species when data are lacking) (Arponen, 2012; Margules & Pressey, 2000). It is also common to give some species or features more importance in the prioritization by giving them a higher weight or conservation target, according to characteristics such as threat category, endemism, evolutionary uniqueness or economic value. Decisions about how to weight some features relative to others are by their nature subjective (De Grammont & Cuarón, 2006; Miller et al., 2006), and the consequences of applying different weighting schemes are often poorly explored (Arponen, Heikkinen, Thomas, & Moilanen, 2005). Concerns have also been raised about the lack of justification behind arbitrarily set species weights and/or targets and their influence on the effectiveness of conservation outcomes (Di Minin & Moilanen, 2012; Marsh et al., 2007; Possingham et al., 2002).

Another poorly explored aspect of spatial prioritization is how the spatial characteristics of an individual species distribution, and the spatial correlations between species distributions, influence the allocation of conservation actions in space. When balancing conservation options across multiple species and locations, these spatial characteristics, including the rarity of individual species and nestedness of species distributions (Wright & Reeves, 1992) will influence prioritization outcomes, with different species having differing amounts of influence in the spatial prioritization outcome. It is likely that these factors will also interact with the total number of species used in the analysis, given that the characteristics of any individual species distribution may influence the prioritization differently as trade-offs need to be settled between a greater number of species. However, there has been little work to explore this in a systematic way.

Here, we quantify the relative impact of individual species on the stability of a spatial prioritization, and how this interacts with the spatial relationships between the species involved in the prioritization. Although conservation practitioners often need to compare solutions that differ by multiple species, mapping the impact of a single species is the key for understanding the link between species attributes and the extent to which they influence spatial priorities. This, in turn, can be used to reveal information about: (1) how the influence of an individual species changes with the number of species used in the prioritization; (2) the stability of a prioritization result and how this might change with additional species, and; (3) the impact on prioritization results of giving some species additional weight in the analysis. We explore these issues using datasets from Australia and Finland and draw a number of conclusions, with potential implications for real-life conservation problems and making spatial prioritization more transparent.

2 | MATERIALS AND METHODS

2.1 | Data

We used two independent datasets: (1) a multi-taxa group of modelled species distributions in the region of Greater Hunter on east coast Australia, and (2) a single-taxon atlas data on observed occurrences of birds at the national scale in Finland, Europe. The two datasets differ in their geographical extent, data type and spatial resolution (Figure 1).

The Greater Hunter (GH) data includes modelled distributions at 1-ha resolution for 504 threatened species (35 amphibians, 258 birds, 58 mammals, 106 plants and 47 reptiles). The models have been built using MaxEnt (Phillips & Dudík, 2008) and presence-only point occurrences obtained from online public databases for species with a minimum of 20 occurrence records within the region. The species distribution modelling is described in Kujala, Whitehead, Morris, and Wintle (2015). Here, we used the MaxEnt logistic outputs of the species

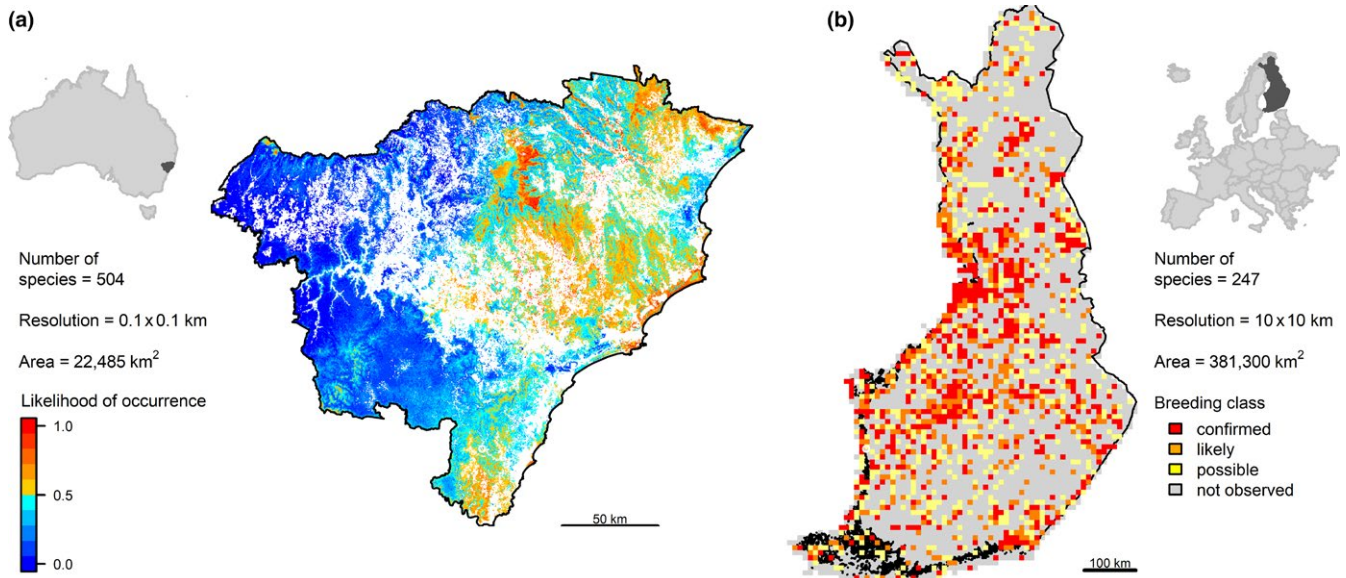


FIGURE 1 The two study regions and examples of the data used. (a) The Greater Hunter region and the modelled distribution of *Dasyurus maculatus*. (b) An example of breeding distribution of *Anas acuta* in Finnish atlas data

distribution models, which scale between 0 and 1. Each species distribution map constitutes of approximately 6.7 million pixels with data.

The second dataset is the combined first and second atlas of breeding birds of Finland (FIN). It comprises breeding observations for 248 bird species, as recorded during surveys in the 1970s and 1980s (Hyytiä, Kellomäki, & Koistinen, 1983; Väisänen, Lammi, & Koskimies, 1998), and is publicly available under Creative Commons Attribute 3.0 licence (<http://atlas3.lintuatlas.fi/background/copyrights>). The data have a uniform grid of 100 km² cells, with each species distribution map containing 3,813 data pixels. These data therefore have a larger geographical extent, but notably lower resolution, and is of a different data type than the Greater Hunter data. The atlas provides a breeding index value for each species in each atlas cell, ranging from 0 = “not observed” to 4 = “confirmed breeding.” Following recommendations from data coordinators (Väisänen, pers. comm.), we rescaled the raw data to values between 0 and 1, so that cells with 4 = “confirmed breeding” were given the value of 1, cells with 3 = “likely” or 2 = “possible” breeding the values of 0.67 and 0.33, respectively, and cells with 1 = “unlikely” and 0 = “not observed” combined and given a value of 0.

2.1.1 | Data resampling

To test how the spatial characteristics of species distributions affect prioritization patterns and how this might depend on the total number of target species, we created several species sets, m , of varying sizes. From both datasets, we first randomly selected 12 sets of 10 species with replacement. Each 10-species set was then increased to comprise a total of 20, 50 and 100 species, by adding new species that were randomly selected from the remaining respective species datasets. We therefore ended up with 96 species sets m , constituting of 24 replicates (12 for each dataset) of four nested groups of species (10, 20, 50, and 100 species), where each smaller group was a subset of a larger group.

2.2 | Methods

2.2.1 | Spatial prioritization analyses

For spatial prioritizations, we used a maximum-utility type algorithm (Camm, Polasky, Solow, & Csuti, 1996), which is one of the most commonly used spatial prioritization algorithm types (Kukkala & Moilanen, 2013). These algorithms aim to maximize the representation value of all included species within an area or budgetary constraint. Here we used an heuristic, non-target-based, maximum-utility type algorithm in the widely used conservation prioritization software, ZONATION (Moilanen et al., 2012). It is a backward algorithm that starts by assuming that the entire study area is protected and then proceeds to iteratively rank and remove all sites (grid cells), always removing the site with the lowest conservation value. After each iteration, the distribution remaining for each feature is recalculated, and the conservation values of remaining grid cells updated. ZONATION includes several alternatives for aggregating conservation value across features. Here we used a method called ‘Core Area Zonation’, in which the conservation value δ_i , across all species, is recalculated for each site i at each removal step as:

$$\delta_i = \max_j \frac{p_{ij}}{\sum_{s \in S} p_{sj}}, \quad (1)$$

where p_{ij} is the value of species j in cell i , and $\sum_{s \in S} p_{sj}$ is the sum of values of species j in cells s included in the remaining set of cells S at each removal step. The removal order creates a hierarchical ranking of grid cells, where increasing rank values from 0 to 1 indicate increasing priority for conservation. The maximum structure of the function increases the likelihood that the highest value cells for all species are maintained in the solution as long as possible, and the proportional structure means that the rarer a species becomes during the cell removal process, the more difficult it is to remove any of its remaining values.

We used Jackknife resampling to analyse how the spatial characteristics of individual species drive the spatial priorities in a multi-species analysis and the potential trade-offs in conservation outcomes between species. For each of the 96 species sets m , we first ran a full prioritization, including all species in the set. We then iteratively dropped out one of the original 10 species at a time, re-ran the prioritization with the remaining species and compared the results to the full prioritization. This resulted in total of 960 spatial prioritizations across the two datasets (96 species sets \times 10 runs missing one species), which could each be used to measure the impact of dropping out one species and how this varies with the characteristics of the dropped species. Within each of the 24 replicates (12 from both datasets), we also measured the differences between the full runs (produced using 10, 20, 50 or 100 species), to understand how the influence of a single species compares to adding multiple species in the prioritization.

2.2.2 | Measuring impact

We used three metrics to measure the impact of leaving out (or including) any single species j from a spatial prioritization (Figure 2). First, we calculated the *summed absolute difference* in the priority ranking of all grid cells, given by

$$\frac{\sum_{i=1}^S |pri_i^n - pri_i^{n-j}|}{0.5 \times S}$$

where S is the total number of grid cells, pri_i^n is the priority ranking of cell i with all species included and pri_i^{n-j} is the ranking of cell i with species j removed from the prioritization. The denominator is a normalizing factor and represents the maximum possible average difference in ranks, which results when two priority rankings are the exact mirror

images of each other. Hence the final values are scaled between 0 and 1, where 0 means that the results are identical (species j makes no change to the spatial priorities) and 1 means they are mirror images.

Second, as conservation planning typically focuses only on a proportion of the entire study area, typically the highest priority locations, we explored how the inclusion or exclusion of a single species j might change the geographical distribution of the top-ranked grid cells. For each solution, we identified the top areal proportions, ranging from the top 1% ranked cells to the top 50% ranked cells in 5% increments, and recorded the spatial overlap between solutions that include or exclude species j (Figure 2). We also repeated this for the bottom 1%–50% ranked cells, as spatial prioritizations are increasingly used to identify not only the most important conservation areas, but also the least important areas, for example to guide regional development (e.g. Gordon, Simondson, White, Moilanen, & Bekessy, 2009; Whitehead, Kujala, & Wintle, 2017). We refer to this metric as *overlap of top and bottom priority areas*.

Finally, we measured how the inclusion/exclusion of species j changes the conservation outcome for other included species. As multi-species prioritizations necessarily involve trade-offs between species that have different geographical distributions, removing one species can, in theory, relax some of these trade-offs and increase the representation of the remaining species under constant areal constraints. Hence, for all other species k in a species set, we measured the *change* in area under the curve (AUC) between the two solutions, where the AUC gives the proportion of the distribution captured for species k as a function of proportion of study area protected per the cells rankings (Figure 2). By averaging the AUC values across all other species k , we can quantify the average change in conservation outcomes for all other species k in the species set, when species j is included/excluded from the prioritization, irrespective of the area of the top priorities that is being investigated.

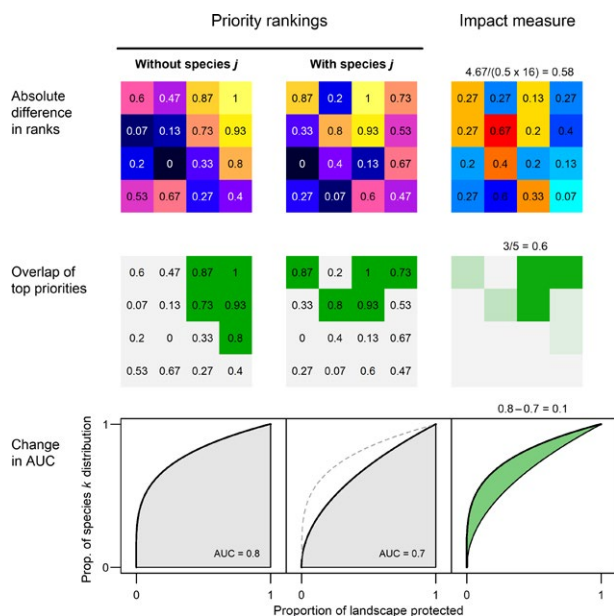


FIGURE 2 Illustration of how impact measures are derived. For each measure (rows) the first two panels (columns) give example results when species j is excluded from or included in, respectively, to the prioritization. The third panel shows how the information is used to calculate the differences between the two results

2.2.3 | Species characteristics

We examined four spatial characteristics of the included/excluded species j and compared these to their impact on the prioritization (Table 1). Relative *regional coverage* was calculated as the distribution size (sum of cell values within distribution) divided by the number of grid cells in the study region. We also explored how each species j co-occurs with all other species k in each species set m , by estimating the average relative *species richness within distribution* of species j and the *mean Jaccard similarity* index (calculated using the R package “PICANTE” v.1.6.-2, Kembel et al., 2010) between species j and species k (Table 1). Finally, we calculated the Spearman rank *correlation* coefficient between the spatial distribution of species j and the priority ranks of the solution without species j (Table 1). Species with high a correlation are assumed to have a lesser impact than those with low or negative correlation, though this relationship is not well understood in multi-species optimizations. We note that by comparing the correlation coefficient to the observed changes in priorities, which both share data elements (species j), we aim to explore how this assumed relationship plays out in real data, rather than to draw formal statistical inferences. We also acknowledge that the relative likelihood values produced by presence-background models such as MaxEnt do not correctly indicate species

TABLE 1 List of variables measured to characterize species distributions

Variable	Equation	Description
Regional coverage	$\frac{\sum_{i=1}^S p_{ij}}{S}$ <p>p_{ij} = value of species j in cell i S = number of data cells i</p>	Proportion of study area covered by species distribution, reflecting spatial rarity or commonality of species. Scaling against total number of data cells makes the values comparable between the two study regions
Within distribution richness	$\frac{p_{ij} \sum_k r_{ik}}{\sum_i p_{ij}} / n_m$ <p>r_{ik} = value of species k in cell i n_m = total number of species in a species set m $k \neq j$</p>	Average species richness within species j 's distribution, weighted by species j 's values in each grid cell i and scaled against total number of species in each species set m . Indicates whether species occupies species-rich or species-poor areas within the study region. Scaling against total number of species in a set makes the values comparable between sets and study regions
Mean Jaccard similarity	$\sum_k \left(1 - \frac{2d_{jk}}{1+d_{jk}} \right) / n_m - 1$ <p>where</p> $d_{jk} = \frac{\sum_i p_{ij} - r_{ik} }{\sum_i p_{ij} + \sum_i r_{ik}}$	Index describing how species co-occur with other species in a species set m . Varies between 0 and 1, with 0 indicating a complete absence of [spatial] relationship between species, and 1 indicating identical distributions. The index is calculated for each species pair j and k in a species set m , and then averaged across species k
Spatial correlation with priority (Spearman's ρ)	$\frac{\text{COV}(rg_j, pri_{n-j})}{\sigma_{rg_j} \sigma_{pri_{n-j}}}$ <p>rg_j = rank converted values of species j pri_{n-j} = priority ranks in a solution without species j $\text{cov}(rg_j, pri_{n-j})$ = covariance of rg_j and pri_{n-j} $\sigma_{rg_j}, \sigma_{pri_{n-j}}$ = standard deviations of rg_j and pri_{n-j}</p>	Spatial correlation between species j and the spatial prioritization produced without species j . Measures how well the distribution of species j is already covered by a priority solution produced without it

prevalence nor are they comparable between species (Guillera-Arroita et al., 2015). However, for this study we assumed that they provide a reasonable representation of the biodiversity patterns in the Greater Hunter and treat them as if they were probabilities of occurrence.

3 | RESULTS

3.1 | Species spatial characteristics

All species in both datasets occupied the landscape partially, with only a few species occupying >50% of their study area (Supplementary Information, Figure S1). The spatially most common species in the Finnish data tended to occupy larger proportional areas (up to c. 90% of the area) than those in the Greater Hunter data (up to c. 45%), where species seemed to have slightly higher average similarity across distributions (max. Jaccard index: GH = 0.4; FIN = 0.3). Despite comprising different types of data, the relationships between the spatial characteristic of species showed very similar patterns across the two datasets: The Jaccard similarity index of a species increased exponentially with increasing regional coverage. The within distribution average species richness showed a nonlinear relationship with the other metrics, both regional coverage and mean Jaccard index peaking at intermediate levels of richness. Hence, in both datasets, the rarest, and most dissimilar

species dominated both the most species-rich and species-poor sites (Figure S1).

3.2 | Influence of species in the spatial allocation of priorities

3.2.1 | Absolute difference in ranks

The impact of excluding/including a single species from/in a spatial prioritization depended on both the characteristics of the included/excluded species and the total number of species included in the prioritization. As the number of species included to the prioritization was increased, the solutions across species sets became visibly similar in both datasets (Figure 3). Increasing the species pool also effectively decreased the change incurred by any single species (Figures 4, S2a,b and S4). When prioritization was done for 10 species, the change in priority rankings incurred by any single species varied between <1%–26% in the Greater Hunter and 1.2%–34% in the Finnish dataset (Figure S2a,b). As the species pool was increased to 20, 50 and 100 species, the maximum observed change in priority ranks dropped to 19.5%, 11.5%, 7.2% in Greater Hunter and 21.4%, 9.7%, 7.5% in Finland, respectively (Figures 4 and S2a,b), with the average changes being clearly lower. Indeed, comparisons between full prioritizations within a set m confirmed that the greater the relative change in the number of included/excluded species,

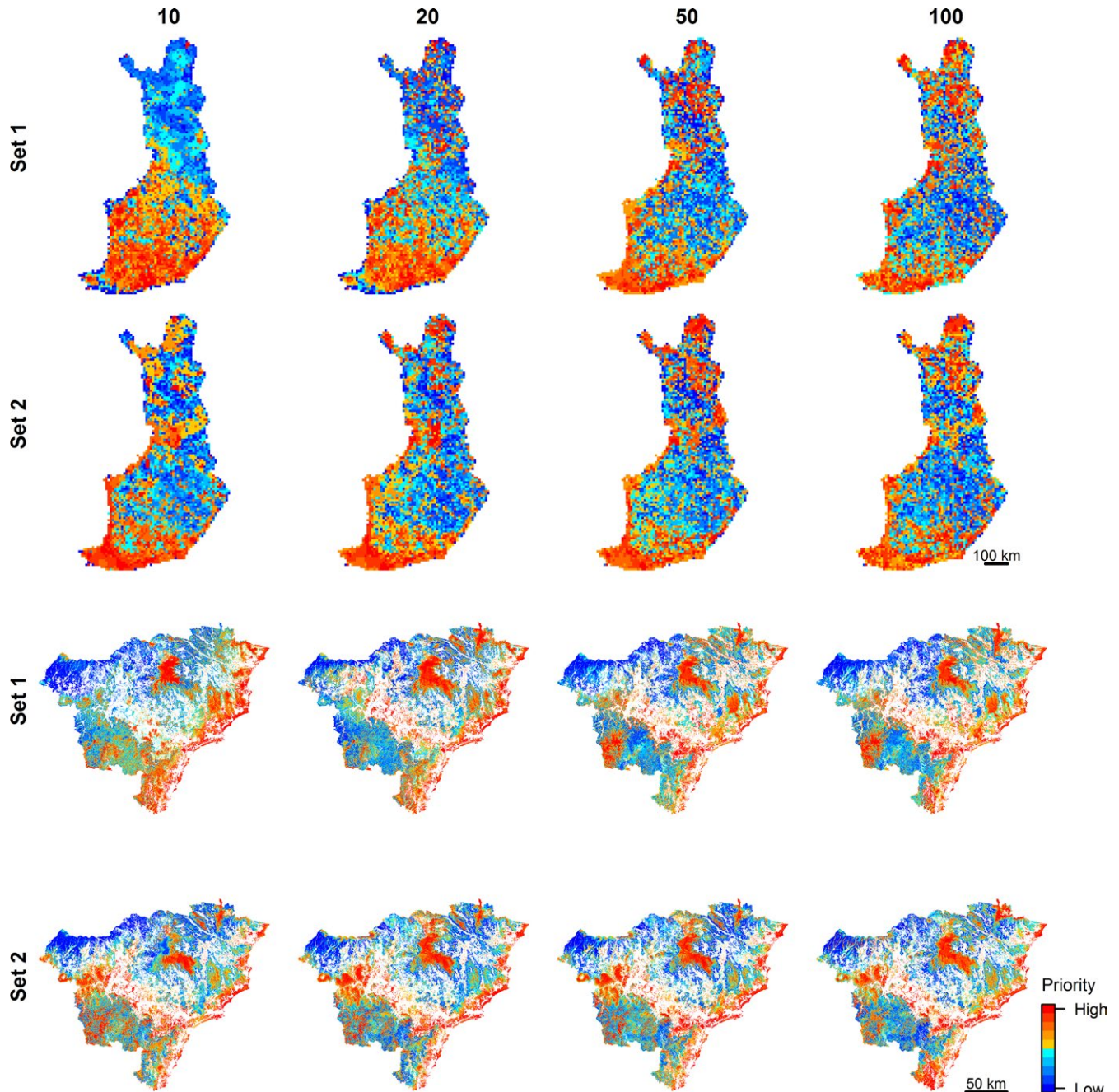


FIGURE 3 Examples of spatial prioritization results for two species sets from the two datasets: Finland (upper two rows) and Greater Hunter (lower two rows). For each set, the prioritization was initially done with just 10 species (first column) after which the species pool is increased to 20, 50 and 100 (remaining columns), respectively, by adding new species from the remaining dataset

the larger the change in priorities, however, the impact does not increase linearly with increasing number of new species (Figure S2c,d).

Two of the tested species characteristics, the average species richness within distribution and the Spearman correlation between the distribution of species j and a prioritization done without species j , had a negative linear or exponential relationships with the observed changes in priority ranks (Figure 4). Hence, species which tended to occupy species-poor locations and which had distinct or even opposing distribution patterns from a priority solution done without them, caused largest changes in the priority ranking when included to the analyses.

Regional coverage and the average similarity with other species distributions (as measured by Jaccard index) showed similar patterns, where impact on priority rankings peaked at intermediately low coverage and/or similarity (Figure 4). Hence, both the rarest and/or most dissimilar species, as well as the most common and/or similar species tended to have less of an impact on priority patterns when included to the species pool. In the case of the Finnish birds, the impact on priorities did tend to increase again at very high levels (>70%) of regional coverage, although this pattern emerged only when prioritization was based on a small number of species ($n = 10$). Interestingly, species with

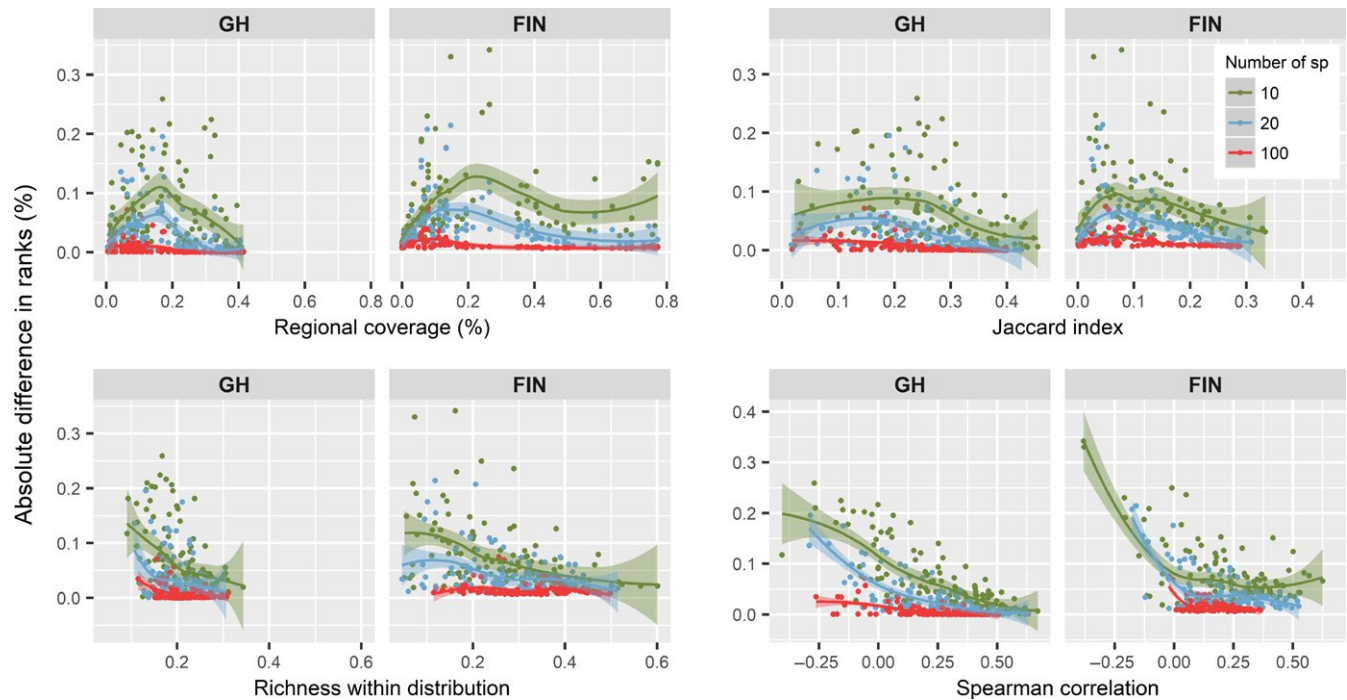


FIGURE 4 Changes in the influence of an individual species on priority ranks as the total species pool is increased, shown for 120 species (12×10 -species sets), as part of different sized collections of species (green = 10, blue = 20, red = 100 species). The Y-axis gives the absolute difference in the priority ranks across all grid cells when species j is excluded, plotted against the characteristics of the excluded species. Lines give the locally weighted smoothing (LOESS) with approximated 95% confidence intervals across all 12 sets and for each species pool size. For clarity, the group size of 50 species has been omitted, for results with this group size see Figure S3. Data is shown for both Greater Hunter (GH) and Finland (FIN)

greatest impact changed together with increasing species pool, with the peak impact shifting towards rarer and more dissimilar species as species number was increased. We note that whereas the regional coverage of species j is constant through different species sets, the Jaccard index of species j depends on the other species in the pool, and thus changes as the species pool is changed.

All four characteristics showed considerable variation across species, suggesting that species influence is likely driven by the interaction of several attributes. For example species with very similar correlation with existing priorities still had very different impact when included in/excluded from an analysis.

3.2.2 | Spatial overlap of top and bottom priority areas

The overlap of top and bottom ranked priority areas varied depending on the species characteristics, the species pool size and the size of the top/bottom proportion considered (Figure 5). In general, the smallest top/bottom proportions, that is, the very highest and lowest priority areas, tended to have the lowest overlap between solutions where species j is either included or excluded. As the size of the top/bottom proportion was increased, the two solutions became increasingly similar: average overlap for the top and bottom 50% fractions was 95.1%, respectively, across the two study areas and 10-species sets, and 99.4% for 100-species sets. When the prioritization was done only for a small number of species, the very lowest

priority areas (e.g. bottom 1%) had notably lower overlap between the two solutions than did the very highest priority areas (top 1%). This pattern tended to reverse as the number of species increased to 50 or 100 species, although in the Greater Hunter dataset some individual species still affected the distribution of the lowest ranking cells much more than the distribution of the equivalently highest ranking cells. The overlap of the highest and lowest priority areas was also lower in the Finnish dataset than in the Greater Hunter dataset, likely driven at least partly by the smaller number of grid cells in the Finnish data.

When a species j was either included or excluded, the overlap of the top and bottom priority areas changed to a similar degree as observed with all cell ranks (Figure S5): the overlap between the two solutions tended to be smaller for those species for which large changes across all cell ranks were observed, and *vice versa*, although towards the most top and bottom proportions (<5% of the study areas) the correlation became weaker or disappeared, particularly in the coarser grained Finnish data.

3.3 | Influence of a single species on the conservation outcomes for all other species

On average, the inclusion/exclusion of any single species j tended to have a relatively small impact to the potential conservation outcomes for the remaining species, particularly when prioritizing areas for many species (Figure S6). In the majority of the cases, including a

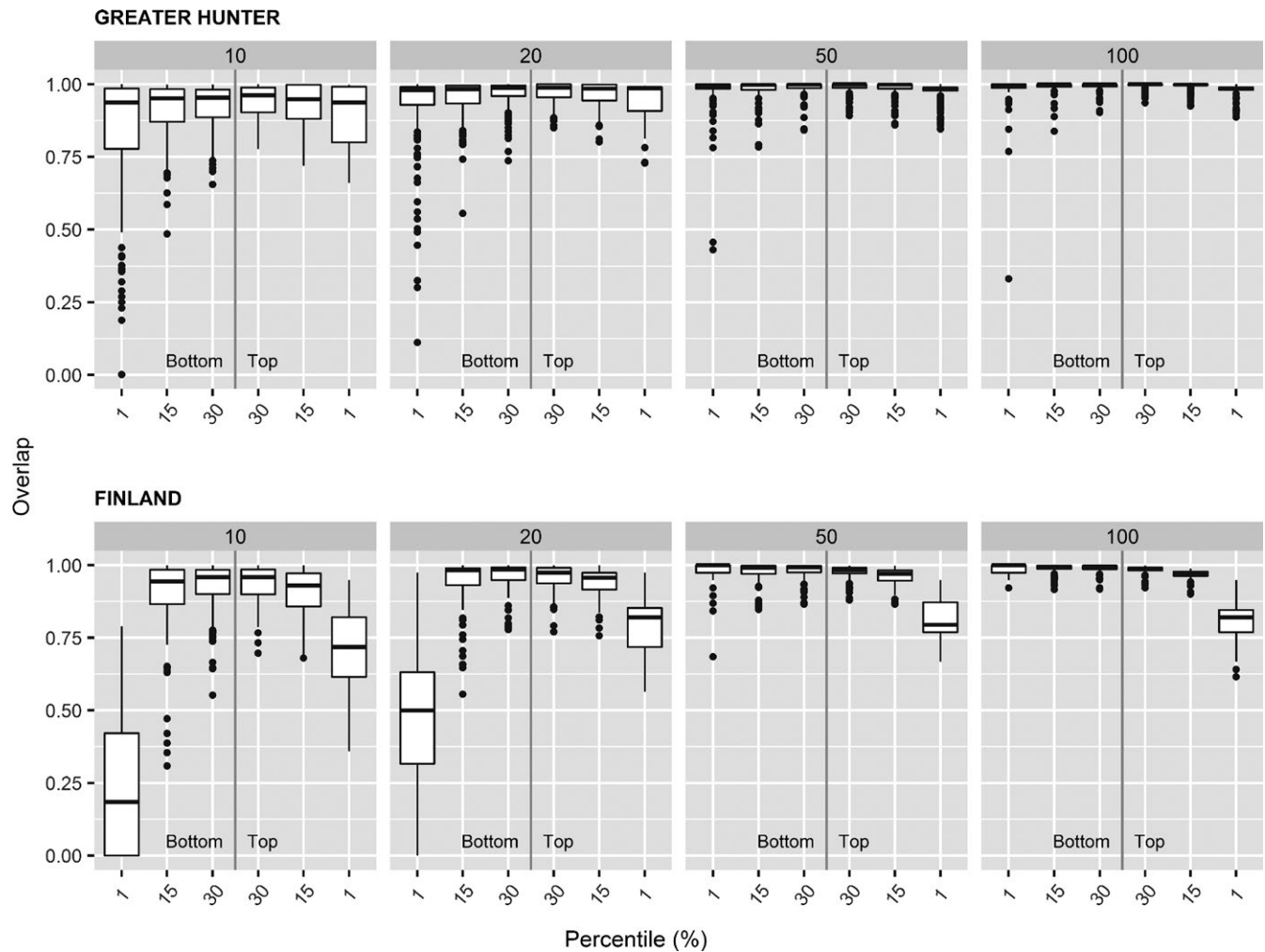


FIGURE 5 The spatial overlap between the top and bottom priority areas when a species j is included/excluded from the prioritizations. Each panel shows results for a different total number of species in the prioritization. The boxplots show the distribution of the observed proportional overlaps when comparing both top and bottom ranked 1%, 15% and 30% of the study area

new species j to the prioritization did reduce the proportion of distribution protected for other species k , but the average reduction was small and decreased in both datasets with increasing species pool size: the average reduction for groups of 10, 20, 50 and 100 species was 0.4%, 0.12%, 0.03% and 0.007% less for species k distributions covered at any level of protection in the Greater Hunter data, and 0.5%, 0.23%, 0.06% and 0.015% in the Finnish data respectively. However, the level of impact varied greatly, not only across the included/excluded species j , but also across the impacted species k , and the level of protection considered. Figure 6 shows the most extreme observed case across all prioritizations, where the inclusion of single species j (the Whimbrel, *Numenius phaeopus*) in one of the 10-species groups in the Finnish dataset reduced the AUC values of all other species on average by 0.045. Across species k this translates to an average of 4.5% less distribution protected at any level of protection, the most impacted species (the Black bird, *Turdus merula*) experiencing an average reduction of 9.8% (Figure 6, shaded area) when species j is included. The greatest single trade-off occurred when 15% of the area was protected, where the inclusion of the Whimbrel resulted in 32% less distribution protected for the Reed bunting (*Arenaria interpres*)

(Figure 6, orange arrow). Nevertheless, the majority of single-species alterations in both datasets had notably smaller impact, some even marginally improving the average outcome for other species, when included to the prioritization (Figure S6).

The change in the conservation outcomes for other species correlated positively with the observed spatial changes in priority ranks: species with the greatest impact on the distribution of priority ranks also reduced the conservation outcomes for all other species the most (Figure S7). The relationships between species spatial characteristics and the mean change in AUC values were nearly identical to those observed with priority rank changes (Figure S8).

4 | DISCUSSION

Our results provide some of the first steps towards understanding how the spatial allocation of conservation priorities across multiple species is driven by the interaction between the number and type of species included to the prioritization. For both datasets, the stability of priority areas increased rapidly as the total number of species included

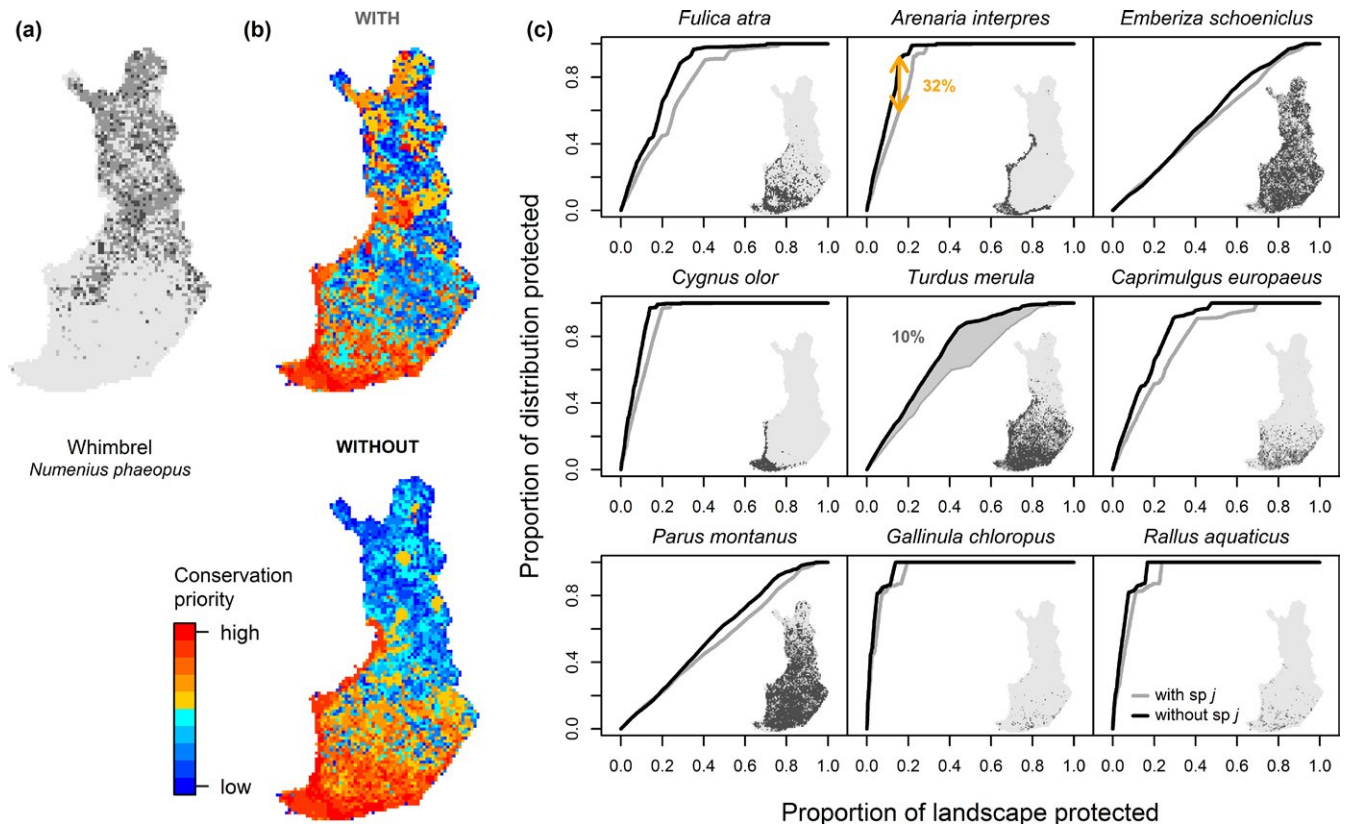


FIGURE 6 An example of how the inclusion/exclusion of a species (illustrated here with Whimbrel *Numenius phaeopus*) in a spatial prioritization can impact the distribution protected for all other species, shown for one of the 10-species sets from the Finnish dataset. The line plots (c) show the proportion of distribution captured at increasing levels of protection (based on the priority ranking) for each of the other 9 species k , when species j (Whimbrel) (a) is either included (grey line) or excluded (black line) in the prioritization (b). Maps of the distributions of each species k are shown in dark grey inside each line plot. The Whimbrel has a spatially different distribution in comparison to the other 9 species and, when included in the prioritization, creates trade-offs at each point of the ranking process, resulting in less area available to protect the other 9 species. The largest trade-off across all levels of protection (shaded area) and at any single level of protection (arrow) are shown

in the prioritization was increased (Figure 3) and after 50 species, the impact on adding a new species to the solution tended to be marginal (Figures 3 and S2-S4). We found that when increasing the species pool size to 250 species in the larger Greater Hunter data, further stability in priority rankings could be achieved, but with diminishing returns (Figure S2). Comparisons between the full runs in each species set m (Figure S2c,d) confirm that not only the starting group size and species characteristics but also the relative change in the number of added or removed species dictate the extent of changes in priority ranks. Hence, changing multiple species will incur larger changes over single-species alterations, but the magnitude of the impact will depend on the starting size, number of species added and the aggregate spatial characteristics of the species.

Understanding the relative impact any single species is likely to have on a conservation plan is nevertheless advantageous for conservation scientists and practitioners for several reasons. Firstly, it helps to disentangle the different drivers that dictate how priorities for multiple species become distributed in space, making the process and outputs more transparent and easier to communicate, and providing a starting point from which to explore impacts of changing multiple species. Second, understanding the link between species influence and

its spatial attributes helps to anticipate potential changes (or the lack of) when considering including new data into analyses. Third, mapping the relative influence of individual species may help to clarify how additional weights given to species shape the prioritization results: for example giving a high weight to already highly influential species may not result in greatly improved outcomes for that species. Finally, understanding which species most drive spatial priorities is highly relevant from the perspective of input data uncertainty and value of information: uncertainties, gaps in the distribution data and the assumptions made in the modelling of a highly influential species are most likely to be of greater interest than those of less influential ones.

An important finding from our results is that, when the number of species included to a prioritization is low, the least important areas are even more sensitive to just single-species changes in the species pool than the top priority areas (Figure 5). As the number of species was increased, the stability of the least important areas also increased, but individual species could still cause larger changes in the least important areas compared to the most important areas (Figure 5). Our explanation for this is as follows: Given that many species, particularly the relatively rare ones, co-occur with other species in local clusters of diversity (Figure S1), many species in a randomly

selected set tend to result in the same top-priority areas. In this case adding or removing one species does not necessarily make much of a difference to the top-ranked grid cells. In contrast, the core habitat of species that tend to occur in isolation are not likely to be captured in high priority areas unless explicitly included in the analysis. As these same areas are of low value to other species, adding such species to a prioritization can make a proportionally large change to the previously low priority areas.

These findings have important implications to some of the current practices in local and regional planning where both environmental impacts and conservation plans are commonly based on just a handful of key species, conservation flagships or surrogates (Gontier, Balfors, & Mörtberg, 2006; Hawke, 2009; Whitehead et al., 2017). Our results suggest that undertaking a prioritization with less than 50 species (or biodiversity features in general) is likely to be an undesirable practice as the resulting prioritization will be more sensitive to the set of species chosen for the analysis. Particularly, when exploring potential development impacts, using only a small number of species runs the risk that impacts on non-included species are not correctly captured. With a larger number of species, the prioritization is more likely to better represent the overall biodiversity patterns of the region, and to increase the robustness of the proposed conservation plan, assuming that the included species are not environmentally biased towards specific habitats. However, further investigation is needed to fully understand the stability of spatial prioritization to adding or removing multiple species to the species pool.

Our results show how the spatial characteristics of species can dictate the influence they have on the spatial allocation of priority areas (Figure 4), particularly when the prioritization is done with only 10–20 species. We found the distribution of priorities to be most influenced by intermediately rare species that have somewhat dissimilar distribution patterns with other species, and which occupy comparatively species-poor areas. Hence, conservation priorities are less driven by species that are very rare and dissimilar or, widespread and very similar with other species. As very rare species occur in only a small number of locations, their inclusion leads to priority changes in very few grid cells and hence to only marginal changes to the overall priority patterns. Therefore, priority areas in a multi-species prioritization are typically not greatly influenced by very rare species, particularly if these species occupy areas of high species richness. Similarly, if a species is widespread, then almost any configuration of priority areas is likely to capture parts of its distribution, resulting in it having a minor influence on the distribution of priority areas. A species' influence on spatial priorities is also dependent on the number of species included to the prioritization. For example with an increasing number of species, the importance of rarity tends to peak at lower levels (Figure 4): with large datasets (>50 species) species that occur within <10% of the study area are most influential, whereas with small datasets (<20 species) most influential species occupy approximately 20% of the study area.

Of the metrics used to measure species' impact on spatial priorities (Table 1), the summed absolute difference in ranks is somewhat specific to our chosen prioritization algorithm, requiring a conservation priority ranking for all locations in the study area. On the other

hand, the overlap of priority areas with and without a species, and its implication for the conservation outcome of all other species are widely generalizable metrics across all types of spatial prioritizations. In general, the impact of the number and type of species included to a prioritization was very similar across all three metrics (Figures S4 and S6). We note that although our work includes only two case studies, it combines two datasets that differ vastly in data type, area extent, resolution and taxonomic composition (Figure 1). Despite these differences, our findings across both datasets are strikingly similar, implying that the outcomes may be generalizable to other locations and data types when the same or a similar prioritization algorithm is used.

In this work, we used an algorithm that maximizes the remaining locally high quality areas for all species at each step of the prioritization process (Moilanen et al., 2012). We chose this option as, beyond the individual species distributions and the underlining philosophy that the important areas of *all* species need to be protected, the solutions are not influenced by other factors, such as species richness of candidate sites or pre-defined conservation targets. It is therefore well-suited for exploring the influence of species characteristics and the trade-offs that arise in a multi-species prioritization. How generalizable our findings are to results created with other approaches depends on their similarities and differences to the algorithm used here. For example algorithms that sum values across species in a cell (e.g. the Additive Benefit Function option in ZONATION, Moilanen et al., 2012) typically give higher priority to areas of high species richness, potentially resulting in solutions that are less sensitive to additional species (Moilanen, Anderson, Arponen, Pouzols, & Thomas, 2013).

Similarly, using conservation targets (e.g. target-based algorithms such as Marxan, Ball, Possingham, & Watts, 2009) may further influence, in interaction with the species distributions, how priorities are distributed (Di Minin & Moilanen, 2012). Expanding the prioritization to include costs, threats, actions and/or socio-political factors will introduce additional drivers that will interact with those presented here. All these drivers may influence not only how priorities are distributed across locations but also their stability (e.g. Bode et al., 2008).

Our work provides clarity in how spatial conservation priorities are formed in multi-species prioritizations and which factors might drive trade-offs when dividing conservation resources between spatially non-overlapping species. As rule of thumb, our results indicate that including at least 50–100 species in regional biodiversity mappings is a good starting point, as prioritization with less species seem sensitive to just single-species alterations. This is particularly important when using spatial prioritization to identify least important areas. Examining factors such as regional coverage, spatial correlation with any existing protected area networks, or even richness within distribution may reveal information on the drivers behind identified priority areas, and how additional species might change them. In general, improved data for very common or very rare species, particularly those that occur in species-rich areas, is unlikely to cause large changes in spatial priorities, whereas improving mapping of the distributions of intermediately rare species that share their space with comparatively few other species will likely be more important.

The methods developed here can be extended to biodiversity data from other regions, scales, and approaches to spatial prioritization. Having a greater understanding of the generality of the findings presented here will be important for most effectively implementing the results of conservation prioritizations around the world.

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AUTHORS' CONTRIBUTIONS

H.K. and A.G. conceived the idea, and H.K., A.G. and A.M. designed methodology; H.K. analysed the data; H.K. led the writing of the manuscript with equal contributions from A.G. and A.M. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data produced in this work has been made available via figshare online repository <https://doi.org/10.4225/49/5a01806212b0c> (Kujala, Moilanen, & Gordon, 2017).

ORCID

Heini Kujala  <http://orcid.org/0000-0001-9772-3202>

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