

Opinion

Measuring Terrestrial Area of Habitat (AOH) and Its Utility for the IUCN Red List

Thomas M. Brooks,^{1,2,3,*} Stuart L. Pimm,⁴ H. Resit Akçakaya,⁵ Graeme M. Buchanan,⁶ Stuart H.M. Butchart,^{7,8} Wendy Foden,^{9,10,11} Craig Hilton-Taylor,¹² Michael Hoffmann,¹³ Clinton N. Jenkins,¹⁴ Lucas Joppa,¹⁵ Binbin V. Li,^{4,16} Vivek Menon,¹⁷ Natalia Ocampo-Peñuela,¹⁸ and Carlo Rondinini¹⁹

The International Union for Conservation of Nature (IUCN) Red List of Threatened Species includes assessment of extinction risk for 98 512 species, plus documentation of their range, habitat, elevation, and other factors. These range, habitat and elevation data can be matched with terrestrial land cover and elevation datasets to map the species' area of habitat (AOH; also known as extent of suitable habitat; ESH). This differs from the two spatial metrics used for assessing extinction risk in the IUCN Red List criteria: extent of occurrence (EOO) and area of occupancy (AOO). AOH can guide conservation, for example, through targeting areas for field surveys, assessing proportions of species' habitat within protected areas, and monitoring habitat loss and fragmentation. We recommend that IUCN Red List assessments document AOH wherever practical.

Rigour and Dynamism in the IUCN Red List

The IUCN Red List of Threatened Species [1] aspires to assess the extinction risk of the world's species, and to serve as a 'barometer of life' of the state of nature [2]. Of the approximately 2 million named species [3], the IUCN Red List has assessed 98 512 species (having increased from fewer than 20 000 in 2002). The process of assessment classifies species in different categories of extinction risk. It does so through an open, rigorously defined process [4] that is objective and transparent. Petitioners can challenge decisions made by Red List Authorities. An important use of the IUCN Red List is the assessment of changes in species extinction risk to monitor changes in the status of individual species, classes and other groups of species, and species-level biodiversity overall [5,6]. These are essential, for example, in reporting on the Aichi Targets [7] and Sustainable Development Goals [8], as well as progress in conserving species [9].

The need for rigour and consensus in assessing extinction risk can potentially bring the process into conflict with those who seek to harness rapidly expanding geographic databases and remote sensing technologies to assess species' status [10–12]. Numerous publications have illustrated how increasingly sophisticated and high-resolution regional and global remote sensing and spatial datasets or models can inform the existing Red List criteria [13,14]. The many-fold growth in the availability of these data over the last decade, coupled with increasing computing power to process them, has allowed the development of methods for estimation of the **Area of Habitat (AOH)**, (see **Glossary** and Supplemental Information) remaining for terrestrial species. It is therefore timely to review, standardise, and stabilise how AOH is measured, how it relates to the Red List criteria, and sources of error in its derivation. Specifically, we show here that AOH is equivalent to neither **extent of occurrence (EOO)** nor to **area of occupancy (AOO)**. Rather, the area of the minimum convex polygon around a species' AOH can be used to estimate the upper bound of EOO. Moreover, if a species' AOH is measured at (or scaled to) a 2 × 2 km reference scale it can be used to estimate the upper bound of AOO. We conclude by highlighting the relevance of measurement of terrestrial species' area of habitat in guiding conservation, for example through targeting areas for field surveys, assessing proportions of species' habitat within protected areas, monitoring habitat loss and fragmentation, and increasing consistency between Red List assessments.

Assessment of Extinction Risk, and Its Relationship to AOH

Five different criteria are used to assess a species' extinction risk [15]. In practice, for many terrestrial species [16], the key criterion (the B criterion) is the size of its geographical distribution plus evidence

Highlights

The IUCN Red List of Threatened Species assesses the extinction risk of nearly 100 000 species, including documentation of a range map, habitat, and elevation data for each species.

Numerous recent studies have matched these habitat and elevation data with remotely sensed land cover and elevation datasets to map AOH (also known as extent of suitable habitat) within the range of each species.

AOH differs from the two spatial metrics used in the IUCN Red List criteria for extinction risk assessment: EOO (minimum convex polygon around all present native occurrences of a species); and AOO (area actually occupied by a species).

AOH can be of value in locating target areas for species-specific field surveys, assessing the proportion of a species' habitat within protected areas, and monitoring habitat loss and fragmentation.

¹IUCN, 28 rue Mauverney, CH-1196, Gland, Switzerland

²World Agroforestry Center (ICRAF), University of the Philippines Los Baños, Laguna, 4031, Philippines

³Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, TAS 7001, Australia

⁴Nicholas School of the Environment, Duke University, Box 90328, Durham, NC 27708, USA

⁵Department of Ecology and Evolution, Stony Brook University, Stony Brook, NY 11794, USA

⁶RSPB Centre for Conservation Science, Royal Society for the Protection of Birds, Edinburgh EH12 9DH, UK



of at least two of (i) severe fragmentation, (ii) continuing decline, or (iii) extreme fluctuations. Two spatial metrics of distribution are defined for application of this criterion, both of which have definitions that are both theoretical and empirical [15]. EOO is the area contained within the shortest continuous imaginary boundary that can be drawn to encompass all the current **known localities**, as well as **inferred occurrence** and **projected occurrence** of a species (although it excludes **vagrant localities**). AOO is the area occupied by a species (Figure 1). The intent of EOO is to 'measure the degree to which risks from threatening factors are spread spatially across the taxon's geographic distribution' [17], while the primary intent of AOO is 'as a measure of the "insurance effect", whereby taxa that occur within many patches or large patches across a landscape or seascape are "insured" against risks from spatially explicit threats' [17].

For the IUCN Red List, EOO must be measured as the minimum convex polygon that includes all the identified occupied areas [17,18]. AOO must be measured at (or scaled to) a reference scale of 2×2 km [17,19]. The latter is more demanding of data, especially for species with large distributions, and consequently used considerably less frequently. Illustrating this, 68% of mammals, birds, amphibians, chondrichthyans, conifers, and cycads assessed as threatened under the B criterion qualify using EOO, 15% using AOO, and 17% both [1]. Thus, a species qualifies for the lowest threatened category, vulnerable, if its EOO is $<20\,000$ km² and there is evidence of at least two of (i) severe fragmentation (or ≤ 10 locations based on threats); (ii) continuing decline (in one or more of EOO, AOO, area, extent and/or quality of habitat, number of locations or subpopulations or mature individuals); or (iii) extreme fluctuations (in the same parameters except habitat). More severely threatened categories have lower thresholds for EOO, AOO, and the number of locations. The thresholds for AOO are 10% of the corresponding thresholds for EOO, for example, <2000 km² for vulnerable.

Required documentation for the IUCN Red List also includes the application of a standard Habitat Classification Schemeⁱⁱ, recording maximum and minimum elevation, and provision of a **range map**

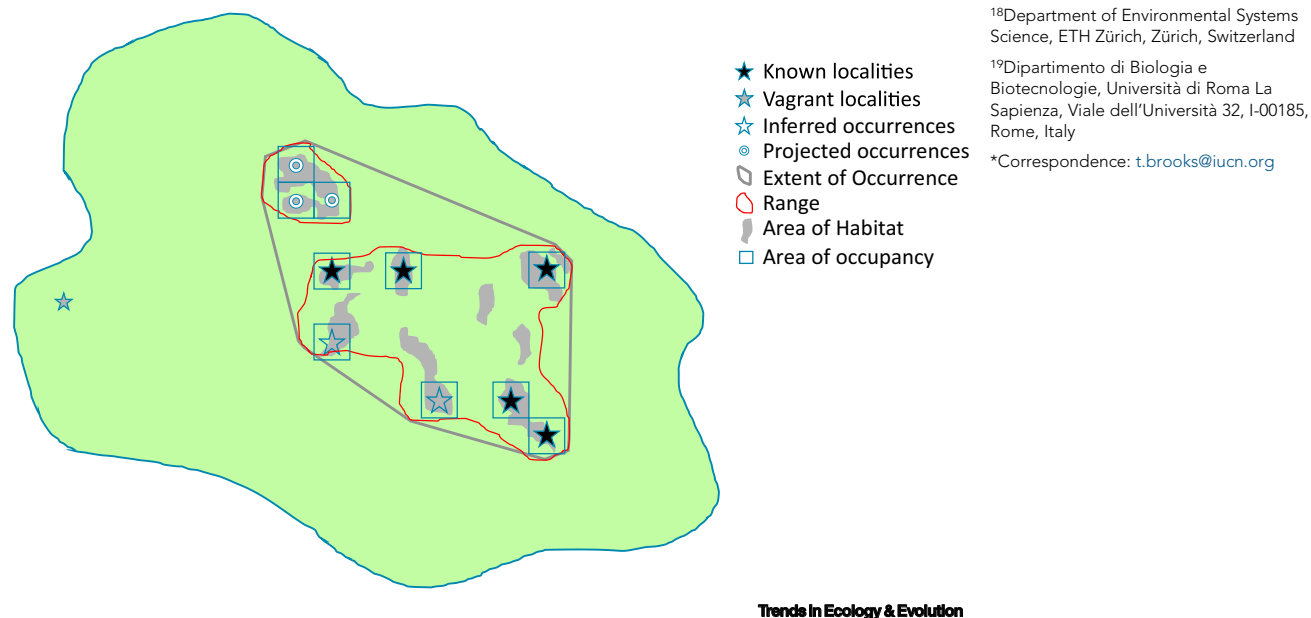


Figure 1. Hypothetical Example of the Relationship between Extent of Occurrence, Mapped Range, Area of Habitat, and Area of Occupancy.

All of these encompass all known localities and inferred and projected occurrences, but not vagrant localities. For a Figure360 author presentation of Figure 1, see the figure legend at <https://doi.org/10.1016/j.tree.2019.06.009>. The green polygon simply represents the region within which the species is found.

⁷BirdLife International, David Attenborough Building, Pembroke Street, Cambridge CB2 3QZ, UK

⁸Department of Zoology, Downing Street, University of Cambridge, Cambridge CB2 3EJ, UK

⁹South African National Parks, Cape Research Centre, Tokai Park, Cape Town, South Africa

¹⁰Global Change Biology Group, Department of Botany and Zoology, Stellenbosch University, Matieland, South Africa

¹¹Climate Change Specialist Group, Species Survival Commission, International Union for Conservation of Nature, Gland, Switzerland

¹²IUCN, David Attenborough Building, Pembroke Street, Cambridge CB2 3QZ, UK

¹³Conservation and Policy, Zoological Society of London, Regent's Park, London NW1 4RY, UK

¹⁴IPÊ - Instituto de Pesquisas Ecológicas, Nazaré Paulista, São Paulo 12960-000, Brazil

¹⁵Chief Environmental Scientist, Microsoft, One Microsoft Way, Redmond, WA 98075, USA

¹⁶Environmental Research Centre, Duke Kunshan University, Kunshan, Jiangsu 215316, China

¹⁷Wildlife Trust of India, F-13, Sector-8, Noida 201301, India

¹⁸Department of Environmental Systems Science, ETH Zürich, Zürich, Switzerland

¹⁹Dipartimento di Biologia e Biotecnologie, Università di Roma La Sapienza, Viale dell'Università 32, I-00185, Rome, Italy

*Correspondence: t.brooks@iucn.org

[20]. Mapped range has no theoretical definition, just an empirical one – the range map ‘should aim to provide the current known distribution of the taxon within its native range. The limits of distribution are determined using known occurrences of the taxon, and knowledge of its habitat preferences, remaining suitable habitat, elevation limits, etc’ [20] (Figure 1). Like EOO, the range should include inferred and projected occurrences. Coding of spatial data according to a species’ presence [20] separates current mapped range from areas where the species has been extirpated.

The last 15 years have seen a rapid increase in the availability of regional and global scale spatial data sets that are available in geographic information systems to strengthen the quantification and repeatability of estimates of species ranges. These include detailed global maps of elevation at 30-m resolution [21], global land-cover maps [22], and global forest cover at 30-m resolution [23,24]. By converting species’ habitat requirements, as documented by application of the IUCN Red List Habitat Classification Scheme, to land-cover types, these can be applied along with the range map of any given terrestrial species to derive the area of habitat falling within a species’ altitudinal limits (Box 1). While some work has used the term ESH to describe this measure [13,14,18,25], we establish the term AOH here because using the term ‘suitable’ is a tautology (habitat is, by definition, suitable for the species in question). Moreover, area is more accurate than extent: the latter implies spread, as in extent of occurrence. Conceptually, AOH is defined as the habitat available to a species, that is, habitat within its range. However, in practice, AOH is often based on mapped range, habitat preferences, and altitudinal limits (Box 1), giving the areas likely to be suitable for the species within its mapped range.

Thus, for the azure-breasted pitta (*Pitta steerii*; Vulnerable [26]; Figure 2), a species endemic to lowland rainforests in the Southern Philippines, the EOO is estimated as 251 695 km² and the mapped range as 177 484 km², while the AOH is estimated to be only 31 377 km² (AOO is not known for the species). It is typical of 586 bird species analysed globally, for which the AOH averaged 23% of the mapped range [11]. Beresford *et al.* [27] found a similar percentage of 28% for 157 species of threatened African birds, while Rondinini *et al.* [28] found it to be 55% for 5027 terrestrial mammal species. For Southeast Asian species, Li *et al.* [29] derived percentages of 39% for birds, 36% for mammals, and 13% for amphibians. The analysis of Tracewski *et al.* [14] found AOH was 41.2% of mapped range across 6283 forest bird species, but differed between resident species (43%), and the breeding and nonbreeding range of migrants (26% and 28% respectively). Such percentages of AOH within mapped range vary considerably, presumably due partly to underlying biological differences between taxa, partly due to different sampling biases between taxa, and partly due to the exact methods used (e.g., for defining habitat requirements for each species). Even for some species assessed as “Least Concern”, the percentages can be <5% of the range [11].

We stress that AOH is equivalent to neither EOO nor to AOO [11,48]. Therefore, as noted in the IUCN Standards and Petitions Subcommittee guidelines [17], AOH cannot be compared directly to the thresholds for EOO or AOO used for determining the extinction risk of a species based on the IUCN Red List criteria. For example, comparing estimates of AOH with the IUCN Red List EOO thresholds would overestimate the number of species potentially qualifying under each Red List category. However, a species’ AOH can estimate upper (i.e., maximum) bounds to its EOO and AOO as follows. The area of the minimum convex polygon (the convex hull) that includes a species’ total AOH (including within inferred or projected sites of occurrence) represents an upper bound to the estimate of EOO. Meanwhile AOH, if measured at (or scaled to) a 2 × 2 km reference scale, is an upper bound on the estimate of AOO. The latter approach was applied by, for example, Tracewski *et al.* [14], who used it to inform extinction risk assessments for forest-dependent mammals, birds, and amphibians worldwide (11 186 species in total).

Importantly, AOH may shift over time due to genuine changes (since habitats themselves are changing in extent and location due to changes in land use by humans and from climate change) as well as improvements in knowledge (such as refinements to land-cover maps and knowledge of species’ habitat preferences). Trends over time in AOH (excluding changes owing to improved knowledge) can therefore be used to inform estimates of the rate of population decline under Red List criterion

Glossary

Area of habitat (AOH): habitat available to a species, that is, habitat within its range. Also known as ESH. This is consistent with the definition of habitat itself as ‘the area, characterized by its abiotic and biotic properties, that is habitable by a particular species’ [17].

Area of occupancy (AOO): ‘area which is occupied by a taxon, excluding cases of vagrancy’ [15], measured as the occupied cells of a grid with the standard scale of 2 × 2 km.

Extent of occurrence (EOO): ‘area contained within the shortest continuous imaginary boundary which can be drawn to encompass all the known, inferred, or projected sites of present occurrence of a taxon, excluding cases of vagrancy’ [15], measured as the minimum convex polygon that includes all such native occurrences.

Inferred occurrence: indirect evidence of occurrence of a taxon, given its ‘habitat characteristics, dispersal capability, rates and effects of habitat destruction and other relevant factors’ [17].

Known localities: localities from which there are ‘confirmed extant records of the taxon’ [17].

Projected occurrence: indirect evidence of occurrence of a taxon extrapolated in space ‘on the basis of habitat maps or models’ [17].

Range: the current ‘limits of distribution of a species, accounting for all known, inferred or projected sites of occurrence’ [25].

Vagrant localities: localities where ‘the species is/was recorded once or sporadically, but it is known not to be native’ [20]

Box 1. Specific Approaches Used to Calculate AOH

Various approaches have been used to calculate AOH. The most widely applied approach [10–14,18,27,29–39] (Figure 1) has been to use geographic information systems to select those areas in a land-cover map that (i) fall within the mapped range of a terrestrial species; (ii) fall within the bounds of the altitudinal limits of the species' distribution; and (iii) that map to the known habitat preferences of the species. Most approaches have restricted the latter to habitats coded as suitable or of major importance by IUCN, although habitats of unknown or marginal importance have also been included for analyses requiring a less conservative approach [28,34].

Rondinini *et al.* [28] and Ficetola *et al.* [40] used a slightly different approach, defining the habitat suitability of all land-cover classes of areas meeting (i) and (ii) above as high, medium, or low suitability depending on the match to habitat type and a separate score for level of tolerance to human impacted natural habitat types (degraded or mosaic). Suitability scores for specific land-cover classes were then modified manually in some cases if more detailed information was available. In addition, for species whose distribution is restricted to within a small distance to water bodies, all areas farther than 1 km from water bodies were classified as unsuitable.

The land-cover products used all derive from remote sensing and include Global Land Cover 2000 [27,34,35] and GlobCover [28,40]. Typically, the land-cover classes of these maps are matched to preferred habitat types (or scored for suitability) usually from information in the literature supplemented by expert opinion. Studies generally publish these crosswalks to enable readers to review decisions. Validation of AOH maps following these approaches is increasingly recognised as important.

We reserve AOH for the approaches described here, and so differentiate it from approaches to modelling species distributions or ecological niches [41,42], sometimes characterised as deductive and inductive approaches, respectively [37]. While these may predict substantially larger areas than the recorded distribution of a species [43], and so may be less useful than AOH for many conservation applications, they can be especially appropriate when projecting future expansion of a species beyond its current range; for example, in considering climate change impacts [17]. Such models allow calculation of the area above a threshold value of probability or suitability. Depending on the number of records, the threshold may be based on the lower tail of the distribution of suitability values of the occurrences, or on balancing sensitivity and specificity [17,44]. New-generation point-process approaches to species distribution modelling also take sampling biases into account [45–47].

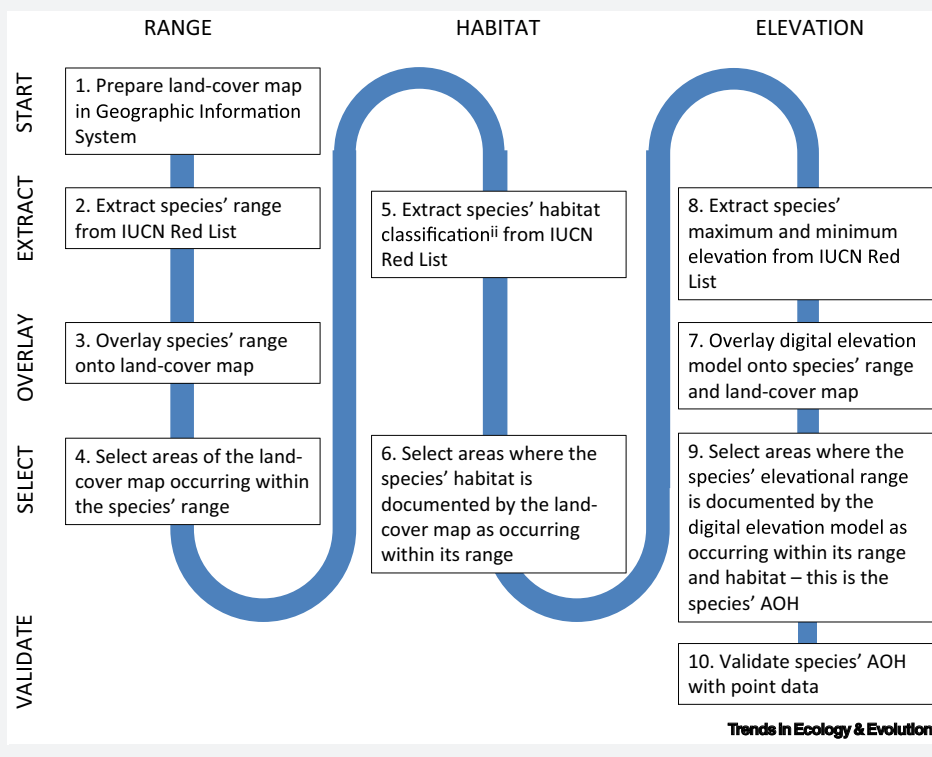


Figure 1. Flowchart Showing Process for Spatial Derivation of AOH.

This uses geographic information systems to select those areas in a land-cover map that (i) fall within the mapped range; (ii) fall within the bounds of the altitudinal limits of the species' distribution; and (iii) that map to the known habitat preferences of the species. See Figure 1 in [10] for a graphical flowchart. Also seeⁱⁱ in the Resources section. Abbreviations: AOH, area of habitat; IUCN, International Union for Conservation of Nature.

A [13,14,49], while modelled future trends can inform projections of the Red List Index [5,50] into the future [39]. If such analyses are based on data from satellite remote sensing, these should be dedicated assessments of land-cover change, rather than the comparison of land-cover maps from multiple time periods. Projecting how such habitat changes will affect species under future scenarios of change, for example, using dynamic global vegetation model predictions, presents a further important application of AOH (see Outstanding Questions).

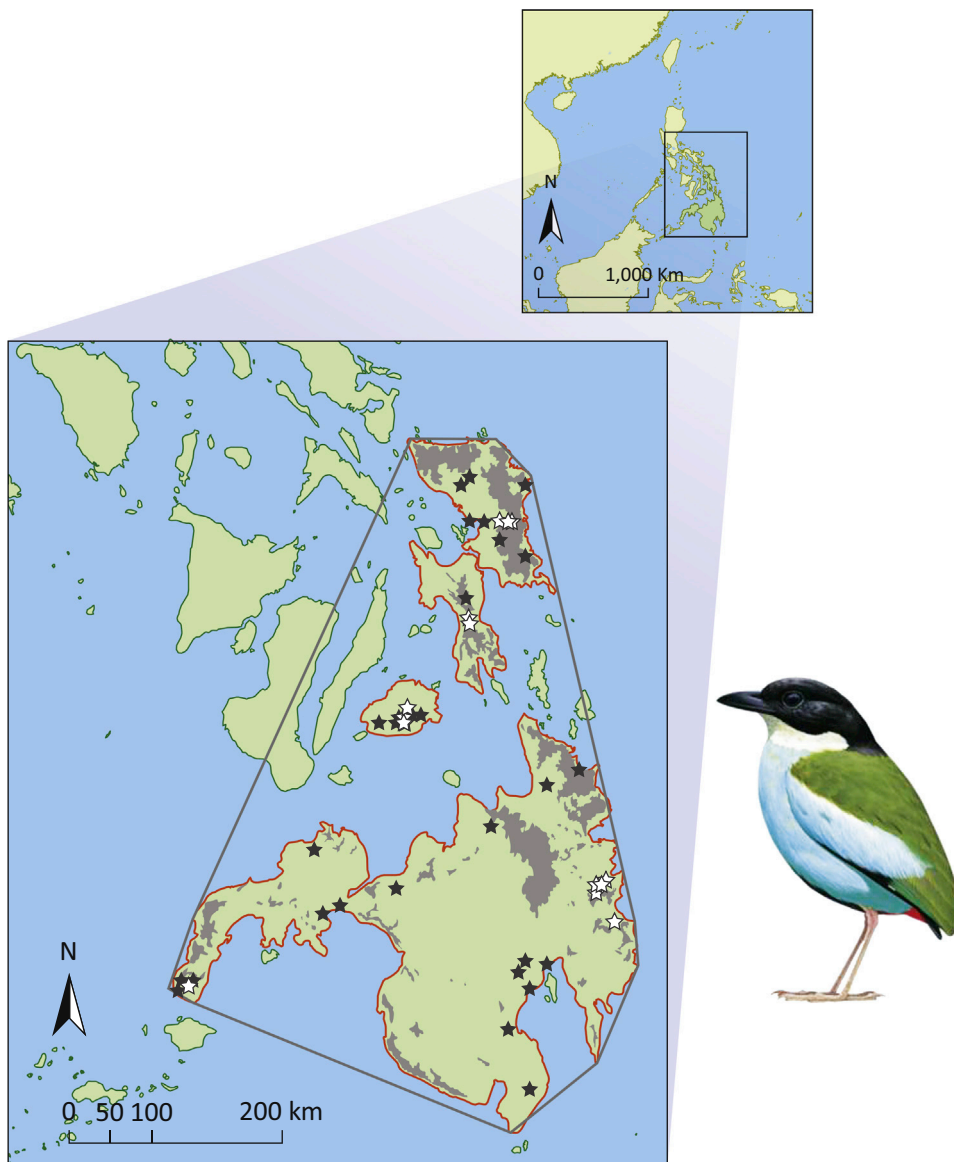
Finally, AOH can provide important insights into how fragmented a terrestrial species' habitat may be [51]. Initial work has shown that species differ considerably in the extent of their habitat fragmentation – and that it can be extreme in some cases [38,52]. However, this does not necessarily correspond to severely fragmented as defined in the IUCN Red List criteria, because the latter has a specific definition that refers to fragmentation of population, not habitat [17] (see Outstanding Questions).

Errors in and Limitations of Measurement of AOH

There are a number of potential sources of error in AOH maps (see Outstanding Questions), including the accuracy of: (i) the range maps (which may extend beyond the true range of the species, or omit areas within which the species is currently distributed); (ii) the altitudinal limits (which may under- or overestimate the altitudinal range occupied by the species at particular locations, especially for species with ranges that span large latitudinal gradients); (iii) the habitats and their importance coded for the species (which may include unoccupied habitats or omit occupied habitats, and may under- or overestimate their importance); (iv) the land-cover classification map (which may misclassify a proportion of pixels and/or have gaps in coverage owing to cloud cover); (v) the crosswalk between land-cover classes and habitat types; (vi) the lack of geographic information system layers for critical habitat variables, for example, availability of temporary water for amphibian reproduction; and (vii) the mismatch of resolution between the geographic information system layers and the species' perception of the environment (e.g., a species may use a habitat fragment that is not mapped because it is much smaller than the map resolution, or, conversely, a species may not use a pixel of habitat if it is surrounded by unsuitable areas).

Beresford *et al.* [30] attempted to quantify the scale of such errors by comparing the total commission and omission errors for AOH versus range maps, using data on known occurrences of species in important bird and biodiversity areas. They found that AOH was more accurate for 37% of species, and less accurate for 16% due to an increase in omission errors, although these averaged just 1.8 sites per species. Ficetola *et al.* [40] assessed the accuracy of AOH maps for 115 amphibian species using a subset of high-quality data from the Global Biodiversity Information Facility. They found that 94% of occurrence points fell within 1 km of a cell classified as having high or medium suitability habitat. Rondinini *et al.* [28] found that for 263 terrestrial mammal species with point data, 77% of point occurrences fell within the AOH, and for 92% of species, the AOH predicted point occurrences better than the mapped range. Such validation tests are important to verify the accuracy of all AOH estimates [53] (see Outstanding Questions).

Calculation of AOH for a given species does not provide information on why a given area is or is not occupied by that species. Such absence could result from ecological factors (e.g., competition) or anthropogenic causes (e.g., extirpation due to unsustainable harvest). Indeed, the reasons why a species does not occupy a given area may be the same within the AOH as in otherwise apparently similar habitat outside the range.



Trends In Ecology & Evolution

Figure 2. Spatial Measures of Different Aspects of the Distribution of the Azure-Breasted Pitta (*Pitta steerii*) in the Philippines [26].

(i) Known localities, encompassing both a cleaned dataset (black stars; [60]) and raw occurrence data from the Global Biodiversity Information Facility (white stars^{vi}). (ii) Range map (red line); 177 484 km². (iii) EOO (grey line); 251 695 km². (iv) AOH (grey shading); 31 377 km². Note that a minimum convex polygon drawn around the AOH (which includes projected occurrences, e.g., in the little-surveyed far northern portion of the species' range) or mapped range would yield a marginally larger value for EOO (approximating a maximum estimate for EOO) than would be generated by a minimum convex polygon around known localities and projected occurrences (approximating a minimum estimate for EOO). The species' altitudinal range is 0–750 m; its habitat is subtropical/tropical moist lowland forest. AOH is calculated using 30 arc second Shuttle Radar Topography Mission data [61] and the European Space Agency Climate Change Initiative Land Cover map for 2015^{viii}. Illustration by Chris Rose from Handbook of the Birds of the World Alive, Lynx Edicions^{ix}. Abbreviations: AOH, area of habitat; EOO, extent of occurrence.

Much work also remains to assess the applicability of AOH to species beyond terrestrial vertebrates. Species with small ranges, such as many plant and invertebrate species, may respond to particular habitat variables at finer scales than those recorded in the IUCN Red List Habitat Classification Scheme or documented in remotely sensed land-cover products. Moreover, the potential of remotely sensed data for freshwater and marine environments to discern species-relevant habitat remains untested (see Outstanding Questions).

The IUCN Red List criteria use projected changes in potential habitat to infer future population reductions due to climate change. Such projections are impossible with AOH based in part on elevation, because of the expected changes in the elevational ranges of species with climate change. However, modelled habitat based on climatic variables; for example, if estimated using ecological niche models or species distribution models [17] would allow consideration of climate change impacts. Similarly, potential habitat may change because of changes in land use by humans or changes in land cover as a result of climate change and elevated atmospheric CO₂. Such changes could be incorporated into AOH estimates using dynamic global vegetation models [54]. Given these caveats, AOH estimates are not automatically integrated into Red List assessments, but rather are reviewed by independent experts on a case-by-case basis before they are accepted for use in informing IUCN Red List assessments [14,26]. Validation of each species' AOH map using independent point locality data should become standard. This is increasingly feasible with the growing availability of geo-referenced citizen science data, such as eBirdⁱⁱⁱ and iNaturalist^{iv} [53], although one must recognise that sometimes large fractions of these data lack sufficient geographical precision [43].

Importance of Consistent Measurement of AOH for Policy and Practice

Since the adoption of the IUCN Red List Categories and Criteria in 2001, satellite remote sensing has revolutionised the availability of data on environmental characteristics (e.g., land cover and topography), and these data are now integral in biodiversity conservation [55]. It makes sense to utilise these new data to guide conservation in general, and to inform the application of the IUCN Red List Categories and Criteria specifically, especially where these data are widely accepted, readily available, and of known provenance. There are multiple ways to use these data but if outputs are to be globally comparable (e.g., among species, across space, or over time) there need to be some standards and guidance. Consolidation of the AOH measure is a step towards the production of such guidance.

Measuring AOH provides rich information about where terrestrial species likely live, that is both geographically and taxonomically comparable. AOH assessments can be of great value for guiding conservation actions; examples include locating target areas for species-specific field surveys to inform the identification of key biodiversity areas [25] and assessing the proportion of habitat for any given species that falls within protected areas [56]. While AOH maps do not establish conservation priorities per se, they can serve as valuable inputs into prioritisation, as with the IUCN Red List itself [57,58]. By using such AOH maps, Ocampo-Peñuela and Pimm [10] revised priorities for bird conservation in the Colombian Andes, enabling them to advise SavingSpecies^v on their land purchases. The same process underpins guidance offered to Chinese authorities on the efficacy of using the giant panda (*Ailuropoda melanoleuca*) to protect a wider variety of species [36]. Range maps of remaining habitat for species are a potential input to the upcoming update of databases of priority conservation areas in Brazil^{vi}. Derivation of AOH should also improve the utility of species distribution maps in informing business decision making [59]. However, publicly accessible versions of such maps do not yet exist for most species and need to be generated case by case. If such maps were available for species assessed for the IUCN Red List, such applications could advance more rapidly and with wider transparency. When these AOH maps are produced periodically with updated habitat maps, conservation practitioners can track species distribution changes and identify critical areas of habitat loss and fragmentation where urgent conservation action is needed.

In short, mapping AOH is a useful contribution to understanding the distribution of species, monitoring habitat loss, and hence guiding conservation actions for them. Currently, the IUCN Red List

includes a range map as required documentation. This requirement should remain unchanged, and IUCN Red List assessors should continue to strive to map species' ranges as accurately as possible. Over time, we anticipate that this mapped range may move closer, and increasingly equate, to AOH, as our methods and abilities to map with ever increasing accuracy continue to improve. Importantly, for species with known elevational ranges and terrestrial habitats, AOH estimates are already readily obtained and validated with the application of standard GIS tools to freely available, global data. Further work is necessary to develop methods for measurement of AOH in freshwater and marine environments. We recommend that validated AOH maps and changes in these should be part of the materials provided online in a species' IUCN Red List assessment wherever practical.

Acknowledgements

We are very grateful to Amy Chernasky, Josep del Hoyo, and Adrian Long for their help sourcing the illustration used in Figure 2, Ackbar Joolia and Janet Scott for data extraction from the IUCN Red List, and Charlotte Boyd, Paul Donald, Jon Hutton, Roland Kays, Daisy Larios, Eugenie Regan, Malin Rivers, Jon Paul Rodríguez, and five anonymous reviewers for comments on the manuscript.

Supplemental Information

Supplemental information associated with this article can be found online at <https://doi.org/10.1016/j.tree.2019.06.009>

Resources

ⁱ<https://www.iucnredlist.org/resources/summary-statistics>

ⁱⁱ<http://www.iucnredlist.org/technical-documents/classification-schemes/habitats-classification-scheme-ver3>

ⁱⁱⁱ<http://www.ebird.org>

^{iv}<http://www.gbif.org>

^v<http://www.savingspecies.com>

^{vi}<http://areasprioritarias.mma.gov.br/>

^{vii}<https://www.gbif.org/species/2489456>

^{viii}<http://maps.elie.ucl.ac.be/CCI/viewer/index.html>

^{ix}<https://www.hbw.com/>

References

1. International Union for Conservation of Nature. (2018) *The IUCN Red List of Threatened Species (Version 2018-1)*, <https://www.iucnredlist.org>
2. Stuart, S.N. et al. (2010) The barometer of life. *Science* 328, 177
3. Scheffers, B.R. et al. (2012) What we know and don't know about Earth's missing biodiversity. *Trends Ecol. Evol.* 27, 501–510
4. International Union for Conservation of Nature. (2016) *Rules of Procedure for IUCN Red List Assessments 2017–2020 (Version 3.0)*, https://nc.iucnredlist.org/redlist/content/attachment_files/Rules_of_Procedure_for_IUCN_Red_List_Assessments_2017-2020.pdf
5. Butchart, S.H.M. et al. (2004) Measuring global trends in the status of biodiversity: Red List indices for birds. *PLoS Biol.* 2, e383
6. Rodrigues, A.S.L. et al. (2014) Spatially explicit trends in the global conservation status of vertebrates. *PLoS One* 9, e113934
7. Secretariat of the Convention on Biological Diversity. (2014) *Global Biodiversity Outlook 4. Convention on Biological Diversity*
8. United Nations. (2017) *The Sustainable Development Goals Report 2017*, United Nations
9. Hoffmann, M. et al. (2010) The impact of conservation on the status of the world's vertebrates. *Science* 330, 1503–1509

Outstanding Questions

How are species' AOHs likely to change under ongoing global change, and how might these changes impact extinction risk? This question could be explored using dynamic global vegetation model predictions, and potentially expanded to incorporate projections of land-use change derived from integrated assessment models.

How can AOH be most effectively applied in freshwater and marine environments? This will require development of a global map of aquatic habitats, classifying areas into categories that can be cross-walked to the IUCN habitat classification schemeⁱⁱ for freshwater and marine environments. Bathymetry data would be used in a similar way to the way in which elevation data are used for terrestrial species.

Can the measurement of AOH strengthen the measurement of species' habitat fragmentation, and how does this relate to application of the subcriterion for severe fragmentation in the IUCN Red List criteria?

Which of the various sources of error are the most severe in the measurement of AOH, do these vary systematically (e.g., with habitat association), and how can these best be reduced?

How can AOH be best deployed to target specific-specific surveys to fill data gaps among known localities for a given species, and validate uncertain records in species occurrence databases such as the Global Biodiversity Information Facility?

10. Ocampo-Peñuela, N. and Pimm, S.L. (2014) Setting practical conservation priorities for birds in the Western Andes of Colombia. *Conserv. Biol.* 28, 1260–1270
11. Ocampo-Peñuela, N. et al. (2016) Incorporating explicit geospatial data shows more species at risk of extinction than the current Red List. *Sci. Adv.* 2, e1601367
12. Ramesh, V. et al. (2017) IUCN greatly underestimates threat levels of endemic birds in the Western Ghats. *Biol. Conserv.* 210, 205–221
13. Buchanan, G.M. et al. (2008) Using remote sensing to inform conservation status assessment: estimates of recent deforestation rates on New Britain and the impacts upon endemic birds. *Biol. Conserv.* 141, 56–66
14. Tracewski, Ł. et al. (2016) Toward quantification of the impact of 21st-century deforestation on the extinction risk of terrestrial vertebrates. *Conserv. Biol.* 30, 1070–1079
15. International Union for Conservation of Nature. (2012) *IUCN Red List Categories and Criteria (Version 3.1)*, <https://portals.iucn.org/library/node/10315>
16. Collen, B. et al. (2016) Clarifying misconceptions of extinction risk assessment with the IUCN Red List. *Biol. Lett.* 12, 20150843
17. International Union for Conservation of Nature Standards and Petitions Subcommittee. (2017) *Guidelines for Using the IUCN Red List Categories and Criteria (Version 13)*, https://nc.iucnredlist.org/redlist/content/attachment_files/RedListGuidelines.pdf
18. Joppa, L.N. et al. (2016) Impact of alternative metrics on estimates of extent of occurrence for extinction risk assessment. *Conserv. Biol.* 30, 362–370
19. Keith, D.A. et al. (2018) Scaling range sizes to threats for robust predictions of risks to biodiversity. *Conserv. Biol.* 32, 322–332
20. International Union for Conservation of Nature. (2013) *Documentation Standards and Consistency Checks for IUCN Red List Assessments and Species Accounts (Version 2)*, https://nc.iucnredlist.org/redlist/content/attachment_files/RL_Standards_Consistency.pdf
21. Jarvis, A. et al. (2008) *Hole-filled SRTM for the Globe Version 4*, <http://srtm.csi.cgiar.org>
22. Bartholomé, E. and Belward, A. (2005) GLC2000: a new approach to global land cover mapping from Earth observation data. *Int. J. Remote Sens.* 26, 1959–1977
23. Hansen, M.C. et al. (2013) High-resolution global maps of 21st-century forest cover change. *Science* 342, 850–853
24. Sexton, J.O. et al. (2013) Global, 30-m resolution continuous fields of tree cover: Landsat-based rescaling of MODIS vegetation continuous fields with lidar-based estimates of error. *Int. J. Digit. Earth* 6, 427–448
25. International Union for Conservation of Nature. (2016) *A Global Standard for the Identification of Key Biodiversity Areas (Version 1.0)*, International Union for Conservation of Nature
26. BirdLife International. (2018) *IUCN Red List for Birds*, <http://www.birdlife.org>
27. Beresford, A. et al. (2011) Minding the protection gap: estimates of species' range sizes and holes in the protected area network. *Anim. Conserv.* 14, 114–116
28. Rondinini, C. et al. (2011) Global habitat suitability models of terrestrial mammals. *Phil. Trans. R. Soc. Lond B* 366, 2633–2641
29. Li, B.V. et al. (2016) Remotely sensed data informs Red List evaluations and conservation priorities in Southeast Asia. *PLoS One* 11, e0160566
30. Beresford, A. et al. (2011) Poor overlap between the distribution of protected areas and globally threatened birds in Africa. *Anim. Conserv.* 14, 99–107
31. Bird, J. et al. (2011) Incorporating projected deforestation estimates into conservation priority-setting in Amazonia. *Divers. Distrib.* 18, 273–281
32. Buchanan, G.M. et al. (2011) Identifying priority areas for conservation: a global assessment for forest-dependent birds. *PLoS One* 6, e29080
33. Butchart, S.H.M. et al. (2015) Shortfalls and solutions for meeting national and global conservation area targets. *Conserv. Lett.* 8, 329–337
34. Foden, W.B. et al. (2013) Identifying the world's most climate change vulnerable species: a systematic trait-based assessment of all birds, amphibians and corals. *PLoS One* 8, e65427
35. Harris, G. and Pimm, S.L. (2008) Range size and extinction risk in forest birds. *Conserv. Biol.* 22, 163–171
36. Li, B.V. and Pimm, S.L. (2016) China's endemic vertebrates sheltering under the protective umbrella of the giant panda. *Conserv. Biol.* 30, 329–339
37. Rondinini, C. et al. (2005) Habitat suitability models and the shortfall in conservation planning for African vertebrates. *Conserv. Biol.* 19, 1488–1497
38. Schnell, J.K. et al. (2013) Quantitative analysis of forest fragmentation in the Atlantic Forest reveals more threatened bird species than the current Red List. *PLoS One* 8, e65357
39. Visconti, P. et al. (2016) Projecting global biodiversity indicators under future development scenarios. *Conserv. Lett.* 9, 5–13
40. Ficetola, G.F. et al. (2015) Habitat availability for amphibians and extinction threat: a global analysis. *Divers. Distrib.* 21, 302–311
41. Franklin, J. (2010) *Mapping Species Distributions: Spatial Inference and Prediction*, Cambridge University Press
42. Peterson, A.T. et al. (2011) *Ecological Niches and Geographic Distributions*, Princeton University Press
43. Pimm, S.L. et al. (2017) Unfulfilled promise of data-driven approaches: response to Peterson et al. *Conserv. Biol.* 31, 944–947
44. Guillera-Aroita, G. et al. (2015) Is my species distribution model fit for purpose? Matching data and models to applications. *Glob. Ecol. Biogeogr.* 24, 276–292
45. Renner, I.W. et al. (2015) Point process models for presence-only analysis. *Methods Ecol. Evol.* 6, 366–379
46. Evans, M.E.K. et al. (2016) Towards process-based range modeling of many species. *Trends Ecol. Evol.* 31, 860–871
47. Schank, C.J. et al. (2017) Using a novel model approach to assess the distribution and conservation status of the endangered Baird's tapir. *Divers. Distrib.* 23, 1459–1471
48. Rondinini, C. et al. (2006) Tradeoffs in different types of species occurrence data for use in systematic conservation planning. *Ecol. Lett.* 9, 1136–1145
49. He, F. (2012) Area-based assessment of extinction risk. *Ecology* 93, 974–980
50. Butchart, S.H.M. et al. (2007) Improvements to the Red List Index. *PLoS One* 2, e140
51. Pfeifer, M. et al. (2017) Creation of forest edges has a global impact on forest vertebrates. *Nature* 551, 187–191
52. Crooks, K.R. et al. (2017) Quantification of habitat fragmentation reveals extinction risk in terrestrial mammals. *Proc. Nat. Acad. Sci. U. S. A.* 114, 7635–7640
53. Peterson, A.T. et al. (2017) Assumption-versus data-based approaches to summarizing species' ranges. *Conserv. Biol.* 32, 568–575

54. Prentice, I.C. et al. (2007) Dynamic global vegetation modeling: quantifying terrestrial ecosystem responses to large-scale environmental change. In *Terrestrial Ecosystems in a Changing World* (Canadell, J.G. et al. eds), pp. 175–192, Springer
55. Leidner, A.K. and Buchanan, G.M. (2018) *Satellite Remote Sensing for Conservation Action: Case Studies from Aquatic and Terrestrial Ecosystems*, Cambridge University Press
56. United Nations Environment Programme-World Conservation Monitoring Centre and International Union for Conservation of Nature. (2017) *Protected Planet*, <http://www.protectedplanet.org>
57. Miller, R.M. et al. (2006) Extinction risk and conservation priorities. *Science* 313, 441
58. Rodrigues, A.S.L. et al. (2006) The value of the IUCN Red List for conservation. *Trends Ecol. Evol.* 21, 71–76
59. Bennun, L. et al. (2018) The value of the IUCN Red List for business decision-making. *Conserv. Lett.* 11, e12353
60. BirdLife International. (2001) *Threatened Birds of Asia: The BirdLife International Red Data Book*, BirdLife International
61. United States Geological Survey. (2017) *Shuttle Radar Topography Mission*, <https://lta.cr.usgs.gov>