

An integrative indicator linking area-based actions to national and global outcomes for forest biodiversity

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Indicators supporting implementation of the post-2020 Global Biodiversity Framework (GBF)¹ are likely to be used not only to monitor progress toward achieving agreed goals and targets, but also to help prioritise specific actions to address shortfalls in this achievement as efficiently as possible². To perform this dual role, adopted indicators must be derived from data of sufficient rigour and spatial resolution to inform decision-making at national and subnational scales. They also need to account for relevant interdependencies between, and within, individual goals and targets³. Here we focus on a particularly prominent set of such dependencies – the impact that area-based actions under draft GBF Targets 1, 2 and 3 will have on outcomes for ecosystem area and

integrity (including connectivity) under Goal A, and for the flow-on effect that these changes will, in combination, have on the persistence of species diversity. We show how these various linkages can now be addressed across all forests globally, by coupling state-of-the-art mapping of ecosystem integrity with the integrative analytical capability of an advanced habitat-based biodiversity indicator. Results generated for the world's forest-supporting countries demonstrate that rigorous consideration of the above interdependencies can profoundly alter understanding of the present state of forest biodiversity, and of the spatial distribution of priorities for area-based action, relative to that based on an indicator of ecosystem extent alone.

With a new post-2020 Global Biodiversity Framework (GBF)¹ expected to be adopted at the 15th Conference of the Parties to the Convention on Biological Diversity (CBD) in 2022, attention is shifting from debating goals and targets to the challenge of implementing actions to achieve real change against these aspirations⁴. While there appears to be broad acceptance of the role indicators will play in monitoring progress toward the achievement of agreed targets, surprisingly little focus is being placed on the other major contribution they can, and should, make to informing the prioritisation of specific actions (e.g. spatial planning), particularly actions taken by individual countries^{5,6}. For the world to avoid a further worsening of the biodiversity crisis, it is vital that actions implemented by nations over the remainder of this decade address shortfalls in goal and target achievement as efficiently and effectively as possible⁷.

If indicators are to perform this dual role well, two key challenges need to be overcome in their design and use. The more widely recognised of these challenges is that such indicators must be able to be derived with sufficient accuracy at the spatial resolution at which actions

will be planned and implemented by member countries of the CBD^{2,4}. In the terrestrial realm this will be particularly important for actions to protect, restore, or otherwise zone or manage specific areas of land under draft GBF Targets 1, 2, and 3. The second challenge arises from the existence of strong interdependencies between the various outcome-oriented goals and action-oriented targets of the GBF and, in some cases, between multiple components defined within any one of these elements^{3,8}. Particularly significant linkages exist within and between draft Goal A and Targets 1, 2 and 3. Any area-based action implemented under these targets will have an impact on the overall area and integrity of ecosystems under Goal A. Changes in these ecosystem attributes will, in turn, have flow-on consequences for the persistence of species and genetic diversity, the other major components of this same goal.

These interdependencies will not be addressed adequately by indicators focused narrowly on measuring progress for each of these components individually, in isolation from the rest of the interlinked system⁸. For example, an indicator of change in the extent (total area) of broad ecosystem types (e.g. forests) will convey little about expected impacts on the persistence of species dependent on these systems, without simultaneously considering how persistence will also be affected by the integrity of the areas of habitat making up this overall extent, and by the spatial distribution of these areas relative to how individual species are distributed within the ecosystem.

These same interdependencies pose a significant challenge for any use of indicators assessing progress against Targets 1, 2 and 3 purely in terms of the proportional coverage of area-based actions – e.g. the areal percentage of degraded ecosystems subjected to restoration under Target 2; or the percentage of land and sea areas protected through area-based conservation measures, under Target 3. Any individual area-based action will make at least some contribution to retaining or enhancing the overall area, connectivity and integrity of natural ecosystems, with some level of benefit flowing through, in turn, to improving prospects for

retaining species and genetic diversity in accordance with Goal A. The problem is that the magnitude of these benefits is not a simple function of the magnitude of the action itself – e.g. the action’s contribution to incrementing the proportion of an ecosystem type protected or restored. This will also depend on the precise location of the action relative to underlying spatial patterns in the distribution of biodiversity⁹⁻¹¹, and on spatial relationships between the area being protected or restored and other areas of natural ecosystems in the surrounding landscape¹². The net contribution made by actions of a given type will further depend on how their effects complement, or offset, those of other types of actions and ongoing threatening processes^{13,14}. Failing to account for these interdependencies when prioritising actions to achieve individual targets will reduce the efficiency with which countries, and the world as a whole, can work towards achieving multiple targets and goals under the GBF.

An integrative forest indicator

Major forest-focused initiatives and agreements including the Bonn Challenge and New York Declaration on Forests¹⁵, and the recent Glasgow Leaders’ Declaration on Forests and Land Use¹⁶, have added particular urgency to overcoming the above challenges in forest ecosystems globally. Here we describe a new indicator covering all of the world’s forests which can address key interdependencies between multiple components of draft GBF Goal A and associated area-based action targets. This indicator is derived from data of sufficient spatial resolution and accuracy to support both subnational prioritisation of area-based actions, and national and global monitoring of progress toward achievement of targets and goals, during GBF implementation.

Our approach builds on high-resolution mapping of the Forest Landscape Integrity Index (FLII), a globally consistent measure of the state of forest ecosystems estimated from best-available spatial data and analysis¹⁷. The FLII already integrates all three dimensions

(ecosystem area, connectivity and integrity) of the ecosystem-focused component of draft GBF Goal A at 300m grid-resolution globally by combining data on forest extent, and a wide range of human pressures, observed or inferred from remote sensing and spatial mapping¹⁷. The methodological framework underpinning the FLII is also now being tailored to allow derivation of the index from finer-resolution national and subnational data, where available, thereby strengthening the degree of ownership amongst policymakers and stakeholders at these scales¹⁷.

To address the expected interdependency between outcomes for the ecosystem-focused and species-focused components of Goal A we couple the FLII with the analytical approach underpinning an existing habitat-based biodiversity indicator – the Biodiversity Habitat Index (BHI)¹⁸⁻²². Habitat-based indicators predict the level of species diversity expected to be retained, or to persist, within a given spatial reporting unit as a function of the state and configuration of natural ecosystems, or ‘habitat’, across that unit^{23,24}. Such indicators can be derived either through bottom-up aggregation of separate analyses of the availability of suitable habitat for individual species or, as in the case of the BHI, through top-down assessment of the expected impact of overall habitat losses and gains on the persistence of species diversity at a whole-community level²⁵. A clear strength of the species-by-species approach is that it can assess outcomes explicitly in terms of recognised species. This approach is, however, restricted largely to biological groups for which adequate information on distributions, and habitat affinities, of individual species is readily available. Past research suggests that basing conservation decisions solely on distributional data for species within better-studied biological groups – e.g. vertebrates – may not account effectively for less-studied yet often highly-diverse groups, particularly those groups including many narrow-range species^{26,27}.

Community-level indicators offer a tractable means of assessing actions and outcomes under the GBF for a larger proportion of the planet's species-level diversity than is currently possible using a species-by-species approach. They are intended to complement, rather than compete with, indicators working more directly with species-level information. As for most manifestations of the community-level approach, the BHI uses the species-area relationship – widely regarded as ecology's most "basic law"²⁸ – to predict the proportion of native species within a given region, or ecosystem type, expected to persist as a function of the proportion of natural habitat remaining within that region. While early applications of the species-area approach treated habitat as being either present or absent at any given location²⁹, the BHI allows more subtle variation in habitat condition across a region to be accounted for in estimating the 'effective' proportion of habitat remaining. The BHI has been implemented previously across the entire terrestrial surface of the planet, including both forest and non-forest biomes, using habitat-condition surfaces inferred from downscaled land-use mapping¹⁸⁻²². The indicator derived in our study is therefore effectively a refinement of the BHI for all forest biomes globally (Methods). This refinement is achieved not only through the enhanced spatial resolution and accuracy of the FLII dataset, but also through the rigour with which the FLII integrates the effects of a wider range of pressures, along with that of habitat connectivity¹⁷.

A key strength of the BHI, relative to other species-area-based approaches, is that it recognises that species' persistence will be determined not only by the overall amount and average condition of habitat in a region, but also by the precise spatial configuration of that habitat^{25,30}. Generalised dissimilarity modelling (GDM)³¹ of spatial variation in the species composition of communities is used to assess the extent to which remaining habitat is well distributed across any natural gradients of variation in community composition (beta diversity) present within the region, or ecosystem type, concerned as opposed to being biased

towards a particular portion of this variation^{32,33}. Here we employ the same GDM models as those used previously for deriving the BHI globally at 30-arcsecond grid-resolution (approximately 900m at the equator)¹⁹. While these beta-diversity models have been developed for a broader range of biological groups, we focus the initial demonstration of our approach on vascular plants, for which the available models were fitted to data for over 254,000 species worldwide¹⁹ (Methods).

Adding value to ecosystem extent-focused assessments

To gain a better understanding of the potential value of this integrative approach we used available mapping of the FLII for 2019¹⁷ to derive the BHI for each of the world's forest-supporting countries (Methods). This generated predictions of the proportion of forest-associated plant species expected to persist, at two policy-relevant spatial scales: 1) for each 30-arcsecond grid-cell in the country of interest, the proportion of species originally associated with that cell which are predicted to persist anywhere in the country (i.e. avoid extinction at national level); and 2) for the country as a single unit, the proportion of species originally associated with that country which are predicted to persist anywhere in the country.

The 'headline indicators' currently proposed for monitoring progress against the ecosystem component of draft GBF Goal A, and against Targets 1, 2, and 3, focus strongly on assessing change in the extent (total area) of broad ecosystem classes, or of broad types of area-based action (e.g. the total coverage of protected areas, or of ecosystem restoration)³⁴. To help explore the potential for divergence between simple extent-focused indicators such as these, and the more integrative approach advocated here, we contrasted our results with predictions of the proportion of forest-associated plant species expected to persist in each country as a simple species-area-based function of the proportion of original forest extent remaining.

Three important findings emerge. First, the proportion of forest-associated plant species predicted to persist in each country is, on average, greatly reduced once the added effects of ecosystem integrity, and of variation in community composition, are considered alongside that of change in ecosystem extent, with this mean proportion dropping from 0.911 to 0.593 (Fig. 1, Extended Data Table 1). When translated into predictions of the proportion of species therefore committed to extinction in each country, the results for our BHI-based indicator suggest an average (per country) extinction level 4.54 times higher than that based on ecosystem extent alone. Second, integrating the effects of ecosystem integrity and compositional variation has a greater impact on predicted levels of persistence in some countries than in others (Fig. 1). These levels are therefore not very strongly correlated with those predicted through application of the species-area relationship to the proportion of original forest extent remaining in each country (Pearson correlation = 0.763; $R^2 = 0.582$). These two findings, in combination, suggest that considerable caution needs to be exercised in employing a headline indicator based solely on ecosystem extent to monitor progress by CBD member nations toward achievement of the ecosystem-focused component of draft GBF Goal A, especially if this indicator is also expected to account for interlinkages with the species-focused component of this same goal.

The third important finding relates more to the role indicators are likely to play in prioritising where best to focus area-based actions to address shortfalls in the achievement of GBF targets and goals. If an extent-focused indicator were to be employed as the sole foundation for assessing progress toward achievement of the ecosystem component of Goal A, or associated action targets, then any given amount of an action (e.g. restoration, or protection of forest) would contribute equally to improving a country's score against this indicator, regardless of where the action was located within that country. The results for our BHI-based indicator suggest, however, that the expected level of persistence of species diversity often varies

dramatically between different parts of the same country (Figs. 1, 2). When the BHI is assessed at the scale of individual grid-cells – i.e. predicting the proportion of species originally associated with a given cell expected to persist anywhere in the country – the level of extinction predicted for the 5th percentile of BHI values within a country is, on average, 2.61 times higher than that for the 95th percentile of BHI values within that country (Fig. 1, Extended Data Table 1). This result confirms that past reduction in the extent and integrity of natural ecosystems is distributed neither uniformly nor randomly within most countries, but is instead biased towards particular environments supporting particular assemblages of a country's species^{33,35-37}. The contribution that a given amount of an area-based action will make to achieving biodiversity outcomes under Goal A will therefore depend greatly on where that action is located within the country concerned (Fig. 2).

Importance for GBF implementation

Derivation of the BHI from high-quality mapping of ecosystem integrity provided by the FLII offers considerable potential to help address interlinkages within and between draft GBF Goal A, and associated area-based action targets. This would involve coupling derivation of the indicator from observed (past to present) changes in ecosystem state with forward projections of the same indicator, as a function of changes in ecosystem state expected to result from the interplay between proposed or implemented actions, and prevailing threats and pressures^{25,38}. This integrative approach could effectively link three major streams of assessment activity during GBF implementation (Fig. 3). In the first of these, the BHI would be generated from observed changes in the FLII estimated from remote-sensing data collected at different time-points (e.g. successive years). This involves repeating for multiple years the same type of analysis for which we have presented results for a single year (2019) in Figs. 1 and 2. Deriving the indicator in this manner would allow progress against the ecosystem component of Goal A to be reported in terms of the collective impact that observed changes

in ecosystem area and integrity are expected to have on the proportion of species persisting over the long term. From the perspective of the ‘leading/coincident/lagging’ indicator typology commonly employed in economics³⁹, the value of the BHI reported by this activity would serve firstly as a *coincident indicator* of change in ecosystem state, because the indicator is derived directly from observations of change in the ecosystem itself. But it would also serve as a *leading indicator* of change in the persistence of species diversity, because this change is not actually observed, but is instead predicted to result from the causal relationship between ecosystem state and biodiversity persistence.

In the second activity, the BHI would be used to assess progress in relation to area-based action targets in terms of the collective contribution that actions already implemented, up to a given point in time, are expected to make to achieving Goal A outcomes. This involves modifying the observed FLII layer to project how this layer is expected to change into the future as a result of implemented actions. The value of the BHI generated from this projection would therefore serve as a *leading indicator* of change in both ecosystem state and persistence of species diversity, because both of these changes may take some time to play out following the implementation of actions. This approach would allow considerable flexibility in assumptions regarding how the FLII will change in response to any given implemented action, and the rigour with which this change is modelled²⁵. For example, if assessing the contribution of ecosystem restoration it might simply be assumed that all areas subjected to restoration will attain a maximum possible FLII value, while all other areas will retain their present value. If assessing the contribution of protected-area expansion it might instead be assumed that all such areas will retain their present FLII value, while the value of all unprotected areas will drop to zero. Alternatively, a more rigorous option for assessing the collective contribution of implemented actions is to model future change in the FLII of areas

not subjected to these actions as a function of best-available information on the spatial distribution of prevailing threats, such as likelihood of land-use change^{20,40}.

This assessment of the collective contribution of implemented actions toward achieving Goal A outcomes would, in turn, provide a logical foundation for prioritising further actions to advance this achievement as efficiently as possible. This involves calculating the marginal improvement in the BHI for a country (or any other region of interest) expected if a given action, or set of actions, is added to those already implemented (Methods). If, for a given type of action (e.g. restoration or protection), this expected marginal gain is derived separately for each grid-cell within the country, then mapping these results offers a simple means of identifying priority areas for action²⁵. While the details of calculation will vary for different types of action, the gain expected from acting in any given cell will be largely a function of two attributes of that cell: 1) the proportion of species originally associated with the cell which are predicted to persist given the present state of forests across the entire country, as measured by the cell's BHI; and 2) the local state of the forest ecosystem within the cell itself, as measured by its FLII (Methods, Fig. 3).

Conclusions

Good potential exists to extend derivation of the indicator we have described here by incorporating comparable GDM models already generated globally for invertebrates and vertebrates, alongside those for vascular plants¹⁹. These same models have already been used to derive the BHI across all terrestrial biomes globally, as a function of habitat-condition surfaces inferred from downscaled land-use mapping¹⁸. Considerable potential therefore also exists for the level of rigour with which the BHI is now derivable for forests to be extended progressively to other non-forest biomes, once mapping of ecosystem integrity underway across these systems reaches a similar standard to that of the forest-focused FLII⁴¹.

Forthcoming implementation of the GBF stands to benefit greatly from broader adoption and application of integrative indicators of the type we have presented here. Combining the rigour of FLII mapping with the capacity of the BHI to address interdependencies between area-based actions and both ecosystem-focused and species-focused outcomes under draft Goal A opens up unprecedented potential to link GBF decision-making and monitoring activities seamlessly from subnational to global scales.

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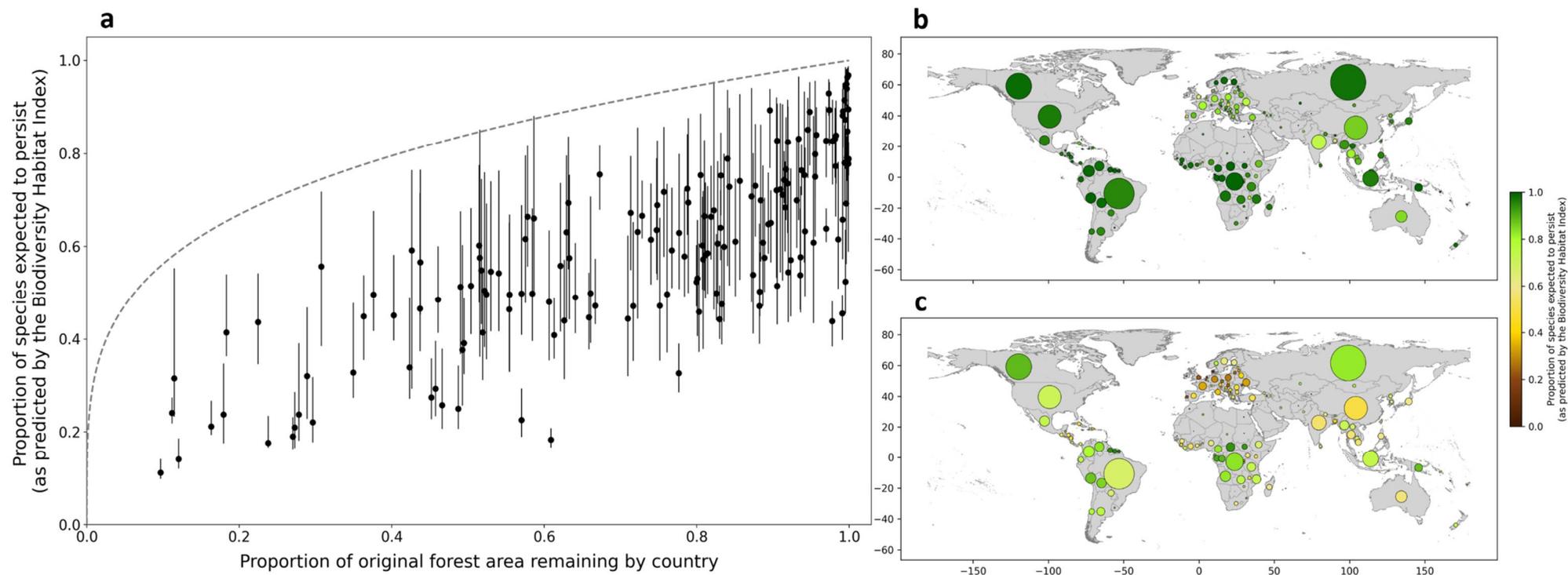


Figure 1. Proportion of plant species expected to persist (i.e. avoid extinction) over the long term, in each of the world’s forest-supporting countries. Results are presented only for countries within which forest originally covered a total area of more than 50km². **a**, The broken-line curve depicts the level of species persistence expected as a simple species-area-based function of the proportion of original forest extent remaining in a country (assuming a species-area exponent of 0.25). Each of the black symbols depicts the proportion of species expected to persist within a given country as estimated by the Biodiversity Habitat Index (BHI) derived from 2019 mapping of the Forest Landscape Integrity Index (FLII). Each of the vertical lines depicts the 5th and 95th percentiles of the distribution of BHI values for all originally forested 30-arcsecond cells within a country (i.e. predictions of the proportion of species originally associated with a given cell which are expected to persist anywhere in the country). **b**, The colour of the circles indicates the proportion of species expected to persist as a simple species-area-based function of the proportion of forest remaining in each country (i.e. values from the broken-line curve in panel a). The size of the circles indicates the relative area originally covered by forest in each country. **c**, As for panel b, except now showing the proportion of species expected to persist as estimated by the BHI derived from mapping of the FLII (i.e. the black symbols in panel a).

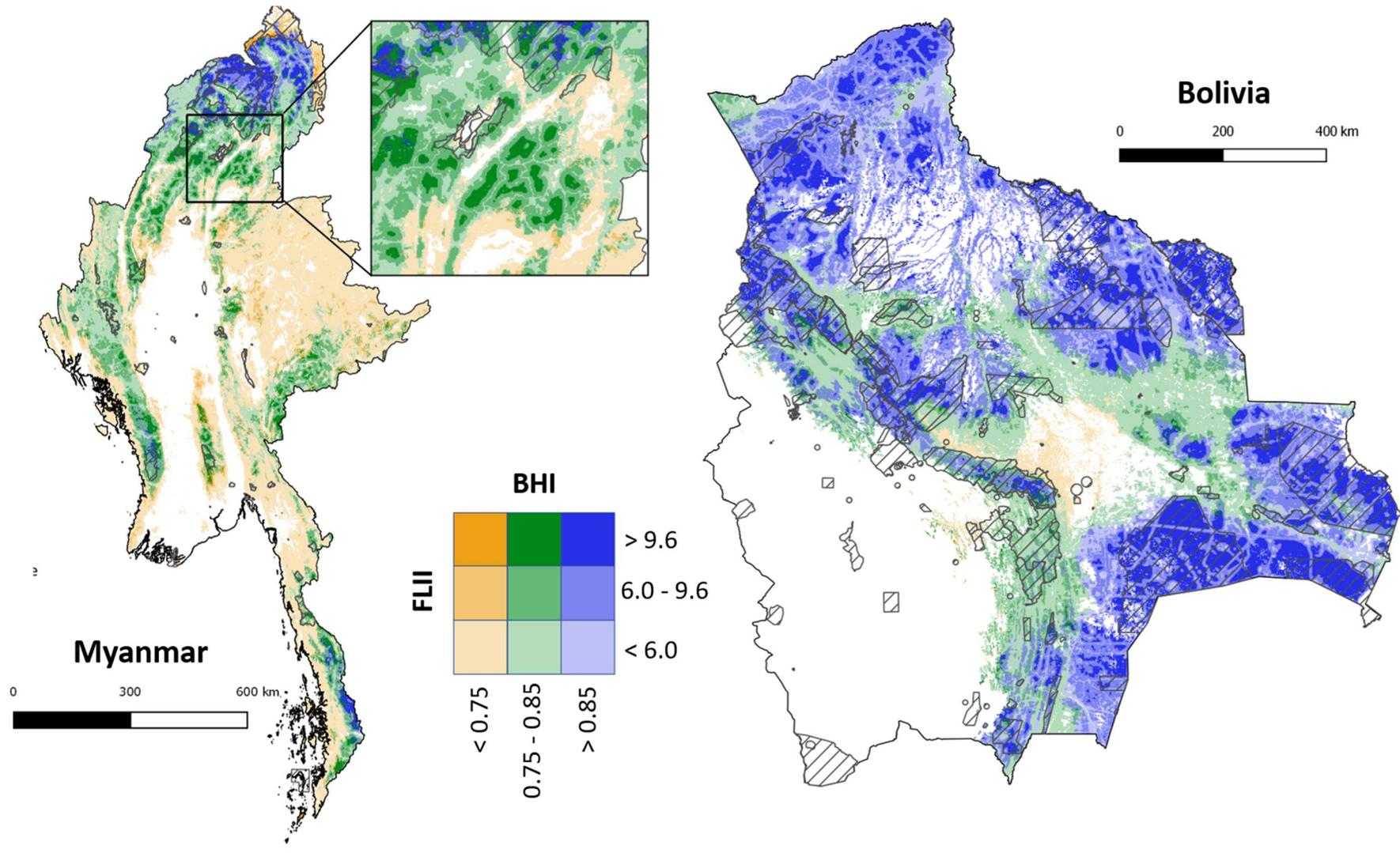


Figure 2. Fine-scale spatial variation in the Biodiversity Habitat Index (BHI) and the Forest Landscape Integrity Index (FLII) within two example countries: a, Myanmar; b, Bolivia. The two variables are mapped for all 30-arcsecond cells containing forest in 2019 (i.e. cells with FLII > 0). Existing protected areas recorded in the World Database on Protected Areas are delineated with black hatching. While both the BHI and the FLII are derived as

continuous variables, each is here divided into three classes to aid interpretation of mapped patterns. The BHI estimates, for each cell, the proportion of species originally associated with that cell which are predicted to persist anywhere in the country of interest, given the present state of forests across that country. It therefore indicates the relative need for action across different types of forest in different parts of the country. The FLII is instead a measure of the local state of forest within the cell itself, and therefore indicates the contribution that different types of action within that cell (e.g. protection or restoration) might make to promoting the persistence of species originally associated with the cell. These two variables, in combination, provide a logical foundation for prioritising actions to advance the achievement of draft GBF Goal A outcomes as effectively and efficiently as possible (Methods).

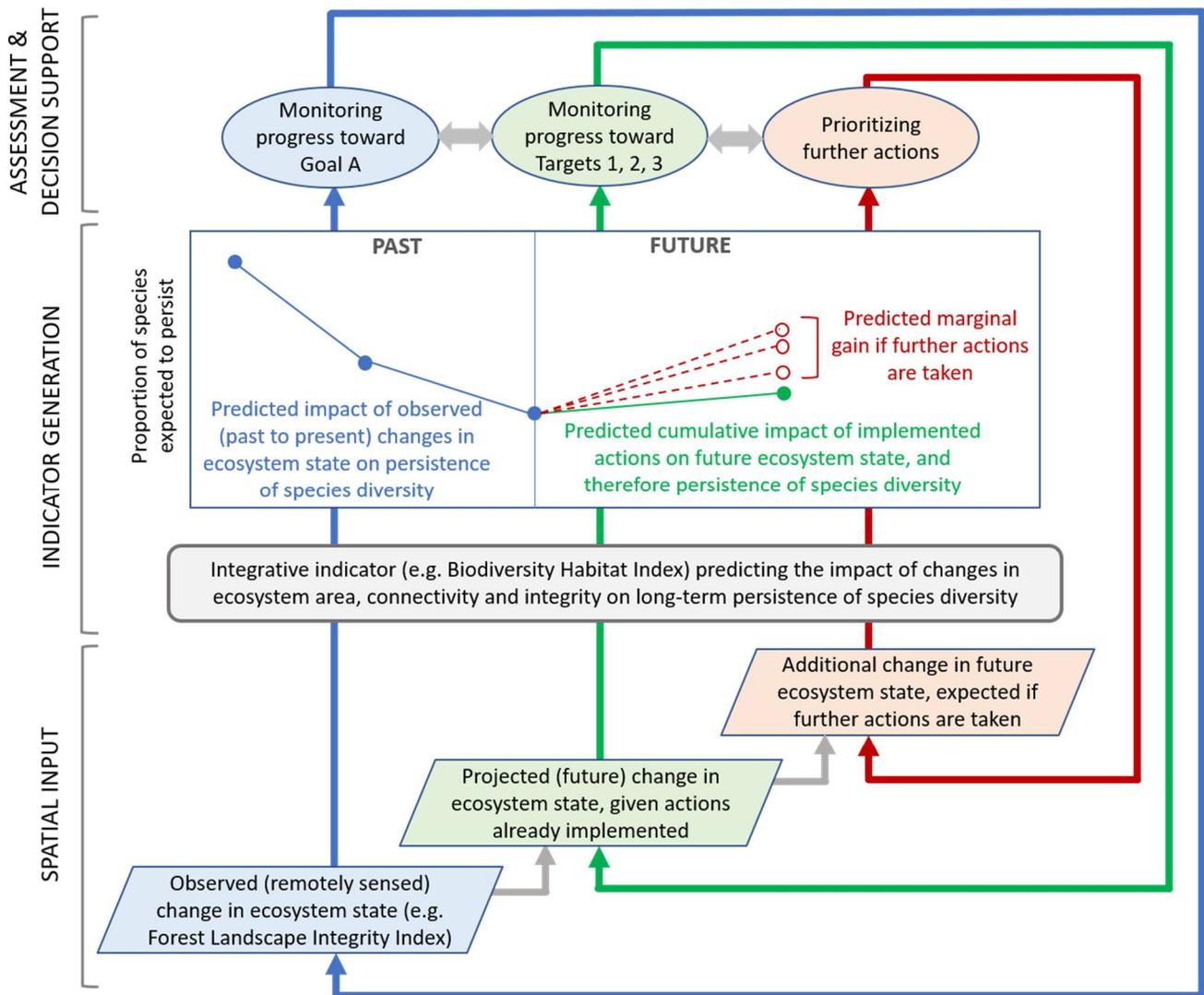


Figure 3. Proposed framework for using the Biodiversity Habitat Index (BHI) to address interlinkages within and between Goal A, and associated area-based action targets, during GBF implementation. This integration would be achieved by deriving the same indicator from three different spatial inputs describing observed or projected changes in ecosystem state across a given country, or any other region, of interest: **Blue pathway** – derivation of the BHI from observed remotely-mapped changes in ecosystem state, in this case using the Forest Landscape Integrity Index, thereby informing monitoring of actual progress made toward achieving Goal A outcomes; **Green pathway** – derivation of the BHI from the projected (future) change in ecosystem state expected as a consequence of actions already implemented, thereby informing monitoring of progress in relation to area-based action targets in terms of the contribution that these combined actions are predicted to make to achieving Goal A outcomes; **Red pathway** – derivation of the additional (marginal)

improvement in the BHI expected if a given action, or set of actions, is added to those already implemented, thereby informing prioritization of further actions to advance the achievement of Goal A outcomes as effectively and efficiently as possible.

Methods

Forest extent and integrity data

We used existing Forest Landscape Integrity Index (FLII) data for 2019, derived at 300m grid-resolution across all forests globally by Grantham et al.¹⁷. The FLII incorporates four spatial datasets: (i) forest extent; (ii) observed human pressures; (iii) inferred human pressures; and (iv) lost forest connectivity. Forest extent in 2019 is derived largely from the remotely-sensed Global Tree Cover and Tree Cover Loss products⁴² using a canopy threshold of 20%¹⁷. Observed human pressures are also derived largely from remote sensing and include impacts of 41 types of infrastructure, agriculture, and deforestation¹⁷, combined through weighted summation using an adaptation of the Human Footprint methodology⁴³. Inferred human pressures are those pressures for which no directly observed datasets are available, and are used to represent edge effects and other diffuse processes such as hunting and forest exploitation. These are modelled collectively as a function of spatial proximity to observed pressures¹⁷. Loss of forest connectivity is quantified using a method adapted from Beyer et al.⁴¹ in which the connectivity of a given grid-cell to forested cells in the surrounding landscape is expressed as a proportion of the connectivity estimated to have existed prior to extensive human modification¹⁷. The FLII score for each forested cell is derived through summation of the three metrics for observed pressure, inferred pressure, and lost forest connectivity, and is scaled to range between 0 (most modified forest) and 10 (least modified forest).

We derived a spatial layer estimating the original distribution of forest, prior to extensive human modification, as the union of two datasets generated by Grantham et al.¹⁷: (i) forest extent in 2019 (as described above); and (ii) potential extent of the forest zone, based largely on mapping by Laestadius et al.⁴⁴. All of the layers sourced or derived from the Grantham et

al.¹⁷ study were then resampled from 300m to 30-arcsecond grid-resolution (approximately 900m at the equator) to match the resolution of the beta-diversity modelling used to derive the BHI (see below). For each 30-arcsecond cell this yielded three values for use in our subsequent analyses: (i) the proportion of the cell originally covered by forest; (ii) the proportion of the cell covered by forest in 2019; and (iii) the mean FLII of this 2019 forest cover. All subsequent analyses were undertaken only for those countries for which forest was estimated to have originally covered a total area greater than 50km² – herewith referred to as “forest-supporting countries”.

Beta diversity models

We employed global modelling of spatial variation in the species composition of terrestrial ecological communities previously undertaken by CSIRO’s ‘Biogeographic modelling Infrastructure for Large-scale Biodiversity Indicators’ (BILBI) initiative¹⁹, and used in several existing global analyses^{20,21,40,45-48}. These models predict the dissimilarity in species composition (pairwise beta diversity) expected between any two 30-arcsecond grid-cells on the planet as a function of fine-scaled spatial variation in climate, terrain and soils, and of the spatial distance between cells. The models are fitted using *obs-pair*GDM¹⁹, an extension of generalised dissimilarity modelling³¹ designed to work effectively with relatively unstructured, or ‘presence-only’, species-occurrence data. To account for major global-scale biogeographic discontinuities, separate models are fitted for each of 61 unique combinations of terrestrial biomes and biogeographic realms¹⁹, as defined by the World Wildlife Fund’s ecoregional framework⁴⁹.

While these beta-diversity models have been developed for a broader range of biological groups, we focused the initial demonstration of our approach on vascular plants, for which the available GDM models have been fitted to over 52 million occurrence records for

254,145 species worldwide, accessed through the Global Biodiversity Information Facility (GBIF)¹⁹. Good potential exists for future work to extend derivation of our indicator to incorporate GDM models already fitted to data for 24,442 species of vertebrates, and 132,761 species of invertebrates worldwide¹⁹.

Biodiversity Habitat Index derivation

We coupled the 2019 FLII dataset and beta-diversity models for vascular plants (described above) to derive the Biodiversity Habitat Index (BHI) for each of the world's forest-supporting countries. The BHI uses an extended form of species-area analysis to estimate the proportion of species expected to persist (i.e. avoid extinction) over the long term as a function of the extent, condition and spatial configuration of natural habitat remaining in any given region or area of interest. Early applications of the species-area approach to predicting species loss treated habitat as a binary variable²⁹ – i.e. natural habitat was deemed to be either present or absent at any given location. More recent applications have typically allowed more subtle variation in the condition of habitat across a region to be accounted for in predicting proportional species' persistence as a function of the 'effective' proportion of habitat remaining⁵⁰⁻⁵². However, most such applications rely strongly on the assumption that the area of interest (e.g. an ecosystem type, an ecoregion, or a country) is biologically homogenous or, at least, that habitat loss and degradation is distributed randomly relative to any spatial pattern in the distribution of species within the area concerned. The analytical approach underpinning the BHI is unique in its ability to account explicitly for well-known biases^{33,35-37} in the distribution of habitat transformation toward particular environments, and therefore particular assemblages of species, within any given region.

In this approach each grid-cell is viewed not as belonging to a homogeneous set of cells forming a discrete ecosystem type, ecoregion, or country, but rather as sitting within a

continuum of spatial variation in environmental conditions, and therefore variation in species composition^{20,32,33,53}. The BHI score assigned to a given ‘focal cell’ is therefore calculated as a function of the average state of all ecologically-similar cells to that cell. The contribution any other cell makes to this calculation is weighted according to the predicted level of similarity in species composition expected if both it, and the focal cell, were in a perfectly natural state. If the state of habitat is scaled between 0 and 1, with 0 corresponding to a complete loss of local habitat for native species originally associated with a given cell, and 1 corresponding to a complete retention of local habitat for these species, then the BHI for focal cell i is calculated as:

$$BHI_i = \left[\frac{\sum_{j=1}^n s_{ij} h_j}{\sum_{j=1}^n s_{ij}} \right]^z \quad (1)$$

where s_{ij} is the expected similarity (proportional overlap, 0 to 1) in species composition between focal cell i and each cell j within the region of interest; h_j is the state of habitat in cell j ; and n is the total number of cells in the region.

The regions used for calculating and reporting the BHI – in this case countries – can be treated as either ‘open’ or ‘closed’ systems for the purpose of the analysis undertaken. Most previous applications of this approach have treated any reporting regions as open systems^{20,32,53} – i.e. the calculation of ecologically-similar habitat to a focal cell includes the contribution of cells both inside and outside the region containing that focal cell. However, for the present study we opted to treat each country as a closed system, as we felt this would best reflect the emphasis that national governments are likely to place on setting targets and prioritizing actions within their own borders, largely independently of those being pursued by other countries. This also allowed us to directly compare country-level estimates of species persistence obtained using the BHI approach with those based solely on the proportion of

original forest extent remaining in each country. In Equation 1, n is therefore the number of cells which were originally covered by forest, within the country containing focal cell i (including the focal cell itself). This means that the division within the square brackets of this equation estimates the ‘effective’ proportion of habitat remaining, across the country concerned, for species originally associated with that focal cell. While the BHI can optionally be reported as this estimate^{18,21} – i.e. in units of the proportion of habitat remaining – for many applications, including our present study, further value can be added by using the species-area relationship to translate this proportion of habitat into a prediction of the proportion of species, originally associated with the focal cell, expected to persist over the long term – in this case, anywhere within the relevant country. This is achieved by raising the effective proportion of habitat remaining to the power of z , which we set to 0.25, in keeping with previous applications of this approach^{20,32,33,47,53}.

We estimated the state of habitat in each cell – h_j in Equation 1 – as a direct function of the FLII value of that cell. Values for the FLII ranged between 0 and 10, and we therefore linearly rescaled these to range between 0 and 1. We then further transformed these rescaled values through an inverse of the power function employed in the species-area relationship:

$$h_j = (FLII_j/10)^{1/z} \quad (2)$$

This transformation was motivated by the need to ensure that values for h were expressed on an additive scale, and therefore made ecological sense when summed across multiple cells to estimate effective proportions of habitat remaining. For example, the result of summing 50 cells with an h value of 0 together with 50 cells with a value of 1, needed to be ecologically equivalent to summing 100 cells all with an h value of 0.5. Descriptions of the ecological characteristics of forest areas assigned different FLII values in Grantham et al.’s original publication¹⁷, suggested that the raw scale of this index is inherently non-additive. This was

also reflected by that publication's choice of thresholds for rating FLII values as 'low' (≤ 6.0), 'medium' (>6.0 and <9.6), and 'high' (≥ 9.6) based on benchmarking against reference locations worldwide. Further advice from the two authors on our present study who were also closely involved with the Grantham et al. study (H.S.G and J.E.M.W.) suggested that the scale of the FLII indicates, albeit approximately, the proportion of native species expected to remain in a continuous expanse of forest with a given FLII value. In other words, an expanse of forest with an FLII value of 6.0 might reasonably be expected to retain 60% of native species, while an area with an FLII of 9.5 would retain 95% of species. Raising FLII/10 to the power of $1/z$ therefore ensured that the summation of values for h yielded an estimate of the proportion of habitat remaining, rather than the proportion of species remaining, prior to the subsequent transformation of this proportion using the species-area relationship (Equation 1). The aggregate BHI for any given country was calculated as a weighted geometric mean of the individual BHI values for all n cells within that country which were originally covered by forest:

$$BHI_{country} = \exp \left[\frac{\sum_{i=1}^n w_i \ln(BHI_i)}{\sum_{i=1}^n w_i} \right] \quad (3)$$

As for previous applications of this approach^{20,32,33,53}, the contribution of each cell was weighted according to the predicted overlap in species composition between this cell and all other cells, and therefore the compositional uniqueness of the cell:

$$w_i = \frac{1}{\sum_{j=1}^n s_{ij}} \quad (4)$$

The aggregate BHI for a given country (Equation 3) ranges between 0 and 1, and is a prediction of the proportion of native species, originally occurring in a country, which are expected to persist over the long term anywhere within that country. This indicator can potentially be used to monitor past-to-present change in the expected persistence of

biodiversity in a country, through repeated application of Equation 3 using data on the state of habitat across that country (h in Equation 1) observed at different points in time. The same indicator can also be used to assess the extent to which the long-term persistence of a country's biodiversity is expected to be altered by future changes in habitat state resulting from the predicted interplay between implemented or proposed area-based actions and ongoing threatening processes²⁵.

A special case of this forward-looking analysis involves predicting, and thereby mapping, the marginal gain in persistence of a country's biodiversity expected if a given action were applied, in turn, to each grid-cell i within that country²⁵:

$$marginal_gain_i = \left[\frac{(\sum_{j=1}^n s_{ij} h_j) + c_i}{\sum_{j=1}^n s_{ij}} \right]^z - \left[\frac{\sum_{j=1}^n s_{ij} h_j}{\sum_{j=1}^n s_{ij}} \right]^z \quad (5)$$

where c_i is the expected change in the local state (h) of focal cell i if the action of interest (e.g. ecosystem restoration or protection) were applied to that cell, and h_j is the state of each and every cell j expected in the absence of further action. The value of c_i will depend on the type of action being considered, but will typically be estimated as some function of the currently observed state and/or the expected future state of the focal cell. For example, to assess the marginal gain in country-level biodiversity persistence predicted to result from adding a given cell to the existing protected-area system, c_i could be estimated as the difference between the present state of that cell (derived from its observed FLII value) and the counter-factual state expected in the future if the cell remains unprotected. In the most basic form of such an analysis, this counter-factual state might be assumed to be zero – i.e. any unprotected cell is assumed to lose all of its present habitat value. Alternatively, as noted above, the counter-factual state of each cell might be modelled as a function of best-available information on the spatial distribution of threatening processes or pressures (e.g. the likelihood of different types of land-use change)^{20,25,40}. Repeated application of this general

approach to each and every cell within a country can then allow the marginal gain expected from applying a given action to be mapped, and to thereby inform spatial prioritisation of ongoing implementation of that action by the country concerned.

Data availability

References cited^{17,19} provide links to all input datasets used to derive the forest extent and integrity layers, and the vascular plant beta-diversity models, employed in this study. The Forest Landscape Integrity Index can be accessed at <https://www.forestintegrity.com/>. All results for the Biodiversity Habitat Index generated by this study will be made publicly available for download, at 30-arcsecond grid-resolution, when published.

Code availability

Code developed for and used in this analysis are available from the corresponding author upon any reasonable request.

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Author contributions

S.F., J.E.M.W., H.S.G. and T.D.H. conceived and designed the study. C.W. and J.M.A. undertook the analyses, with advice and feedback from S.F., H.S.G., J.E.M.W., and T.D.H.. J.M.A. and S.F. prepared the figures. S.F. wrote the draft manuscript with input and feedback from J.E.M.W., H.S.G., J.M.A., C.W. and T.D.H.

Extended Data Table 1. Results for individual forest-supporting countries, including: the estimated original area of forest prior to extensive human modification, and the area remaining in 2019; the proportion of plant species expected to persist over the long term, as a simple species-area-based function of the proportion of original forest remaining in the country; the proportion of plant species expected to persist as estimated by the Biodiversity Habitat Index (BHI) derived from 2019 mapping of the Forest Landscape Integrity Index; and the 5th and 95th percentiles of the distribution of BHI values for all originally forested 30-arcsecond grid-cells within the country.

Country	Original forest area (km²)	Forest area remaining in 2019 (km²)	Proportion of species expected to persist based on proportion of forest remaining	Proportion of species expected to persist as estimated by the BHI	5th percentile of the distribution of BHI values for individual grid-cells	95th percentile of the distribution of BHI values for individual grid-cells
Afghanistan	4,242	3,173	0.930	0.689	0.528	0.829
Albania	21,244	10,414	0.837	0.513	0.368	0.676
Algeria	23,340	15,367	0.901	0.447	0.378	0.543
Andorra	260	258	0.998	0.456	0.398	0.496
Angola	818,343	741,055	0.976	0.828	0.717	0.908
Antigua and Barbuda	244	199	0.950	0.585	0.498	0.730
Argentina	476,224	383,299	0.947	0.754	0.602	0.886
Armenia	11,121	4,477	0.797	0.451	0.397	0.582
Australia	973,823	501,790	0.847	0.576	0.362	0.852
Austria	68,639	48,713	0.918	0.444	0.320	0.624
Azerbaijan	26,659	16,871	0.892	0.575	0.443	0.754
Bahamas	3,493	3,337	0.989	0.750	0.703	0.810
Bangladesh	111,536	20,399	0.654	0.414	0.364	0.540
Belarus	198,363	121,613	0.885	0.409	0.358	0.490
Belgium	26,540	7,864	0.738	0.221	0.178	0.319
Belize	20,196	18,563	0.979	0.736	0.629	0.917
Benin	22,040	11,338	0.847	0.602	0.479	0.775
Bhutan	31,817	31,115	0.994	0.827	0.734	0.916
Bolivia	690,558	652,911	0.986	0.852	0.748	0.920
Bosnia and Herzegovina	42,463	36,113	0.960	0.611	0.493	0.746
Botswana	644	577	0.973	0.893	0.769	0.939
Brazil	6,797,814	5,589,491	0.952	0.678	0.464	0.955

Brunei	5,708	5,462	0.989	0.841	0.746	0.901
Bulgaria	104,219	56,305	0.857	0.542	0.418	0.763
Burundi	19,556	12,526	0.895	0.490	0.413	0.608
Cambodia	141,665	81,915	0.872	0.664	0.557	0.817
Cameroon	387,017	375,331	0.992	0.828	0.749	0.902
Canada	4,884,192	4,630,148	0.987	0.890	0.774	0.954
Cape Verde	602	69	0.582	0.316	0.234	0.553
Central African Republic	555,853	554,091	0.999	0.940	0.902	0.971
Chad	20,536	14,957	0.924	0.666	0.618	0.742
Chile	237,141	199,246	0.957	0.789	0.559	0.937
China	3,942,569	2,185,648	0.863	0.497	0.329	0.669
Colombia	939,132	897,041	0.989	0.799	0.622	0.957
Comoros	1,492	1,489	0.999	0.784	0.699	0.896
Costa Rica	49,857	47,530	0.988	0.608	0.435	0.882
Cote d'Ivoire	228,916	214,219	0.984	0.538	0.464	0.682
Croatia	48,418	31,975	0.901	0.499	0.392	0.708
Cuba	96,435	54,983	0.869	0.498	0.410	0.689
Cyprus	1,281	1,280	1.000	0.789	0.753	0.825
Czech Republic	72,694	33,886	0.826	0.258	0.207	0.379
Dem Rep of the Congo	2,261,690	2,219,765	0.995	0.832	0.748	0.899
Denmark	37,980	3,676	0.558	0.112	0.098	0.142
Dominica	711	405	0.869	0.226	0.190	0.294
Dominican Republic	42,071	32,009	0.934	0.497	0.372	0.735
Ecuador	222,412	209,304	0.985	0.753	0.566	0.934
Egypt	4,887	545	0.578	0.241	0.219	0.275
El Salvador	16,365	13,138	0.947	0.459	0.373	0.607
Equatorial Guinea	26,694	26,624	0.999	0.848	0.786	0.906
Estonia	38,761	32,160	0.954	0.443	0.401	0.517
Ethiopia	342,229	200,704	0.875	0.661	0.500	0.882
Fiji	17,160	16,861	0.996	0.839	0.736	0.914
Finland	244,415	240,888	0.996	0.616	0.509	0.782
France	454,854	192,567	0.807	0.339	0.272	0.490
French Guiana	82,263	82,179	1.000	0.968	0.931	0.988
Gabon	256,356	254,818	0.998	0.915	0.879	0.947
Gambia	916	333	0.776	0.449	0.355	0.538
Georgia	48,648	38,375	0.942	0.695	0.500	0.877
Germany	308,779	141,163	0.822	0.293	0.234	0.396
Ghana	104,159	92,595	0.971	0.576	0.502	0.705
Greece	95,283	50,474	0.853	0.546	0.417	0.741
Grenada	329	327	0.999	0.524	0.456	0.636
Guatemala	99,485	86,950	0.967	0.539	0.412	0.801
Guinea	159,299	149,154	0.984	0.577	0.458	0.729
Guinea-Bissau	23,094	20,640	0.972	0.648	0.585	0.759

Guyana	193,611	192,641	0.999	0.945	0.904	0.986
Haiti	14,168	10,646	0.931	0.472	0.354	0.662
Honduras	100,604	92,561	0.979	0.544	0.437	0.768
Hungary	83,816	23,303	0.726	0.238	0.182	0.392
India	1,601,024	492,448	0.745	0.557	0.385	0.719
Indonesia	1,835,712	1,572,494	0.962	0.741	0.529	0.928
Iran	33,135	20,838	0.891	0.631	0.445	0.796
Iraq	123	121	0.994	0.439	0.385	0.482
Ireland	15,066	4,071	0.721	0.191	0.163	0.232
Israel	322	257	0.946	0.524	0.471	0.604
Italy	228,982	112,794	0.838	0.377	0.258	0.604
Jamaica	10,360	9,564	0.980	0.571	0.449	0.769
Japan	360,380	301,135	0.956	0.599	0.437	0.800
Kazakhstan	47,204	43,283	0.979	0.766	0.657	0.879
Kenya	88,732	46,297	0.850	0.505	0.383	0.760
Kosovo	9,405	5,493	0.874	0.499	0.396	0.682
Kyrgyzstan	5,925	5,918	1.000	0.895	0.873	0.926
Laos	219,811	201,267	0.978	0.684	0.590	0.783
Latvia	56,966	44,218	0.939	0.327	0.286	0.391
Lebanon	1,378	682	0.839	0.392	0.325	0.489
Liberia	95,300	88,743	0.982	0.700	0.598	0.829
Liechtenstein	127	102	0.946	0.531	0.407	0.657
Lithuania	59,845	29,144	0.835	0.250	0.207	0.343
Luxembourg	2,038	1,241	0.883	0.184	0.167	0.209
Macedonia	18,698	10,755	0.871	0.616	0.478	0.796
Madagascar	226,648	200,939	0.970	0.609	0.472	0.774
Malawi	85,231	32,051	0.783	0.496	0.418	0.677
Malaysia	325,523	252,839	0.939	0.629	0.508	0.800
Mali	1,644	1,541	0.984	0.764	0.710	0.819
Mauritius	1,786	1,475	0.953	0.499	0.441	0.627
Mexico	765,018	644,678	0.958	0.729	0.516	0.899
Micronesia	83	81	0.992	0.638	0.609	0.682
Moldova	28,502	4,651	0.636	0.212	0.194	0.267
Mongolia	69,117	46,498	0.906	0.755	0.680	0.818
Montenegro	9,454	8,481	0.973	0.651	0.566	0.721
Morocco	10,159	7,246	0.919	0.672	0.549	0.795
Mozambique	565,783	496,124	0.968	0.731	0.622	0.864
Myanmar	635,633	481,181	0.933	0.718	0.578	0.858
Nepal	105,810	78,274	0.927	0.615	0.518	0.736
Netherlands	21,972	2,646	0.589	0.141	0.121	0.186
New Zealand	128,214	116,631	0.977	0.723	0.545	0.909
Nicaragua	107,862	97,672	0.975	0.515	0.432	0.718
Nigeria	231,677	173,108	0.930	0.635	0.542	0.790
North Korea	99,289	62,707	0.891	0.694	0.552	0.837
Norway	131,075	128,766	0.996	0.773	0.665	0.862
Pakistan	36,445	15,537	0.808	0.592	0.293	0.765

Palau	402	400	0.999	0.791	0.741	0.838
Panama	72,432	66,106	0.977	0.711	0.527	0.907
Papua New Guinea	452,962	448,943	0.998	0.882	0.795	0.939
Paraguay	296,698	240,290	0.949	0.665	0.505	0.830
Peru	800,290	796,112	0.999	0.873	0.767	0.968
Philippines	285,624	236,341	0.954	0.607	0.476	0.783
Poland	289,335	130,693	0.820	0.275	0.228	0.359
Portugal	58,670	16,000	0.723	0.210	0.166	0.286
Republic of Congo	322,738	314,327	0.993	0.894	0.817	0.954
Romania	196,935	103,218	0.851	0.497	0.357	0.693
Russia	9,188,907	8,448,346	0.979	0.825	0.727	0.902
Rwanda	21,244	9,283	0.813	0.466	0.374	0.715
Saint Kitts and Nevis	229	185	0.948	0.572	0.379	0.720
Saint Lucia	595	590	0.998	0.658	0.573	0.797
Saint Vincent and the Grenadines	356	355	0.999	0.693	0.563	0.850
Sao Tome and Principe	890	257	0.733	0.321	0.229	0.469
Senegal	3,915	3,580	0.978	0.743	0.693	0.806
Serbia	72,285	40,038	0.863	0.465	0.332	0.651
Sierra Leone	69,910	61,664	0.969	0.471	0.390	0.650
Singapore	575	137	0.698	0.177	0.167	0.235
Slovakia	46,612	29,194	0.890	0.441	0.315	0.571
Slovenia	18,854	15,703	0.955	0.475	0.389	0.594
Solomon Islands	26,474	26,305	0.998	0.780	0.696	0.862
Somalia	10,861	2,438	0.688	0.437	0.346	0.543
South Africa	117,920	90,461	0.936	0.592	0.510	0.727
South Korea	93,574	73,333	0.941	0.579	0.492	0.723
South Sudan	218,459	212,608	0.993	0.930	0.882	0.960
Spain	214,582	130,067	0.882	0.481	0.354	0.635
Sri Lanka	61,822	51,391	0.955	0.640	0.571	0.721
Sudan	3,917	3,908	0.999	0.964	0.943	0.985
Suriname	141,548	141,050	0.999	0.950	0.897	0.982
Swaziland	13,938	9,296	0.904	0.472	0.432	0.574
Sweden	338,257	318,599	0.985	0.633	0.493	0.813
Switzerland	24,838	17,795	0.920	0.471	0.354	0.653
Syria	2,217	1,151	0.849	0.414	0.312	0.555
Taiwan	35,205	25,438	0.922	0.631	0.444	0.856
Tajikistan	304	304	1.000	0.778	0.589	0.942
Tanzania	562,908	443,439	0.942	0.724	0.625	0.843
Thailand	499,105	218,254	0.813	0.566	0.453	0.765
Timor-Leste	14,683	11,854	0.948	0.602	0.508	0.707
Togo	23,709	12,265	0.848	0.549	0.432	0.745
Trinidad and Tobago	4,993	4,413	0.970	0.700	0.568	0.863
Tunisia	5,708	2,629	0.824	0.485	0.414	0.600

Turkey	277,050	139,509	0.842	0.516	0.411	0.683
Uganda	157,681	127,905	0.949	0.581	0.488	0.738
Ukraine	396,748	138,648	0.769	0.328	0.274	0.478
United Kingdom	135,096	24,214	0.651	0.238	0.176	0.348
United States	3,872,642	3,376,305	0.966	0.708	0.480	0.942
Uruguay	16,646	14,692	0.969	0.503	0.449	0.587
Uzbekistan	629	569	0.975	0.721	0.533	0.921
Vanuatu	11,268	11,176	0.998	0.891	0.813	0.952
Venezuela	659,570	615,922	0.983	0.832	0.657	0.966
Vietnam	288,956	179,538	0.888	0.558	0.416	0.737
Zambia	493,396	410,266	0.955	0.753	0.668	0.846
Zimbabwe	32,976	27,004	0.951	0.664	0.572	0.774