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Quantifying the relative irreplaceability of important bird and biodiversity areas

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Abstract: *World governments have committed to increase the global protected areas coverage by 2020, but the effectiveness of this commitment for protecting biodiversity depends on where new protected areas are located. Threshold- and complementarity-based approaches have been independently used to identify important sites for biodiversity. We brought together these approaches by performing a complementarity-based analysis of irreplaceability in important bird and biodiversity areas (IBAs), which are sites identified using a threshold-based approach. We determined whether irreplaceability values are higher inside than outside IBAs and*

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whether any observed difference depends on known characteristics of the IBAs. We focused on 3 regions with comprehensive IBA inventories and bird distribution atlases: Australia, southern Africa, and Europe. Irreplaceability values were significantly higher inside than outside IBAs, although differences were much smaller in Europe than elsewhere. Higher irreplaceability values in IBAs were associated with the presence and number of restricted-range species; number of criteria under which the site was identified; and mean geographic range size of the species for which the site was identified (trigger species). In addition, IBAs were characterized by higher irreplaceability values when using proportional species representation targets, rather than fixed targets. There were broadly comparable results when measuring irreplaceability for trigger species and when considering all bird species, which indicates a good surrogacy effect of the former. Recently, the International Union for Conservation of Nature has convened a consultation to consolidate global standards for the identification of key biodiversity areas (KBAs), building from existing approaches such as IBAs. Our results informed this consultation, and in particular a proposed irreplaceability criterion that will allow the new KBA standard to draw on the strengths of both threshold- and complementarity-based approaches.

Keywords: complementarity, convention on biological diversity, irreplaceability, key biodiversity areas, restricted-range species, systematic conservation planning, threatened species

Cuantificación del Carácter Relativamente Irreemplazable de las Áreas Importantes para la Conservación de Aves

Resumen: *Los gobiernos del mundo se han comprometido a incrementar la cobertura de las áreas protegidas para el año 2020, pero la efectividad de este compromiso con la protección de la biodiversidad depende de la ubicación de las nuevas áreas protegidas. Las estrategias basadas en umbrales y en la complementareidad se han utilizado independientemente para identificar sitios importantes para la biodiversidad. Juntamos estas estrategias al realizar un análisis basado en la complementareidad del carácter irreemplazable de las áreas importantes para la conservación de aves (AICA), que son sitios identificados con el uso de una estrategia basada en umbrales. Determinamos si los valores de irreemplazabilidad son más altos dentro que fuera de una AICA y si alguna diferencia observada depende de las características conocidas del área. Nos enfocamos en tres regiones con inventarios completos de AICA y en atlas de distribución de aves: Australia, el sur de África y Europa. Los valores de irreemplazabilidad fueron significativamente más altos dentro de las AICA que fuera, aunque las diferencias fueron mucho menores en Europa que en otro lado. Los valores más altos de irreemplazabilidad en las AICA estuvieron asociados con la presencia y el número de especies con extensión restringida; el número de criterios bajo los que se identificó el sitio; y el tamaño promedio de la extensión geográfica de las especies para las cuales se identificó el sitio (especies de activación). Además, las AICA se caracterizaron por valores de irreemplazabilidad más altos cuando se usaron objetivos de representación proporcional de especies en lugar de objetivos fijos. Hubo resultados comparables de manera general cuando se midió la irreemplazabilidad de las especies de activación y cuando se consideró a todas las especies de aves, lo que indica un buen efecto de sustitución de las anteriores. La Unión Internacional para la Conservación de la Naturaleza convocó recientemente a una consulta para consolidar los estándares globales para la identificación de áreas clave de biodiversidad (ACB), a partir de las estrategias existentes como las AICA. Nuestros resultados brindaron información a esta consulta y en particular a la propuesta de un criterio de irreemplazabilidad que permitirá al nuevo estándar de las ACB recurrir a las fortalezas de las estrategias basadas en umbrales y de las basadas en la complementareidad.*

Palabras Clave: áreas claves de biodiversidad, carácter irreemplazable, complementareidad, Convención sobre la Diversidad Biológica, especies amenazadas, especies con extensión restringida, planeación de la conservación sistemática

Introduction

Facing an accelerating rate of biodiversity loss (Butchart et al. 2010), parties to the Convention on Biological Diversity (CBD) have established an ambitious set of 20 targets for the conservation of biodiversity to be achieved by 2020 (Aichi Targets) (CBD 2011). Under Aichi Target 11, signatory nations committed to expand the global coverage of protected areas (PAs) to at least 17% of terrestrial and 10% of coastal and marine environments "especially in areas of particular importance for biodiversity and ecosystem services." Implementing this target could lead

to a dramatic expansion of the global PA estate (Watson et al. 2014). However, biodiversity is distributed unevenly across the earth, so the overall effectiveness of the target in reducing biodiversity loss depends largely on where PA expansion takes place (Venter et al. 2014; Butchart et al. 2015). In addition, in assessing the most appropriate strategies for implementing Target 11, it is important to make the distinction between areas that are important for biodiversity and areas that are priorities for conservation intervention, which are a subset of the former group. The identification of priority sites for PA expansion is not based solely on the distribution of species

(or other biodiversity features) and needs to account for other conservation-relevant factors such as the threats to biodiversity and the cost of conservation interventions (Margules & Pressey 2000). We focused on areas that are important for biodiversity and particularly on comparing threshold- and complementarity-based methods used to identify these areas (Brooks et al. 2006; Moilanen et al. 2009).

Threshold-based approaches have been used to identify sites that support important components of biodiversity based on a set of criteria and associated thresholds. These sites have been broadly referred to as key biodiversity areas (KBA) (Eken et al. 2004; Langhammer et al. 2007). In particular, the approach developed by BirdLife International (2014) to identify important bird and biodiversity areas (IBAs) has been adapted and extended to other taxonomic groups, including important plant areas (PlantLife International 2004), prime butterfly areas (van Swaay & Warren 2006), and Alliance for Zero Extinction sites (Ricketts et al. 2005). Over 12,000 IBAs have been identified worldwide (Supporting Information), considerably more than for any other approach. These areas are globally identified using 4 criteria (Supporting Information), with associated thresholds (e.g. minimum number of species, or individuals), related to the occurrence of globally threatened species (A1), restricted-range species (A2), species assemblages confined to a single biome (A3), and congregations of one or more species (A4). In addition to global criteria, regional criteria have been used in Europe and the Middle East (with numeric thresholds lower than for global criteria). To date, one-fifth of all IBAs (22%) are completely covered by PAs, 45% are partially covered, and 33% are entirely unprotected (Butchart et al. 2015).

In parallel to the development and implementation of threshold-based approaches, systematic conservation planning (SCP) has emerged as a framework to identify cost-effective strategies for identifying areas important for biodiversity and for prioritizing and implementing conservation actions (Margules & Pressey 2000). Within the SCP framework, spatial conservation prioritization (Moilanen et al. 2009) is the process of using spatial analysis to identify locations for conservation investments. This process can include data on threats, costs of conservation actions, and budget availability (Wilson et al. 2006). It can also account for social factors determining the feasibility of actions (Mills et al. 2013). Quantitative conservation targets are applied to identify actions aimed at ensuring the persistence of biodiversity (Knight et al. 2006) or, alternatively, solutions are sought to maximize the protection of biodiversity given a budget constraint (Moilanen et al. 2009). Spatial prioritization incorporates the concept of complementarity, by identifying sites for protection that complement, rather than replicate, each other (Justus & Sarkar 2002), to maximize cost-efficiency of target achievement (Possingham et al. 2000). It also incorporates the concept of irreplaceability, defined as the contribution of a site in achieving biodiversity conservation targets or the extent to which the options for achieving the targets are compromised if the site is lost (Pressey et al. 1994; Ferrier et al. 2000). SCP is recognized as an efficient method to prioritize investments in PA expansion. PAs in South Africa (Cowling et al. 2003), Australia (Fernandes et al. 2005), the Solomon Islands (Game et al. 2011), and the United Kingdom (Smith et al. 2009) have been identified through SCP.

Threshold-based approaches (such as KBAs) and complementarity-based approaches (from SCP) rely in part on subjective decisions. The former identify all sites meeting the thresholds for 1 or more criteria. The latter identify sites based on their relative contribution to the biodiversity targets adopted, and typically there are many potential alternative solutions. The thresholds used by threshold-based approaches are often discretionary, such as the 50,000 km^2 threshold used for defining restricted-range bird species (Stattersfield et al. 1998). Similarly, complementarity-based approaches use discretionary values, for example, to identify spatial representation targets for biodiversity features (e.g., 10% of the distribution range of a widespread species [Rodrigues et al. 2004]).

To date, relatively little interaction has occurred between the KBA community and the SCP community (Bennun et al. 2007; Knight et al. 2007). Recent exceptions include the identification of freshwater KBAs for subsequent use as planning units in a spatial prioritization analysis (Holland et al. 2012) and the use of KBAs to test the local-scale accuracy of a global-scale spatial prioritization analysis (Montesino Pouzols et al. 2014). However, no one has applied complementarity-based techniques to comprehensively assess the irreplaceability of sites identified under threshold-based approaches.

We tested 2 hypotheses: irreplaceability values are higher inside than outside IBAs (H1), and irreplaceability values are correlated with the characteristics of individual IBA sites (H2), such as the criteria adopted to identify the site and the number and characteristics of species for which the site qualified.

Methods

We used bird distribution data to estimate site irreplaceability in 3 different regions of the world: Australia, southern Africa, and Europe. We tested hypothesis H1 by comparing irreplaceability values inside and outside IBAs in each region. We tested hypothesis H2 by comparing the irreplaceability values observed in IBAs with different characteristics. We first conducted these tests focusing on species that triggered the identification of individual IBAs (hereafter trigger species) and then repeated the analyses including all species native to the study regions.
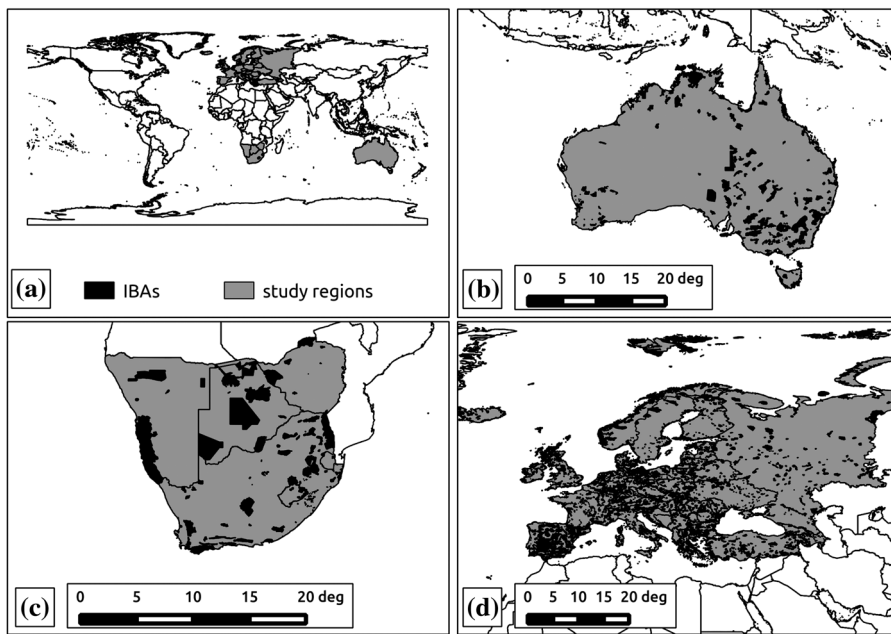
Figure 1. Location of (a) the 3 study regions and distribution of important bird and biodiversity areas (IBAs) within (b) Australia, (c) southern Africa, and (d) Europe. Some of the areas in each region were excluded from analyses due to poor data coverage or difference in regional data resolution (see "Bird Distribution Data and Characteristics of the Study Regions" and Supporting Information).

Table 1. Characteristic of the important bird and biodiversity areas (IBA) networks in the study regions.

Region	No. of IBAs	Mean IBA size (km²)	No. of trigger species*	Total no. of species
Australia	271	1,600	252	749
Southern Africa	173	898	215	821
Europe	4,158	271	241	492

Species that triggered the identification of individual IBAs.

The selected regions provide ideal case studies, being characterized by comprehensive IBA inventories (Birdlife International 2015; Fig. 1, Table 1) and published atlases of bird distributions (see Supporting Information for a consideration of bias in data coverage). These regions also differ in the characteristics of their avifauna and their IBA networks. For example, Australia and southern Africa have more endemic birds than Europe, whereas IBAs are smaller in Europe than elsewhere. This allows for extrapolation of our results to a broader context.

Bird Distribution Data and Study Region Characteristics

In Australia, IBAs were identified mostly during 2008–2009 and were on average larger than IBAs in the other 2 regions (Dutson et al. 2009). We used bird occurrence data from the 2012 version of the Atlas of Australian Birds, a citizen science initiative (www.birdata.com.au). This data set included information on 866 species recorded on 615,500 checklists associated with point locations on the continental mainland, surrounding islands, or at sea (>9.8 million observation records). After removing observations of nonnative species and those obtained in open sea (i.e., from boats), and matching the taxonomy with the IBA data, we analyzed 749 species (one-third of them have been used for the identification of IBAs). We converted the point occurrences in the Atlas of Australian

Birds to 50 km grid-based occurrences. We used a 50 km grid because the reported accuracy of survey locations was up to 50 km in some cases.

In southern Africa, IBAs were identified mostly in 1997–1998 (Barnes 1998). Occurrences of bird species in this region have been systematically recorded since 1987 and published in 2 atlases. The first Southern African Bird Atlas Project (SABAP 1) culminated in the publication of The Atlas of Southern African Birds (Harrison et al. 1997). The atlas covered Botswana, Lesotho, Namibia, South Africa, Swaziland, and Zimbabwe and included information on the occurrence of 847 bird species since 1987 (i.e., approximately the same period during which IBAs were independently identified). We did not use the more recent SABAP 2 atlas (http://sabap2.adu.org.za) because the timing of the data compilation is more recent than (and so less comparable to) the regional IBA data set. We based our analyses on 821 bird species with matching distribution and taxonomic information (one-quarter of them have been used for the identification of IBAs). The data were linked to grid cells with a resolution of 15 arc-min (about 27.7 km at the equator) with the exception of Botswana, where the resolution was 30 arc-min. We excluded Botswana from the analyses to ensure a consistent resolution in the region.

In Europe, IBAs have been identified since the late 1970s; a list published in 2000 represents the most recent

comprehensive compilation (Heath et al. 2000). Europe includes approximately 40% of all existing IBAs (more than any other region), and these are on average smaller than those in the other 2 regions. The EBBC Atlas of European Breeding Birds includes information on the occurrence of 499 bird species, mainly from 1980–1990 (Hagemeijer & Blair 1997). We based our analyses on 492 species with matching distribution and taxonomic information (half of them have been used for the identification of IBAs). The data on observed species occurrences were associated with a grid with a 50 km resolution. This atlas differs from those in the other 2 regions in that it covers only information on breeding occurrences and reports survey data completeness (which we used to exclude grid cells with poor coverage to avoid inclusion of largely under-sampled area). We considered only globally significant IBAs, excluding those identified as regionally significant, with the exception of countries where global thresholds have not yet been applied (Hungary, Lithuania, Romania, Slovakia).

The 3 regions differed in the characteristics of their avifauna. For example, the percentage of IBA trigger species qualifying as restricted range was 30% in Australia, 13% in southern Africa, and 4% in Europe. Consequently, the 3 regions differed in the number of IBAs identified under each IBA criterion (Supporting Information). Individual IBAs can qualify under multiple criteria: on average IBAs met 2 criteria in Australia, 2.5 in southern Africa, and 1.3 in Europe.

Seasonality in Species Geographic Ranges and Representation Targets

For each migratory species, we classified grid cells in the atlas data as relating to non-breeding or breeding plus resident range (hereafter breeding) by matching them to seasonal range maps (BirdLife International and NatureServe 2013). We assigned a representation target to each seasonal part of species' ranges (Rodrigues et al. 2004). In Europe all species occurrences were classified as breeding, given that the European bird atlas data are limited to breeding occurrences.

For each species, we set a proportional representation target (i.e., the proportion of regional species' range to be included in selected areas). The proportional target was scaled with the size of the species' global geographic ranges (Rodrigues et al. 2004; Venter et al. 2014; Butchart et al. 2015). Widespread species (global geographic range >250,000 km^2) had a representation target of 10%, small-range species (range <1000 km^2) had a representation target of 100%, and intermediate-range species had values log-linearly interpolated between the 2 thresholds. We applied these proportional representation targets to define regional targets of global significance.

The results of a spatial prioritization analysis depend largely on the targets. To test the sensitivity of our re-

sults to the use of different representation targets, we focused on Australia as a case study and assigned 3 different targets to species: scaled proportional representation targets (as described above), fixed representation target of 5% (i.e., half the minimum proportional target), and fixed representation target of 20% (i.e., twice as much as the minimum proportional target). We chose Australia because it had the greatest differences between irreplaceability inside and outside IBAs (see Results).

Spatial Prioritization Analysis and IBA Characteristics

Different tools exist to approximate irreplaceability (Moilanen et al. 2009), for example based on statistical techniques (C-Plan) and optimization algorithms (Marxan), and these provide similar results under similar problem settings (Carwardine et al. 2007). We used the selection frequency (SF) metric of the Marxan software (Ball et al. 2009) to estimate the irreplaceability of grid cells (i.e., the planning units) in our regions. Marxan uses a stochastic global search algorithm to identify combinations of planning units that meet the required species targets. Because the process is partially stochastic, each Marxan run can provide different solutions, and the SF represents the proportion of times a cell is selected across all solutions. We ran a full biodiversity-driven analysis, excluding information on costs and threats because these factors are not considered when identifying IBAs. We performed 1000 Marxan runs for each analysis with 1 million iterations each, and the species penalty factor was set at 100. Given the relatively coarse resolution of the atlas data, we did not use clumping functions. The spatial resolution of our analyses was subject to the availability of atlas data. We used a 50 km resolution for Europe and Australia and approximately 28 km resolution for southern Africa. In a recent analysis, Montesino Pouzols et al. (2014) found that the results of a global-scale spatial prioritization analysis were robust to changes in resolution (from <2 km up to 20 km).

We performed separate Marxan analyses for each study region and derived SF values of individual grid cells in each region. We then associated these values with IBAs. Because each IBA may overlap with multiple grid cells, we calculated the mean area-weighted SF value (SF_{mean}) and the maximum SF value (SF_{max}) within IBAs. We used SF_{mean} to test H1 (i.e., irreplaceability higher inside IBAs) because this average value can be directly compared with SF in cells outside IBAs. We used SF_{max} to test H2 (irreplaceability correlates to IBA characteristics) because this indicates the highest irreplaceability contributed by an IBA and it is not affected by the inclusion of areas of lower importance (resulting from the IBA delineation).

By measuring IBA SF values as a combination of the SF values observed in their overlapping grid cells, we may have underestimated the irreplaceability of IBAs as a whole (Supporting Information). This is because the
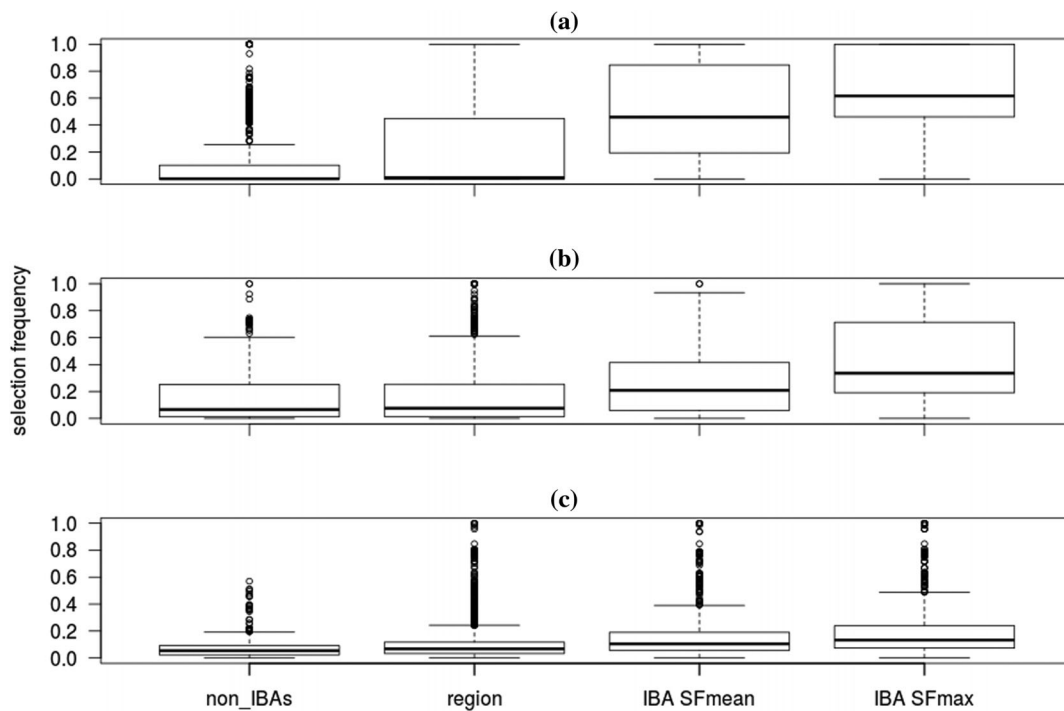
Figure 2. Selection frequency (SF) values measured in the 3 study regions: (a) Australia, (b) southern Africa, and (c) Europe. From left to right box plots represent SF values for cells outside important bird and biodiversity areas (IBAs), SF values for all cells in the region, mean SF values observed in IBAs, and maximum SF values observed in IBAs.

irreplaceability of a given spatial unit is not a simple additive function of the irreplaceability values in its sub-units; an IBA covering 2 grid cells, each including half of the global distribution of a species, is totally irreplaceable (even if neither of the 2 cells are). This may affect the comparison of irreplaceability inside and outside IBAs (H1). To investigate this effect, we performed a comparison of SF values measured in Australia for actual IBAs and for a set of randomly located IBAs (Supporting Information). In this test, SF values were measured in exactly the same way in both actual and random IBA locations; the latter represented background regional SF values. Results were similar (SF significantly higher inside than outside IBAs, Wilcoxon signed-rank test) with the cell approach and the random-location approach (Fig. 2 and Supporting Information). This confirmed that our testing of H1 was robust relative to the use of an alternative (and more computationally intensive) technique.

To test H2 (IBA characteristics influence irreplaceability) we evaluated the relationship of SF_{max} based on criteria under which the IBA qualified (A1 to A4) (Supporting Information); total number of criteria met by each site (1–4); number of trigger species; number of restricted-range trigger species; number of threatened trigger species; and mean geographic range size of all trigger species.

To test the effect of using different pools of species when measuring regional irreplaceability values, we ran two sets of analyses: a trigger-species analysis, where we

aimed at representing only those species triggering IBAs, and an all-species analysis, where we aimed to represent all bird species within a region (Table 1).

Results

The SF_{mean} values inside IBAs were always significantly higher (Wilcoxon signed-rank test, $P < 0.05$) than regional background values (Fig. 2; see Supporting Information for SF maps). The difference between SF values inside and outside IBAs was highest in Australia and lowest in Europe.

The IBA triggering criterion A2 (restricted-range species) showed on average higher SF_{max} values than those triggering other criteria. This pattern was observed in all regions but was most evident in Europe (Fig. 3). The IBAs triggering more criteria had higher SF_{max} values in Australia and southern Africa but not in Europe. In Australia and southern Africa, the SF of sites meeting 3 or 4 criteria was significantly higher than SF of sites meeting only 1 (Wilcoxon signed-rank test, $P < 0.05$).

The relationship between SF_{max} and number of trigger species was weak across all regions and was positive for Australia and southern Africa (Fig. 4). This relationship became stronger when we considered only restricted-range species or threatened species. In Europe a positive relationship with SF values was observed only when
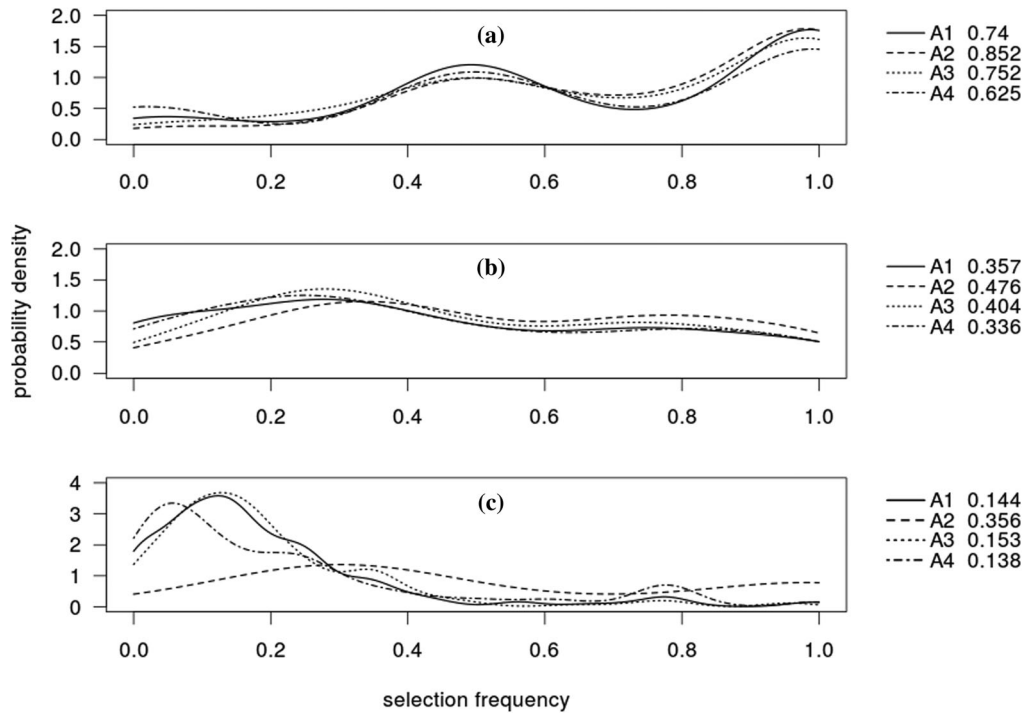
Figure 3. Distribution of maximum selection frequency values (SF$_{max}$) for important bird and biodiversity areas (IBAs) identified under each of 4 global criteria (A1 to A4, described in Supporting Information) in the 3 study regions: (a) Australia, (b) southern Africa, and (c) Europe. The median values of SF$_{max}$ distributions are reported on the right-hand side of the plots. An IBA may meet more than one criterion; hence, there is a partial overlap between sites included in each of the 4 groups (e.g., a site qualifying for A1 and A2 was included in both the solid and the dashed lines).
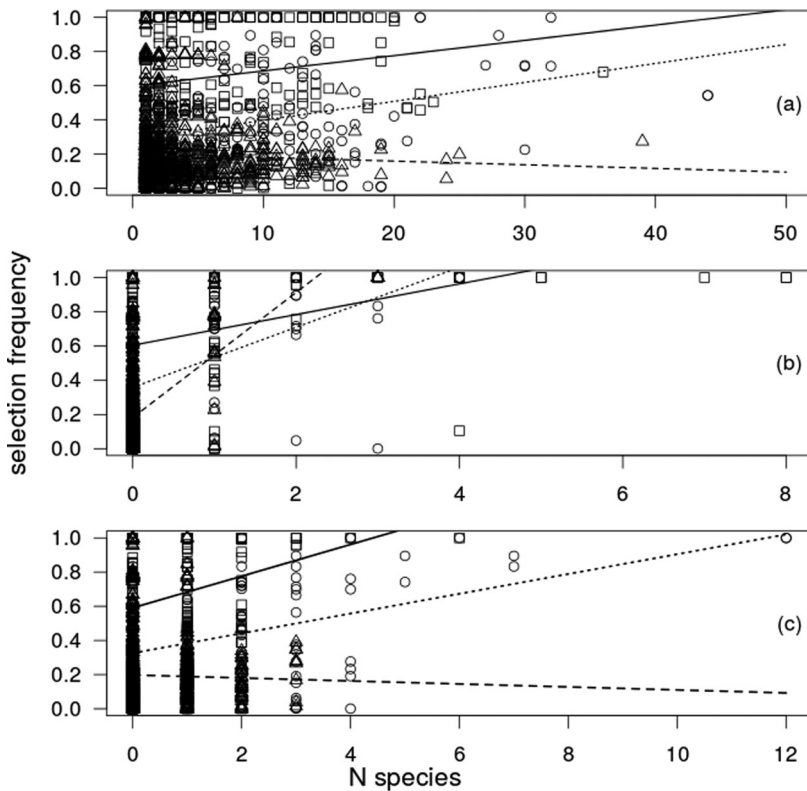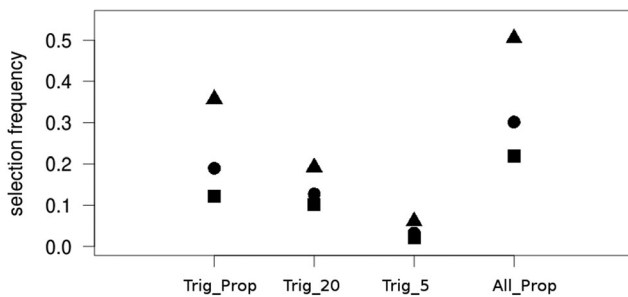

Figure 4. Relationship between important bird and biodiversity areas (IBA) selection frequency values (SF$_{max}$) and number of trigger species (i.e., species that triggered the identification of IBAs). Each shape represents a different IBA, and lines represent fitted linear regressions (squares and solid line, Australia; circles and dotted line, southern Africa; triangles and dashed line, Europe). The plots represent the relationship between selection frequency and (a) total number of trigger species, (b) number of restricted-range trigger species, and (c) number of threatened trigger species.

Figure 5. Selection frequency values measured in Australia under 4 different scenarios: trigger (trig) species (i.e., species that triggered the identification of important bird and biodiversity areas [IBAs]) with representation targets scaled by range size (prop); trigger species with a fixed representation target of 20%; trigger species with a fixed representation target of 5%; and all bird species with representation targets scaled by range size (all) (squares, grid cells outside IBAs; circles, all cells in the region; triangles, grid cells overlapping with IBAs).

considering restricted-range species. The lack of a clear pattern in Europe probably resulted from IBAs in the region having fewer trigger species (i.e., most European IBAs clustered at the bottom left of Fig. 4a). In all regions, there was a negative linear relationship between mean species' range size and SF_{max} ($P < 0.05$ for Europe only).

The SF values in the all-species analysis were similar to those in the trigger-species analyses. This was verified both when comparing SF values inside and outside IBAs (H1) and when investigating the relationship between SF and IBA characteristics (H2). We found only one noticeable exception: in the all-species analysis, IBAs triggering criterion A4 (congregatory species) had relatively higher SF values and showed relatively less difference in SF with respect to IBAs triggering other criteria (Supporting Information).

The SF was always significantly higher inside than outside Australian IBAs ($P < 0.05$ Wilcoxon signed-rank test), but the strength of this pattern depended largely on the target (Fig. 5). Australian IBAs had relatively higher SF values (with respect to the regional context) when we used proportional species representation targets rather than fixed targets, especially when low fixed targets were adopted.

Discussion

We found higher irreplaceability values within IBAs than outside them for all regions, indicating there was concordance between the 2 approaches. However, these differences were more evident in Australia and southern Africa than in Europe. This is likely because Europe has fewer restricted-range species and more IBAs than

other regions. When using representation targets scaled by range size, high SF values tended to be associated with the presence of restricted-range species. A grid cell including a restricted-range species was more likely selected because relatively few cells exist where such a species occurs and a relatively large proportion (up to 100%) of the species' distribution must be selected to meet its representation target. Furthermore, the difference between mean and maximum SF values in IBAs was more evident in Australia and southern Africa than in Europe. This is likely related to the characteristics of the IBA networks; the former 2 regions included relatively fewer and larger IBAs (which may include some areas of lower irreplaceability).

The fulfillment of H1 was influenced by the representation targets assigned to species during the spatial prioritization analysis. The IBAs were characterized by relatively higher SF values when representation targets were scaled with species' range size. The difference was less evident for fixed targets, in particular if these were low (such as 5%). This is likely the result of IBAs themselves being targeted to represent species with restricted distributions (criterion A2) and threatened species (criterion A1), which typically also have small distributions.

We also confirmed H2: in all regions IBAs identified under criterion A2 (restricted-range species) showed higher SF values than those identified under other criteria. This result held when considering all species (not only IBA trigger species). Values of SF were also positively related to the number of criteria triggered by each IBA, with the exception of Europe, where most IBAs met only 1 criterion. In Australia and southern Africa, an increased number of trigger species were associated with higher SF values for IBAs, and this was more evident when looking at restricted-range species or threatened species. This result was not unexpected: an increasing number of species (especially those with small ranges) increased the chances that an individual grid cell was selected by Marxan. European IBAs generally had fewer trigger species than the other 2 regions, and higher SF values in European IBAs were associated only with the number of restricted-range species. In all regions, a negative relationship was observed between mean range size of trigger species and SF values for the IBAs, again confirming the strong link among range size, representation targets, and irreplaceability.

Our results did not depend on the set of species included in the analyses; in general, results were the same when limiting analyses to IBA trigger species and when considering all bird species. This likely resulted from non-IBA trigger species being generally widespread and having low representation targets assigned. Targets for widespread species can be met under many different combinations of grid cells, whereas there are relatively few options for meeting targets for small-ranged species (which typically trigger IBA identification).

Consequently, trigger species proved a good surrogate of bird biodiversity. The only exception was criterion A4 (congregatory species), which was associated with relatively high SF values when all species were considered. Site-level abundance data are used when identifying IBAs under criterion A4, yet comprehensive data on species abundance were not available for our study regions, and we used presence-absence data. This may explain the relatively low SF values observed for IBAs identified under this criterion. Further testing is required to investigate the relationship between IBAs and irreplaceability in regions where comprehensive population abundance data are available.

Our analytical resolution was relatively coarse, depending on the resolution of bird atlas data, and some of the IBAs were smaller than the size of an individual grid cell, especially in Europe. This means that in theory the irreplaceability value of these IBAs could have been overestimated. However, IBAs are specifically delineated to cover the distribution of bird species of conservation concern (the trigger species). It is thus expected that an IBA located in a grid cell where one or more trigger species occur would overlap with the distribution of these species. Consequently, it is unlikely that the irreplaceability value of small-sized IBAs was overestimated.

Reconciling Threshold- and Complementarity-Based Approaches

Threshold-based approaches use simple classification criteria and are applied to 1 site at a time. For example, the identification of an IBA is generally independent from the characteristics of other sites in the same region, and a given species may be used to identify any number of sites, provided that it meets threshold numbers in all those sites. In contrast, to meet species' representation targets through complementarity-based approaches, a set of areas are selected where the targets can be met efficiently (e.g., with few sites). Although all sites where a given species occurs can potentially be selected to achieve the target, in general only a limited number of sites will be selected. Consequently, the selection of a site depends not only on its characteristics, but also on the characteristics of other sites in the region. In other words, the irreplaceability of a site depends on the regional context, whereas the IBA status is an absolute, rather than relative, attribute. In some cases, the 2 approaches are expected to produce convergent results. For example a site that includes the only occurrence of one or more endemic species is identified both as totally irreplaceable and as an IBA. However, the relationship between the 2 approaches in other situations is context dependent and requires testing.

We conducted a comprehensive comparative test of threshold- and complementarity-based approaches for the identification of important biodiversity sites in 3 re-

gions. The correspondence between these 2 approaches depended largely on the characteristics of areas selected under the threshold-based approach and the representation targets adopted under the complementarity-based approach. Sites with species below IBA-threshold levels could still be important to efficiently achieve species' representation targets, especially when they have high levels of complementarity with other sites (Ferrier et al. 2000). Conversely, a site may be of particular importance for a given species (e.g., if the species congregates there for part of the year) and be identified as an IBA even if it has low irreplaceability when aiming for global species representation (e.g., if the species is widespread). For these reasons, we stress the importance of complementing the threshold-based identification of important biodiversity sites (such as IBAs and KBAs more generally) with the systematic identification of irreplaceable sites (through spatial prioritization techniques). Failing to do so may bring about significant gaps in any reserve system built on these sites.

Recently, the International Union for Conservation of Nature convened a consultation to consolidate standards for the identification of KBAs globally (www.kbaconsultation.org); this effort builds on existing approaches like IBAs. Our results have helped inform the new KBA standard in 2 ways. First, the definition of new KBA thresholds was influenced by our identification of the characteristics that trigger higher irreplaceability in a site. Second, our results informed the proposal of a new criterion ('criterion E) in the new KBA standard, allowing sites to qualify as KBAs if they have high levels of irreplaceability (measured using spatial prioritization techniques). This important addition minimizes the possibility of sites with relatively high levels of irreplaceability being left out of a KBA network. The new KBA standard therefore supports identification of important sites for biodiversity based on the strengths of both threshold-based and complementarity-based approaches.

The CBD Aichi Target 11 commits governments to expanding their PA coverage (CBD 2011), and this expansion needs to ensure a significant increase in biodiversity protection in order to be effective. In addition, this PA expansion will directly contribute to the achievement of other CBD targets (Di Marco et al. 2015). Consequently, knowing where important sites for biodiversity are located is an essential first step to inform the allocation of conservation resources. Scientists have proposed several strategies to identify important biodiversity areas for expanding the global PA estate, following threshold-based approaches (Butchart et al. 2012; McCarthy et al. 2012), complementarity-based approaches (Montesino Pouzols et al. 2014; Venter et al. 2014), or a combination of these (Butchart et al. 2015). By bringing together different approaches for sites selection, we have provided guidance on how to identify irreplaceable and important sites for biodiversity.

Acknowledgments

Supporting Information

Supporting text (Appendix S1), description of global criteria used to identify IBAs (Appendix S2), proportion of IBAs in each region of the world (Appendix S3), percentage of IBAs identified under each criterion (Appendix S4), calculation of SF in IBAs (Appendix S5), representation of the IBA randomization procedure (Appendix S6), comparison of observedversus random SF values in Australian IBAs (Appendix S7), maps of selection frequency values in the three study regions (Appendix S8), box plots representing the distribution of SF values for IBAs triggering an increased number of criteria (Appendix S9), relationship between mean species range size SF values (Appendix S10), distribution of SF values for IBAs identified under each of four criteria in the all-species analysis (Appendix S11) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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