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Developing spatially comparable biodiversity indicators using objective scale-dependent species selection

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ABSTRACT

Multi-species indices (MSIs) are an important tool for monitoring progress towards conservation policy targets from the local to the global scale. The choice of constituent species for habitat-specific indicators often reflects context-specific knowledge, policy needs and data availability. This makes direct comparisons of equivalent indicators across various locations challenging, and potentially reduces their representativeness if subsequently applied to other locations or spatial scales. In recognition of this, there is growing demand to develop standardised approaches to species selection that produce more spatially comparable MSIs. Using forest bird species in Europe, we use an objective, niche-based framework for indicator species selection to derive standardised indices at national, regional and pan-European scales, and explore the implications for species composition on indicator trends when adopting three alternative species-selection strategies: selecting species representative of a given spatial scale ("geographically-targeted"), disaggregating a species set representative of a broad-scale for use at smaller scales ("top-down") and aggregating species lists representative of smaller scales for use at larger scales ("bottom-up"). We show that although the composition of indicator sets varied according to the species' selection approach, resultant index trends for a given location were generally comparable. However, "geographically-targeted" indicators tended to be comprised of more specialist species and were more representative of the wider

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community. Whilst existing biodiversity indices provide critical insights into the state of nature across spatial scales, our study provides the basis for the development of complementary, standardised indicators that are spatially comparable.

1. Introduction

Global scale biodiversity losses are driven by anthropogenic activities, including natural habitat loss (Díaz et al., 2019) and over-exploitation of natural resources (Reyers and Selig, 2020). In recent decades, multi-species indices (MSIs) based on relative abundance have been increasingly used to track the effects of these activities on ecosystems (Cairns et al., 1993; Gregory et al. 2008), monitor biodiversity's response to conservation management (Butchart et al., 2010), and track progress towards environmental and sustainable development policy targets (Niemeijer and de Groot, 2008; Bal et al., 2018; Mace et al., 2018).

MSIs aim to summarise results of complex processes occurring within habitats and environments so they can be easily interpreted (Niemeijer and de Groot, 2008). To be robust and policy-relevant, these MSIs must be representative of the wider ecological community, responsive to environmental changes (Zettler et al., 2013; Stevenson et al., 2021) and, ideally, comparable across geographies (McNellie et al., 2020). Habitat-specific MSIs can be developed using three main strategies. Firstly, they can be developed specifically for the habitat in a focal area (hereafter "geographically-targeted", GT, indicators). This allows local species' habitat associations (Zettler et al., 2013), data availability, conservation objectives and policy requirements to be considered when selecting constituent species (Feld et al., 2009; Terrigeol et al., 2022). Whilst this approach ensures the indicator is likely to be representative and responsive to local conditions, such context-dependency can make it challenging to compare GT indicators for various locations, as they may be composed of different sets of species and respond to different drivers (Remme et al., 2016). As an alternative, international targets for halting biodiversity loss have seen broad-scale MSIs being calculated at smaller spatial scales (hereafter "top-down", TD, indicators) (Knight and Cowling, 2007) to monitor national and local-level progress towards these targets. However, because the initial species selection will have been designed to produce MSIs representing broad geographical areas, TD indicators generally do not account for variation in species' habitat associations, making them likely to be less representative of local communities and less responsive to local environmental change (Butler et al., 2012). The final approach is based on an opposite process to the TD indicators development, whereby sets of species included in "geographically-targeted" local MSIs are combined to produce indicators for larger geographical regions (hereafter "bottom-up", BU, indicators) (Fraser et al., 2006; Feld et al., 2009). This approach ensures that species closely associated with a given habitat at smaller spatial scales are accounted for at the larger scale. However, this may result in these MSIs being driven, for example, by the population dynamics of a species with limited distribution, thereby reducing their representativeness for patterns in the wider area.

Birds are often used as biodiversity indicators due to their sensitivity to environmental changes, well-studied ecology, physiology and behaviours, and the relative ease with which they can be monitored (Gregory et al., 2005; BirdLife International, 2020; Fraixedas et al., 2020). For example, the Pan-European Common Bird Monitoring Scheme (PECBMS) collates and integrates national indices for breeding bird species across Europe to produce regional (North, South; Central & East; West) and European-level Forest Bird Indicators (FoBI) that track changes in the population trends of a suite of indicator species (Brlík et al., 2021; https://pecbms.info/), whilst many European countries have also developed equivalent national FoBIs (https://pecbms.info/trends-and-indicators/national-indicators/). Current national and regional FoBIs can be classified as GT indicators as their species composition reflects geographic variation in occurrence, habitat use, data availability and policy drivers. Conversely, the current European FoBI can be classified as a BU indicator, as it is derived from regional-level classifications of occurrence and habitat use *e.g.*, five of the 34 species included in the European FoBI (*Bombycilla garrulus, Cyanopica cyanus, Emberiza rustica, Ficedula albicollis, Tringa ochropus*) only occur in one of the four bio-geographical regions that this indicator represents (https://pecbms.info/methods/).

In Europe, Forest Europe, an organisation central to policy for sustainable forest management (Forest Europe, UNECE and FAO, 2011), is interested in validating and improving the indicators it uses, including for birds (Forest Europe, 2019). In light of the current variation, they are exploring the integration of more objective, niche-based frameworks for indicator species selection to facilitate cross-country indicator comparison and benchmarking (Forest Europe, 2019). In addition, the European Commission has recently proposed a monitoring framework for resilient European forests; 'Forest Monitoring Law', which will likely be underpinned by a set of standardised measures, such as the Forest Bird Indicator (European Commission, 2023). Similarly, the European Commission's recent Nature Restoration Law is the first continent-wide, comprehensive law of its kind, comprising national targets to restore species populations and ecosystems, with specific reference to forest and farmland birds and indicator frameworks (European Parliament, 2024). Such EU regulation places increasing emphasis on the quality of national reporting mechanisms and on national-scale biodiversity indicators.

Against this backcloth, we use European forest birds to explore the consequences for MSI dynamics when employing GT, TD and BU approaches to generate constituent species sets using an objective method which produces representative, responsive and comparable MSIs. Specifically, we ask: (1) Does species selection approach (*i.e.* GT, TD or BU) influence species composition of indicators? (2) Does the species selection approach impact indicator representativeness and responsiveness? (3) Do the MSI trends of GT-, TD- and BU-derived indicators for a given spatial scale differ? (4) Do the MSI trends of GT-, TD- and BU-derived European and regional indicators differ from equivalent trends for the current published European and regional FoBIs?

2. Methods

Forest Europe are exploring the use of an objective, niche-based approach (Butler et al., 2012; Wade et al., 2014) to select species for inclusion in their revised Forest Bird Indicators (Forest Europe, 2019) and we employ that approach here to derive constituent species lists for GT, TD and BU indicators at national, regional and European scales. This approach imposes two core rules; 1) from a defined set of resources used by the wider community, each must be covered by at least one of the species in the indicator and 2) the indicator must be comprised of the most specialised species possible, with each species' specialisation scored according to the number of resource types it uses and its reliance on the target habitat to provide those resources (Butler et al., 2012). These rules ensure that the indicator is representative of the wider community and is sensitive to any changes in land use or resource availability (Butler et al., 2012; Wade et al., 2014; Magg et al., 2019). The approach is based on a standardised resource requirements matrix. This means that, although the species composition of indicators for a given habitat may vary across geographical regions, the indicators will still represent the same underlying resource set, thereby allowing more direct comparisons. To date, applications of this approach have used expert-based opinions to determine the candidate species pool from which indicator species are chosen and to quantify each species' reliance on the target habitat (Butler et al., 2012; Wade et al., 2014). To remove this subjective element, here we replace these steps with an objective assessment of each species' Relative Habitat Use (RHU; Larsen et al., 2011). A species' RHU for a given habitat is calculated as its abundance in that habitat, relative to its mean abundance across all other habitats, weighted by habitat availability. RHU can be used as a quantitative measure of reliance that is comparable across species (O'Reilly et al., 2022). Previous work has shown that RHU and literature-based classifications of species' habitat associations are broadly aligned (O'Reilly et al., 2022).

2.1. RHU calculation

Annual RHU scores for each species were calculated at the European, regional, and national levels following O'Reilly et al. (2022). In brief, we used annual, site-level count data for European common breeding birds (168 species) collected between 1998 and 2017 from 22,777 sites surveyed using either point counts, line transects or territory mapping across 22 countries (Table A.1) (Brlík et al., 2021). Although PECBMS currently do not produce FoBIs for the Southeast, East Mediterranean and West Balkan regions, national monitoring scheme data from countries in these regions contribute to the European FoBI. We therefore decided to include these three additional regions in our study. Following the methods of O'Reilly et al., (2022), each survey site was classified according to the dominant habitat type (forest, farmland, urban, wetland or semi-natural) within a 1 km^2 circular area centred on it. Habitat information was derived from Corine Land Cover 2012 (Copernicus Land Monitoring Service, 2012) (Table A.2); Corine Land Cover 2012 was used as it represents the closest mid-point to the bird monitoring data timeseries. The Corine Land Cover inventory defines areas occupied by forests and woodlands as those composed of native or exotic coniferous and/or broad-leaved trees, and with a canopy closure of at least 30 %. In case of young plantation, the minimum cut-off-point for inclusion in this habitat category is 500 trees by hectare. Given the potential use of agroforestry areas by birds, we also chose to include agroforestry within our definition of forest in this study. In Corine, agroforestry is described as annual crops or grazing land under wooded cover of forestry species with a crown coverage of 10–30 % (*i.e.* agroforestry). Of the 5328 forest-dominated sites, only 64 contain agroforestry and these are all found in Spain. Defining sites by the dominant habitat type assumes that individual birds present in that square are likely to be influenced by processes and management associated with that dominant habitat (O'Reilly et al., 2022). For 82.5 % of sites, the dominant habitat types classified using Corine data from within the 1 km^2 and a 25 km^2 area centred on each site location were the same.

RHU scores can be sensitive to small changes in the relative distribution of individuals across sites of different habitat types, if the total number of sites occupied is small (O'Reilly et al., 2022). Additional exploration found that, for a given habitat, RHU scores stabilised when the total number of sites counted across habitats was between five and ten sites (Fig. A.1). Therefore, for a given species in a given year, RHU scores were only calculated if that species was recorded in at least 35 sites in total in that year, and RHUs were only calculated for an individual habitat if that species was recorded in at least seven sites of that habitat type in that year. These site thresholds also had to be met in at least three years for a species to be included (O'Reilly et al., 2022). Site threshold requirements were the same when calculating RHU scores at European, regional, and national levels, to ensure reliable RHU scores were calculated at each spatial scale.

A limited number of forest-dominated sites prevented national RHU score calculations for species in Latvia and Greece. However, data from these countries remained included in calculations of species' regional and European RHU scores. Note also that the PECBMS splits Germany into East and West for the Central & East and West PECBMS regions, respectively. Therefore, species' RHU scores for the Central & East and West regions included species' counts from East and West Germany, respectively. However, species' counts from East and West Germany were combined when calculating species' RHU scores at the national level. Combining data in this way allowed us to produce an indicator for Germany as a whole.

2.2. Selecting candidate species pools and developing a resource requirements matrix

For Europe, and for each region and country in turn, we identified a candidate indicator species pool by selecting all species with RHU scores $\geq$1 for forest habitat in at least 50 % of the years in which RHU scores were generated for them at the given spatial scale (Fig. 1; Step 1). No species met this threshold in Cyprus or Slovenia, as monitoring schemes in these countries are focused on farmland birds with survey sites located in farmland-dominated landscapes. As a result, no candidate species pools were produced for these countries or for the East Mediterranean or West Balkan regions (Table A.1). Although MSIs could not be created for these countries or regions, species count data from Cyprus and Slovenia still contributed to developing European MSIs.

A resource requirements matrix for all species identified in Step 1 was then constructed (Fig. 1; Step 2). This matrix covered breeding and non-breeding season diets, forest foraging habitat, nest type and nesting habitat (Wade et al., 2014), with a binary code (0/1) defining each species' use of each resource type within these categories (Snow et al., 1998; Storchová and Hořák, 2018) (Tables A.3 and A.4). The resource matrix was constructed at a European level as information on national and regional level resource use was not available for all species. For the derived indicators to be sensitive to changes in the availability of forest-specific resources, species needed to both nest and forage in forest habitat. Therefore, species identified as exclusively having an aquatic diet, or as not nesting and/or not foraging in forest habitats were subsequently removed. Finally, for each candidate species pool in turn, we categorised the constituent species as either resident or migrant at the corresponding spatial scale (BirdLife International and Handbook of the Birds of the World, 2019). Note that a species could potentially be categorised as migrant at a national level but resident at regional and/or European levels. These categories were used to determine the total number of potential resources available to each species at the given scale; 124 possible resource combinations for resident species (breeding and non-breeding season diet resources and nesting resources) and 70 for migratory breeding species (non-breeding season diet resources excluded).

For each species, we calculated the number of resources it uses as the percentage of the total number of resources available. This was rounded to the nearest whole number as the species selection software, *Specsel*, (Wade et al., 2014) requires integers for this metric. Each species' sensitivity score was calculated as the percentage of resources used divided by its reliance on forest habitat at the given spatial scale, with each species' reliance on forest habitat defined as its mean annual forest RHU at that scale. Lower scores were therefore assigned to species assumed to be more sensitive to changes in resource availability in forest (few resources used and/or higher forest mean RHU) and higher values to species assumed to be less sensitive (many resources used and/or lower forest mean RHU) (Butler et al., 2012; Wade et al., 2014; Teufelbauer et al., 2017; Magg et al., 2019).

2.3. Indicator species selection

2.3.1. "Geographically-targeted" indicator approach

We first applied the species selection algorithm (*Specsel*; Wade et al., 2014) to the European candidate species pool to identify the most sensitive species set. Thus, for each possible indicator set size (from the minimum of two species to the number of all species included in the candidate species pool) we identified all possible combinations of species that, between them, exploit all resource types used by the wider community (Fig. 1; Step 3) and ranked them according to the average

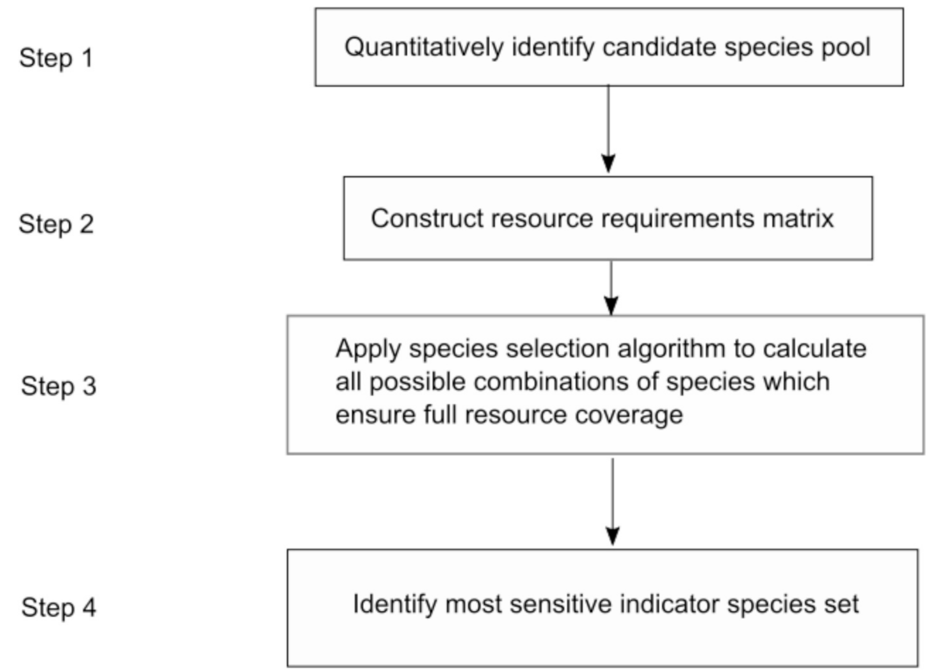

Fig. 1. Outline of the niche-based framework for indicator species selection (adapted from Butler et al., 2012). Each indicator set produced by the species selection algorithm in Step 3 receives an average sensitivity score which is the average sensitivity score across its constituent species. Each species' sensitivity score is calculated as the percentage of resources used divided by its reliance on forest habitat at the appropriate spatial scale. Detailed description of key processes and, where appropriate, quantitative thresholds or requirements to be met in each step of the niche-based framework are outlined in Table A.5.

sensitivity score across constituent species. From this, we identified the *European GT* indicator set as the species combination with the lowest overall average sensitivity score, *i.e.*, comprised of the most sensitive species set possible (Fig. 1; Step 4). We repeated this process for region- and country-specific candidate species pools to identify *regional* and *national GT* indicators.

2.3.2. "Top-down" indicator approach

For each region, species included in the *European GT* indicator set that occur in that region were assigned to the indicator set for that region (hereafter *European – regional TD* indicator). Next, for each of the 18 countries in turn, species included in the *European GT* indicator set that occur in that country were assigned to that country's indicator set (*hereafter European – national TD* indicator). Finally, for each country in turn, species included in the corresponding *regional GT* indicator set that occur in that country were assigned to the indicator set for that country (hereafter *regional – national TD* indicator). Regional indicator sets for Central & East, and West regions both contributed to the *regional – national TD* indicator set for Germany.

2.3.3. "Bottom-up" indicator approach

Using the species selection algorithm for each region in turn, a regional BU indicator set was selected from a composite candidate species pool containing all species included in the *national GT* indicator sets for countries within that region (hereafter *national – regional GT* indicator sets). The *national GT* indicator set from Germany contributed to the *national – regional GT* indicator sets for both Central & East and West regions. Next, a European BU indicator set was selected from a composite candidate species pool containing all species included in the 18 *national GT* indicator sets (hereafter *national – European BU* indicator set). Finally, the same process was applied to select a *regional – European BU* indicator set from a composite candidate species pool produced by combining *regional GT* indicator sets.

All species sets selected for national, regional and European indicators using GT, TD and BU approaches are available in Appendix C. Additional details of the species included in all GT candidate species pools, and of the species excluded at each step during the generation of these candidate species pools, are provided in Appendix B.

2.4. Data analysis

2.4.1. Average sensitivity and resource coverage

We use the average sensitivity of constituent species to quantify indicator responsiveness (lower sensitivity score reflects higher responsiveness) and resource coverage to quantify indicator representativeness (higher proportion of resources covered reflects greater representativeness). The number of resources covered by TD and BU indicators for a given spatial scale was expressed as a percentage of the total number of resources used by species in the GT indicator set for that scale (hereafter referred to as scale-dependent resource coverage); resource coverage of all GT indicators was 100 % due to the embedded rules of the species selection algorithm. For regional and national levels in turn, Wilcoxon signed-rank tests were carried out to test for differences between indicator set types in i) average sensitivity score and ii) percentage of scale-dependent resources covered. Wilcoxon tests were used because species potentially occurred in more than one indicator set for a given spatial scale therefore compositions of individual indicator sets were not necessarily independent. Indicator sets were paired for the same region or country. As there were only three indicator sets produced for Europe (*European GT*; *regional – European BU*; *national – European BU*), statistical comparisons between these could not be made.

2.4.2. Multi-species indices

MSIs for all GT, TD and BU indicator sets described above were calculated using the MSI-tool (Soldaat et al., 2017). For this, first we used the RTRIM-shell package in R (Pannekoek and van Strien, 2001; Bogaart et al., 2020) and the site-level count data to calculate national annual indices (+/- SE) for each species selected in the *national GT* indicator sets for each of the 18 countries. PECBMS provided regional and European-level population indices for each species occurring in any regional- or European-level indicator sets (Brlík et al. 2021). Note that the European and regional species' indices provided by PECBMS include data from six countries (Hungary, Italy, Lithuania, Luxembourg, Portugal, Slovakia) for which site-level count data were not used in this study. Therefore, there are slight differences between the countries that contributed count data for generating species' European and regional level RHU scores in this study, and the countries that contributed to the European and regional level species indices produced by PECBMS. However, our estimates of species' RHUs at the European and regional levels incorporate data from multiple countries to quantify their forest habitat associations across these large spatial scales and it is unlikely that additional count data from these excluded countries would significantly change these estimates.

For each GT, TD and BU indicator set in turn, the first index value in the MSI for all species included in the given indicator was set to 100 and standard error = 0, with 95 % confidence intervals around the yearly indices calculated by resampling individual species indices with replacement 10,000 times, re-calculating the index each time (Buckland et al., 2005). We also used the MSI tool to calculate smoothed trends (LOESS-regression, span = 0.75, degree = 2) for each indicator to best

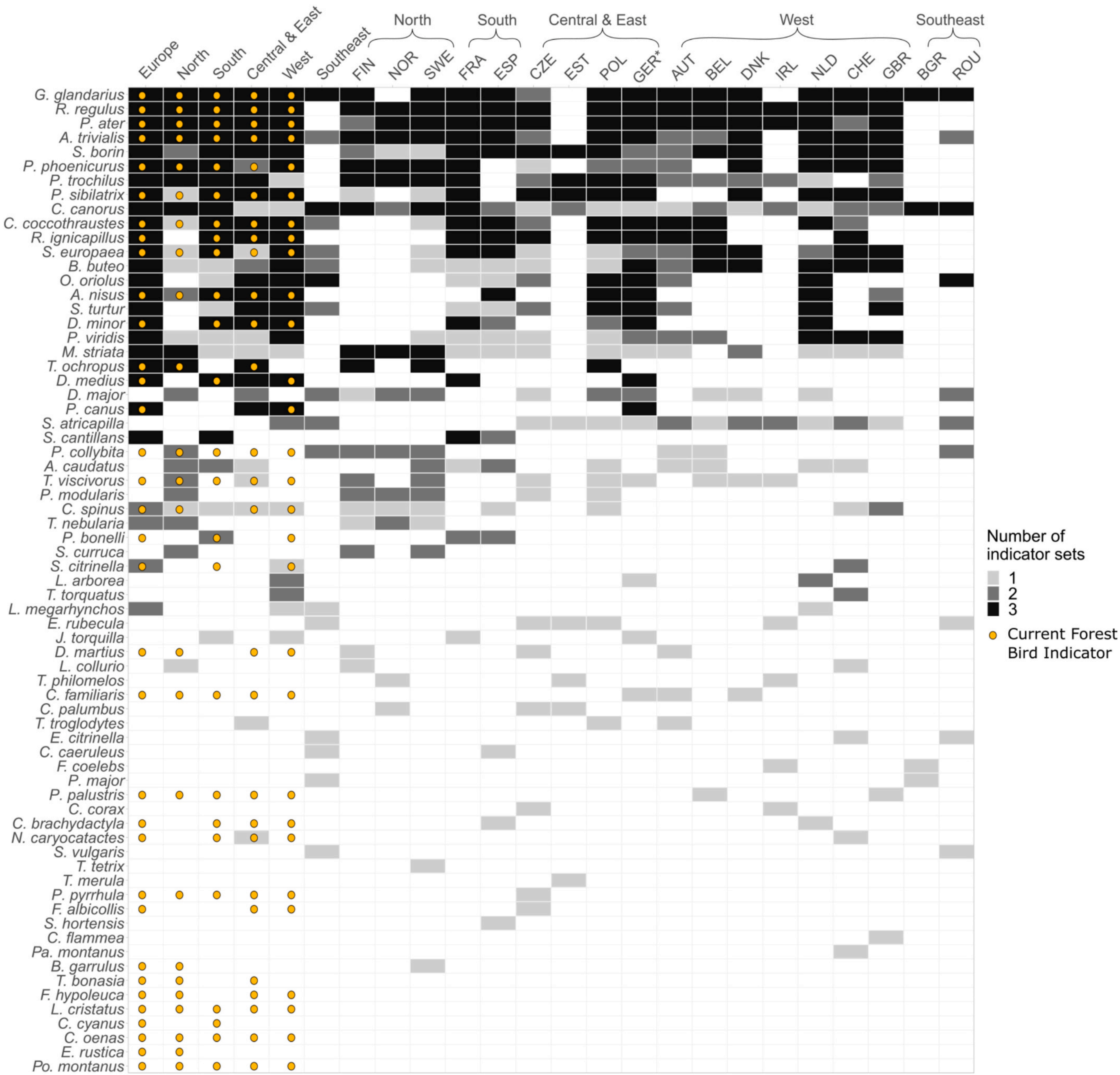

Fig. 2. Frequency of each species occurrence across indicator sets for Europe, for each region and each country. Countries are given a three-letter code (Table A.6) with species full names provided in Table A.7. Species can occur in a maximum of three indicator sets at each spatial scale ("geographically-targeted", "top-down" from European set, "top-down" from regional set for national indicators; "geographically-targeted", "top-down" from European set, "bottom-up" from national sets for regional indicators; "geographically-targeted", "bottom-up" from regional sets, "bottom-up" from national sets for European indicators). For comparison, species that occur in the current European and four regional Forest Bird Indicators (FoBI) are also identified; no current regional FoBI for the Southeast region. *GER: *regional – national TD* indicator set is derived from both the Central & East and West regions of Germany. Equally, the national German indicator set contributes to both the Central & East and West *national – regional BU* indicator sets. The indicators for Belgium only represent the south (Wallonia) as data were not available for northern Belgium. Full details of species included in each indicator set for each spatial scale can be found in Appendix C.

describe the overall population trend, minimising interannual variation (Buckland and Johnston, 2017; Gregory et al., 2019). To test for significant differences between MSIs for indicator sets at a given spatial scale, the TREND_DIFF function (using 1000 iterations), based on Monte Carlo procedures, was used (Soldaat et al., 2017; Gregory et al., 2019). This calculated the average difference between sets of MSIs with standard error and the significance of that difference.

Finally, we compared regional and European MSIs for our GT, TD and BU indicator sets to the current FoBIs at the corresponding scale using the TREND_DIFF function. This comparison was not generated for the Southeast region as PECBMS do not currently produce a FoBI for this region.

All analyses were carried out in R version 4.0.1 (R Core Team, 2020).

3. Results

3.1. Indicator species sets

62 species were selected for at least one of the niche-based indicators across European, regional and national levels. The average species set size for European indicators was 25.67 ± 0.88, 18.13 ± 1.25 for regional and 13.17 ± 0.73 for national (Fig. 2). The average set size for GT indicators was 15.38 ± 0.99, 13.44 ± 0.95 for TD and 20 ± 2.30 for BU. The most frequently selected species were Jay (*Garrulus glandarius*), followed by Goldcrest (*Regulus regulus*) and Coal tit (*Periparus ater*). 16 species in the current European FoBI occurred in at least two of the niche-based European indicators, with 14 of these occurring in all three indicators (*i.e. European GT, regional – European BU* and *national – European BU*), whilst 18/34 species in the current European FoBI did not occur in any of the European niche-based indicators. At the regional level, 13/24, 13/25, 15/27 and 15/29 species in the current North, South, Central & East and West FoBIs (respectively) occurred in at least one of the niche-based indicators for the corresponding region (Fig. 2). It is important to re-emphasise here that some species typical of forest habitat in particular countries or regions may not be included in the respective indicator sets presented here either because of our focus on the indicator sets with the lowest average sensitivity score and/or because limited data excluded them from the candidate species pool in

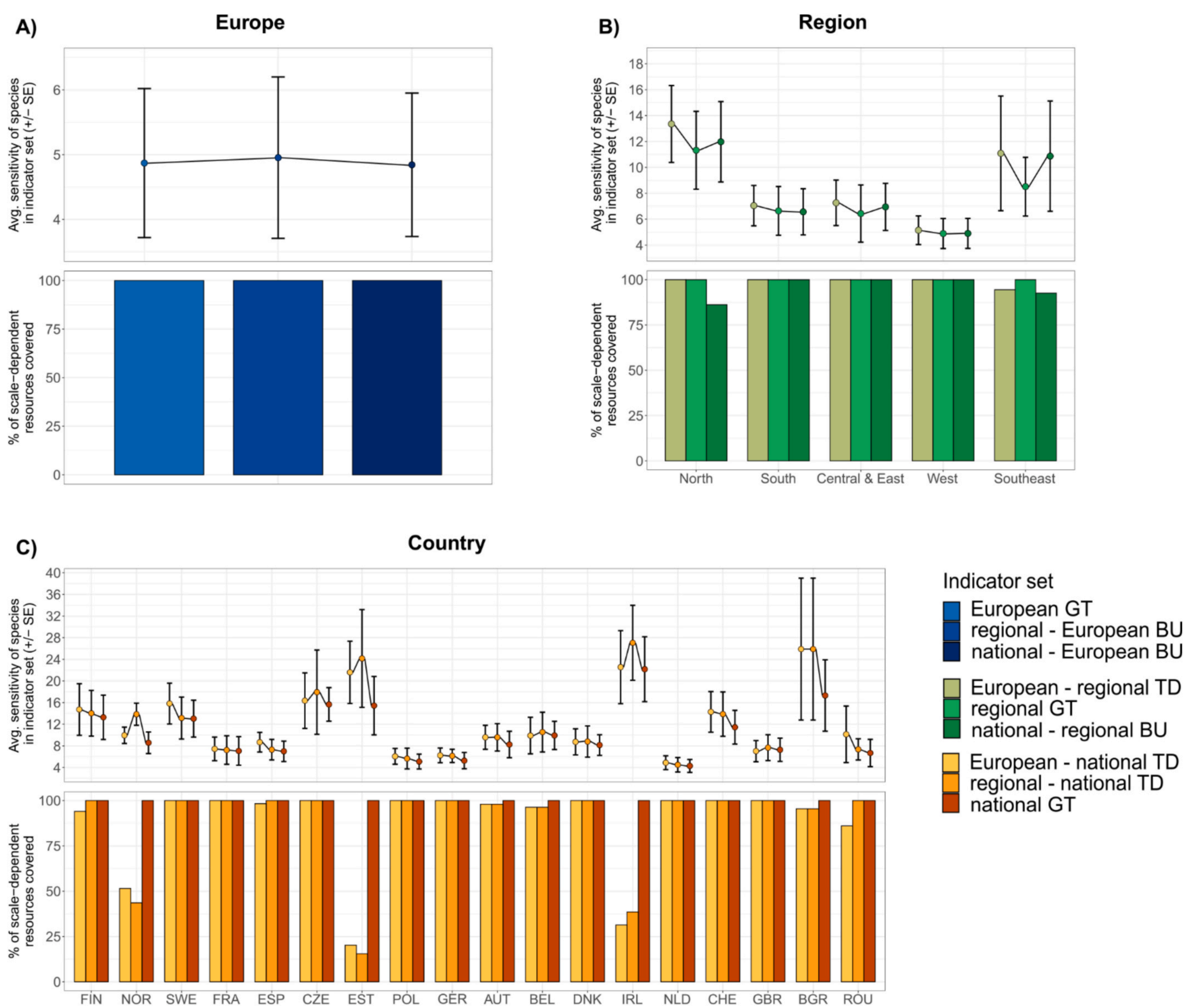

Fig. 3. Average sensitivity score (±SE) (upper graph) and percentage of scale-dependent resources covered (lower graph) by, A) European, B) regional and C) national-level indicator sets. The indicator set type ("geographically-targeted", GT; "top-down", TD; "bottom-up", BU) is provided alongside each indicator set. Each country is denoted by a three-letter code (Table A.6). Note that a higher score value indicates lower sensitivity.

the first place. Full details of the species excluded at each stage of the selection process for each national indicator are provided in the supplementary material (Appendix B).

3.2. Average sensitivity and resource coverage

At both the national and regional levels, GT indicators had lower average sensitivity scores, *i.e.* were more sensitive, than either TD or BU indicators, with these differences significant at the national level (Table A.8). The exception was the South region where the *national – regional BU* indicator had a lower average sensitivity score than its *European – regional TD* or *regional GT* indicator (Fig. 3, Table A.8). At the European level, the *national – European BU* indicator had the lowest average sensitivity score (4.84 ± 1.108), followed closely by the *European GT* (4.87 ± 1.151) and then the *regional – European BU* (4.95 ± 1.246) indicators.

All three European indicators covered 100 % of scale-dependent resources, while at the regional level, there were no significant differences in the percentage of scale-dependent resources covered between indicator set types. At a national level, the percentage of scale-dependent resources covered by *European – national TD* (87.28 ± 5.94) and *regional – national TD* (88.19 ± 6.17) indicator sets were significantly lower than their corresponding *national GT* indicators (100 ± 0.00) (Fig. 3, Table A.8).

3.3. MSIs

3.3.1. European

European MSIs (*European GT, regional – European, BU* and *national – European BU*) remained stable over time (Fig. 4, Tables A.3 and A.9), with no significant differences between their trends (Table A.10) or when compared to the current European FoBI (Table A.11).

3.3.2. Regional

In general, regional MSIs were stable regardless of the species selection approach used. However, the *regional GT* index for the Southeast showed a significant moderate increase, while the West *European – regional TD* indices showed a significant moderate decline (Fig. 5, Table A.9). There were no significant differences between MSIs within regions (Table A.10) except in the West where the *European – regional TD* index was significantly more negative than the current regional FoBI (Table A.11).

3.3.3. National

Within each country, MSIs generally demonstrated similar trends regardless of the species selection approach used. The exceptions were Finland and Czechia. In Finland, the *European – national TD* index showed a significant moderate decline, whilst the *regional – national TD* and *national GT* indices showed significant moderate increases. In Czechia, the *European – national TD* and *regional – national TD* indices showed significant moderate declines, and the *national GT* index showed a significant moderate increase (Fig. 6, Table A.9). Despite similarities in the overall pattern, there were significant differences between MSI trends within eight of the 18 countries (Table A.10).

4. Discussion

This study shows that although "geographically-targeted", "top-down" and "bottom-up" indicators for forest bird populations at a given spatial scale are comprised of different sets of species, the resultant MSIs for that scale generally show similar temporal trends since the late 1990s. Similarly, despite differences in species composition, the indicators developed here generally show comparable trends to the current Forest Bird Indices at the European and region levels. However, we find that GT indicators are composed of more specialised species and cover more resources at a given spatial scale than equivalent TD and BU indicators. This suggests that GT indicators could be more representative

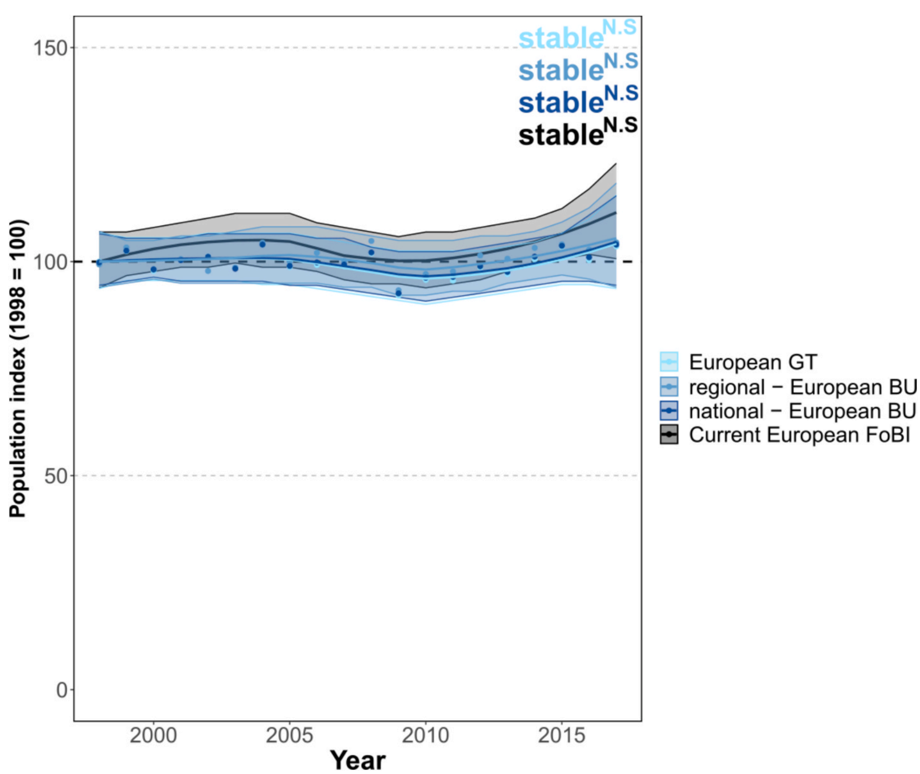

Fig. 4. Smoothed multi-species indices (MSIs), with shaded 95 % confidence intervals, for *European GT, regional – European BU, national – European BU* indicator sets and the current European Forest Bird Indicator (FoBI). Indices were set to 100 and their SEs to 0 in 1998. Description of the overall trend for each index, and significance of those trends, are provided in the upper right corner; N.S. = not significant.

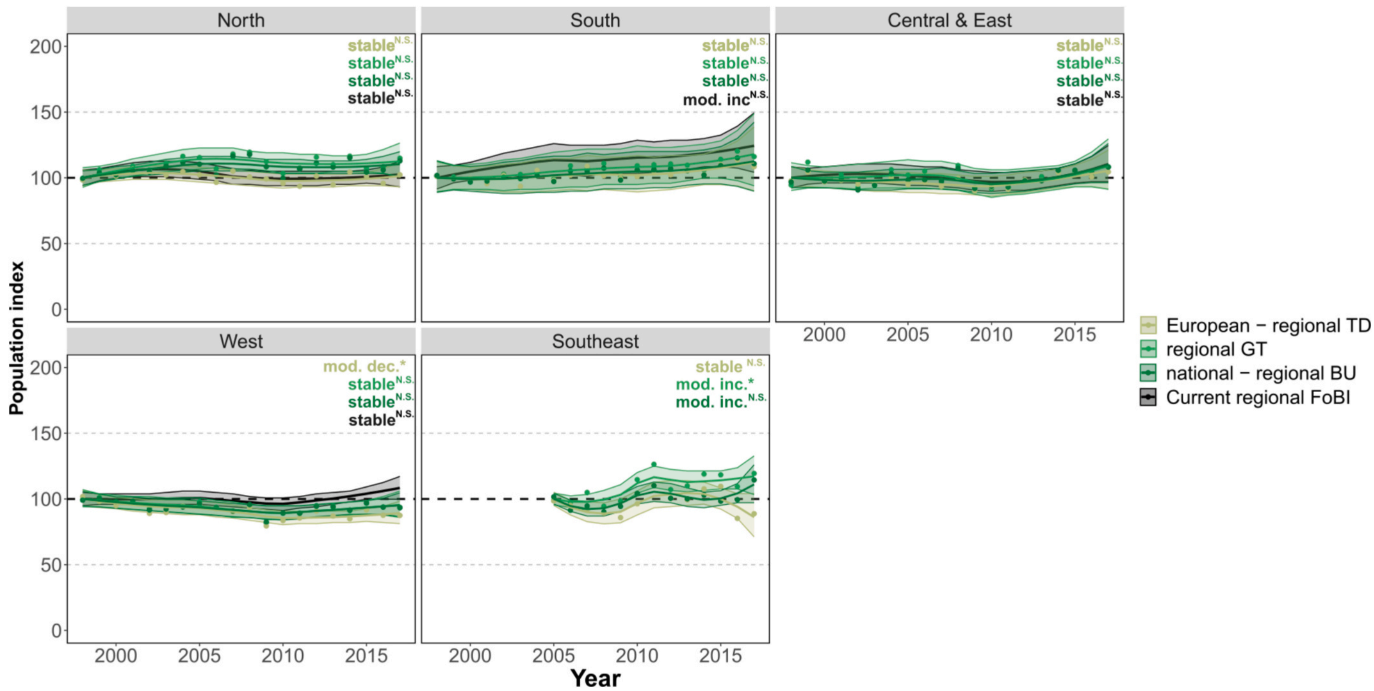

Fig. 5. Smoothed multi-species indices (MSIs), with shaded 95 % confidence intervals, for *regional GT,* European – *regional TD*, national – *regional BU* indicator sets and current regional Forest Bird Indicators (FoBIs) (where available). The *national GT* indicator set from Germany contributed to the *national – regional BU* indicator sets for both Central & East and West regions. Indices were set to 100 and their SEs to 0 in 1998 for North, South, Central & East and West, and in 2005 for Southeast. Description of the overall trend for each index, and significance of those trends, are provided in the upper right corner; * = $p < 0.05$, N.S. = not significant.

of the target community and potentially more responsive to future changes in resource availability.

In general, TD niche-based indicators are composed of less specialised species and cover the same, if not fewer, scale-dependent resources compared to GT indicators. Whilst TD indicators may provide a broad overview of forest bird community health, results suggest that they may be less sensitive than GT indicators to spatial variation in forest bird community dynamics driven by, for example, landscape level characteristics such as forest cover, composition and configuration (Balestrieri et al., 2015; Basile et al., 2021; Hofmeister et al., 2017) or to conservation and management policies and actions that are often applied at local or national scales (Jones et al., 2023). Additionally, BU indicators cover all scale-dependent resources but contain less sensitive species than GT indicators, suggesting that the latter may be more sensitive to changes in availability of those resources. In the North and Southeast regions, BU indicators covered fewer scale-dependent resources than the corresponding GT indicators. *National GT* indicators for countries within these two regions cover fewer resources than the equivalent *regional GT* indicators because some species which cover resources at the regional level are not present at the national level for any constituent countries as they do not meet the site threshold for RHU calculation at the smaller scale. As these species are not in the *national GT* indicators, they do not appear in the composite candidate species pool from which the *national – regional BU* indicators are derived. These species do however meet the site threshold for *regional GT* indicators because count data are combined across countries. Therefore, resources they use will be covered in the *regional GT* indicator but will not be covered in the *national – regional BU* indicator.

Despite the variation in species composition between indicator sets, MSIs for a given spatial scale were generally similar over the time frame of this study, regardless of whether a GT, TD or BU approach to species selection was used. This reflects the standardised selection process that ensures they reflect the status of the same broad resources within forest habitats. Our study also coincides with a period of relative stability in European forest bird populations (Gregory et al., 2019), which may also have limited our ability to detect differences between trends. Additionally, regional and European MSI trends were generally more stable than national MSI trends as underlying species' trends are estimated over a larger area and they tend to include more species, reducing the potential influence of more localised, national variations in individual species' populations. It is important to note here that MSI trends for *national GT*, *regional – national TD* and *European – national TD* indicator sets reported here may differ from the trends for existing national FoBIs reported elsewhere (*e.g.,* Husby and Kålås, 2011; Eaton and Noble, 2023; CBS, PBL, RIVM, WUR, 2024; Lehikoinen et al., 2024). As discussed above, existing national FoBIs have been developed to reflect specific policy and conservation needs, as well as local data availability and species' habitat use. For example, they may include species and/or data that are not included in the PECBMS database. In contrast, the indicator sets presented here were developed to assess the implications of using a GT, TD or BU approach to derive indicator sets when applying a standardised, niche-based species selection method across countries and regions to facilitate indicator comparison and benchmarking. Moreover, we focus specifically on the most sensitive species set identified. This means that some forest species in the candidate pools were subsequently not selected for inclusion because more sensitive species already covered the resource types that those species also used. Increasing indicator set size beyond this most sensitive set would result in the inclusion of these species (see Appendix B). We acknowledge that there will be a trade-off between accommodating national level nuance and standardisation across countries when producing indicators and emphasise that it is both appropriate and logical for indicators using expert-based and objective-based species selection methods to exist side-by-side.

47 % of species in the current European FoBI do not occur in any of the European indicators developed here, and 52 % to 56 % of species in the current regional FoBIs do not occur in the corresponding regional niche-based indicators. Our species selection algorithm identifies the combination of species with the lowest average sensitivity whilst providing full resource coverage as the optimal set. This means that

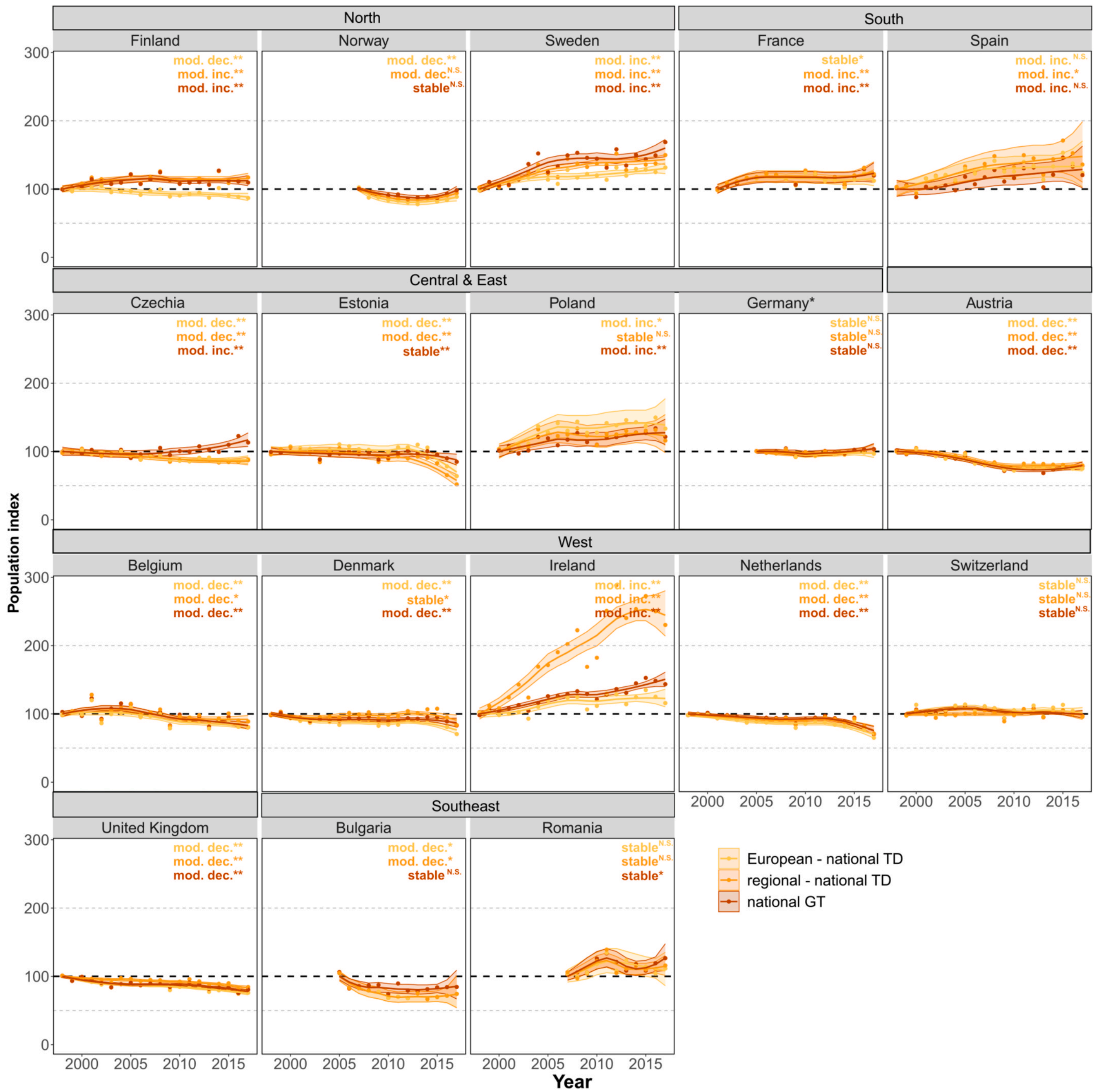

Fig. 6. Smoothed multi-species indices (MSIs), with shaded 95 % confidence intervals, for *national GT*, European – *national TD*, and *regional* – *national TD* indicator sets. The *regional* – *national TD* indicator set for Germany was derived from the aggregated indicator sets for the Central & East and West regions. The indicators for Belgium only represent the south (Wallonia) as data were not available for northern Belgium. Indices were set to 100 and their SEs to 0 in the first year where data were available for each given country. Description of the overall trend for each index, and significance of those trends, are provided in the upper right corner; * = $p < 0.05$, ** = $p < 0.01$, N.S. = not significant. Note: national trends may differ from existing published national FoBIs produced by the countries themselves due to differences in indicator species selection methods employed.

some forest species in the candidate species pools are not selected for inclusion in the indicator sets presented because a more sensitive species already covers the resources that species also uses. If we selected an indicator which contained more species than this, whilst still providing full resource coverage, it would likely include more species which are found in the current European and regional FoBIs but could also produce a less sensitive indicator (Wade et al., 2014); any additional species would negatively impact the overall average sensitivity of the selected indicator. Despite differences in species composition, MSIs for niche-based indicators at the European and regional levels generally do not differ significantly from the corresponding current FoBIs. Although the species selection methods of the current indicators and the niche-based indicators differ, both reflect the same underlying environmental changes in European forests, and it is to be expected that trends should be broadly comparable. However, the standardised framework embedded within our objective, niche-based approach delivers indicators which can be more readily compared as they rely on the same definition of forest (see below) and underlying resource requirements matrix; that is not the case at the moment.

Indicators should be designed to reflect their specific purpose, and the patterns they reveal must be interpreted within this context (Failing and Gregory, 2003; Heink and Kowarik, 2010). The niche-based indicators developed here reflect changes in the range of habitats included in our broad definition for forest (*i.e.,* deciduous and/or coniferous forests and woodlands, canopy closure of at least 30 %, with young plantations and agro-forestry included), because the resource requirements matrix and calculations of RHU are based on this definition. The RHU and niche-based approach can however be adapted to represent forest habitat subsets, or indeed any other habitat, and the specific human pressures they face. For example, increased anthropogenic activity in European forests has led to an interest in monitoring species associated with large tracts of forest and old-growth forest (Ćosović et al., 2020). If the habitat data and resource information are available, the RHU and niche-based approach can be adapted to explore indicator development for these habitat types. This could lead to different sets of indicator species which more accurately represent these specific forest habitats. To demonstrate how indicator species sets can change depending on the specific forest habitat it is representing, we produced *national GT*, *regional GT* and *European GT* indicators that did not include forest edge or early-growth forest specialists and/or were produced using increasingly conservative definitions of forest habitat (Figs. A.2 and A.3). This allowed us to i) determine which species persisted in the indicators if stricter definitions of forest habitat existed and ii) compare MSI trends across indicators using different definitions for forest habitat. Although species composition again varied between indicators, MSIs for a given spatial scale remained broadly similar (Figs. A.4–A.6). It should also be noted that these additional analyses found that when a more conservative definition of forest habitat is used, some countries do not currently have enough data to produce indicators. This is due to spatial variation in the forest cover of surveyed sites across Europe. If we are to succeed in setting a benchmark against which indicators can be compared spatially and we want to target more specific definitions of forest habitat, we need to be aware of both spatial differences in forest cover and the distribution of survey sites across all countries. Some countries will have few survey sites with >50 % forest cover included in their current monitoring schemes. This reduces the number of countries which we can produce indicators for, thereby reducing the comparability across spatial scales. If monitoring schemes were to survey more sites where forest cover was greater, this would reduce those spatial differences across countries, thereby making it more plausible that spatially comparable indicators could be produced for larger tracts of forest, if that is the purpose of the indicator.

The need for robust, geographically-targeted, and comparable indicators extends beyond birds and the objective, niche-based framework reported here has the potential to be used to identify indicator sets across other taxa. However, data availability would be an important consideration. Firstly, the resource requirements matrix will need to be adapted to accurately define the niche space occupied by the community of interest (*e.g.* Butler et al., 2009). Whilst thorough knowledge of species' ecology is needed to complete the resource requirements matrix, the resource categories included can be kept relatively coarse to facilitate populating it. The greater potential constraint to wider application of this approach lies in requiring species distribution and habitat data at the appropriate spatial resolution to quantify RHU. If sufficient data are not available, the time series and occupancy thresholds imposed here when calculating RHU could be relaxed but the implications for the reliability of RHU estimates would need to be recognised. Alternatively, expert opinion could be used to define the extent of species' habitat reliance (Wade et al., 2014), with the caveat that this would reintroduce an element of subjectivity to the indicator species selection process (O'Reilly et al., 2022).

5 Conclusion

Although GT, TD and BU indicators for a given spatial scale generally show similar temporal trends, "geographically-targeted" indicators cover more scale-dependent resources and have a more specialised suite of species compared to "top-down" or "bottom-up" indicators. The species composition of GT indicator sets varies by country and region, yet each set represents the same resource matrix and therefore the same stressors on forest ecosystems, allowing indicators to be compared over space and time. Adopting a standardised, objective indicator selection framework is of high importance on the European policy agenda to facilitate accurate monitoring of progress towards international, regional and national targets. Our study represents a step towards more effective indicator species selection methods and the basis for the development and adoption of spatially comparable biodiversity indicators.

CRediT authorship contribution statement

Enya O'Reilly: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Richard D. Gregory:** Writing – review & editing, Writing – original draft, Supervision. **Marc Anton:** Writing – review & editing, Data curation. **Lluís Brotons:** Writing – review & editing, Data curation. **Virginia Escandell:** Writing – review & editing, Data curation. **Anna Gamero:** Writing – review & editing, Data curation. **Sergi Herrando:** Data curation, Writing – review & editing. **Frédéric Jiguet:** Writing – review & editing, Data curation. **Johannes Kamp:** Writing – review & editing, Data curation. **Alena Klvaňová:** Writing – review & editing, Data curation. **Primož Kmecl:** Writing – review & editing, Data curation. **Ingar J. Øien:** Writing – review & editing, Data curation. **Jean-Yves Paquet:** Writing – review & editing, Data curation. **Jiří Reif:** Writing – review & editing, Data curation. **Eva Šilarová:** Writing – original draft, Data curation. **Bård G. Stokke:** Writing – review & editing, Data curation. **Nicolas Strebel:** Writing – review & editing, Data curation. **Norbert Teufelbauer:** Writing – review & editing, Data curation. **Sven Trautmann:** Writing – review & editing, Data curation. **Thomas Vikstrøm:** Writing – review & editing, Data curation. **Petr Voříšek:** Writing – review & editing, Data curation. **Simon J. Butler:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2025.113327.

Data availability

The authors do not have permission to share data.

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