Evaluating the effectiveness of European protected areas on preserving the diversity and connectivity of bat populations

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Todas as correções determinadas pelo júri, e só essas, foram efetuadas.

O Presidente do Júri,

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Abstract

Habitat fragmentation, climate change and other anthropogenic stressors are leading the world to its 6th mass extinction event. Species range and connectivity between populations plays a key role to mitigate climatic change impacts on species. To tackle biodiversity loss, European Union created a protected areas network based on ecological coherence while covering the unique habitats and ecological values of the European space. Among the several taxa under legal protection status, bats are one of Europe’s most endangered mammal group while also possessing a high taxonomic and ecological diversity. One of the most widespread tool of conservation management has been the creation and maintenance of protected areas (PA) for biodiversity. Nevertheless, continental wide evaluation of PA´s effectiveness protecting chiroptera diversity and connectivity is missing. In this study the main aims were to determine the spatial patterns of European bat diversity and evaluate the coverage of PAs over diversity hotspots. In parallel, a connectivity analyses will be carried to identify which European regions are most relevant for the maintenance of connectivity and also evaluate the PA coverage of those areas. To access species and connectivity diversity in Europe, species distribution models (SDM) and connectivity analyses were performed. In addition, gap analyses were performed to evaluate PA´s effectiveness in covering bat diversity and relevant areas for connectivity maintenance.

From all European bat species, 26 species have been selected because they were considered suitable for analyses. Bat presence data was obtained through online databases and collaborators. SDM´s have been used to assess each bat species potential distribution over Europe, calculated in MaxEnt software. For that purpose, it was selected a set of climatic variables acknowledged to influence bat distribution. In parallel, connectivity analyses were performed in Conefor software to spatially determine which European regions are contributing most to the maintenance of bat’s ecological connectivity. Conefor measures the total connectivity through three metrics: intra, flux and connector. Intra (patch) connectivity is a measure of intrinsic patch connectivity, thus identifying which patches possess larger suitability for each species. Flux connectivity relies on patch intrinsic importance translated into number of links to other patches – the importance increases with the number of links. Finally, connector connectivity is a measure of patch importance considering the maintenance of overall connectivity and depends on the number of patches that become isolated with each

other. Patch importance is measured through the removal of that patch from analysis and measuring the change on overall connectivity prior to removal. To represent potential pathways of connectivity it was calculated a connectivity surface over which all Conefor calculations were made. A number of linear features, like rivers/streams or mountain summits together with the amount of available suitable habitat are acknowledged to promote the movement of bats. Therefore, distance to river/stream and distance to high slope were calculated for the European space and integrated into the connectivity surface.

SDM results identified high species diversity areas in north of Iberian Peninsula, southern part of central Europe and central part of Italian peninsula. On the other hand, low diversity areas were identified in northern Europe and in northern Italy. Intra connectivity main hotspots were found in the north of the Iberian Peninsula and central Europe. Intra diversity in central Italian peninsula and United Kingdom were also relevant. Flux connectivity showed higher diversity in northern Iberian Peninsula and central Europe. On other hand, lower diversity flux areas occur mainly in northern and eastern Europe as well as in smaller islands. Only two areas have shown high diversity in connector connectivity. These areas are the central northern part of Iberian Peninsula and the Alps area in southern central Europe. Gap analyses results suggests low effectiveness on species diversity protection. Furthermore, gap results showed an increase on the coverage of PAs on all connectivity metrics, though overall percentage cover is still low.

The outcomes emphasize the importance of current PA´s range expansion to protect high species and connectivity diversity areas. Bat diversity hotspots were identified on the southern European peninsulas which is in line with current knowledge. Yet, gap analyses indicated that PA coverage was low over Europe and on those areas in particular. Regarding the ecological connectivity of European bat populations, PA coverage of most relevant areas for connectivity maintenance was lower than the coverage of bats’ hotspots. Results also indicated that the central northern part of Iberian Peninsula and the Alps were the most relevant areas for the maintenance of ecological connectivity – a likely consequence of the overlap between bat diversity hotspots and areas of fragmented distribution. Overall, this study has identified flaws on PA coverage of bat populations while also drawing attention to the need of also considering the connectivity of those areas to the PA design. Through the employment of new technological and methodological tools it may be possible to identify areas for conservation action while also considering its sustainability for the whole species range.

Resumo

A fragmentação de habitats, as alterações climáticas e outros fatores antropogénicos estão a levar o mundo a 6ª extinção em massa. A área de distribuição duma espécie bem como a conectividade entre as populações desta, têm um papel fundamental na mitigação do impacto das alterações climáticas. Para fazer face a redução da biodiversidade, foi criada pela união europeia uma rede de áreas protegidas suportadas em coerência ecológica, cobrindo valores e habitats únicos do espaço europeu. Entre os diversos taxa sob estatuto de proteção legal, os morcegos são dos mamíferos mais ameaçados na Europa, apesar de possuírem elevada diversidade ecológica e taxonómica. Uma das ferramentas mais difundidas para a proteção da biodiversidade é a criação e gestão de áreas protegidas (AP´s). No entanto, está em falta uma avaliação continental da eficácia das AP´s na protecção da diversidade e conectividade de chiropteros. Entre os principiais alvos deste estudo encontra-se a determinação dos padrões espaciais da diversidade de quirópteros, bem como a avaliação da cobertura, pelas AP´s, das zonas de elevada diversidade. Em paralelo, foram realizadas análises de conectividade, de modo a identificar as áreas mais relevantes para a manutenção da conectividade, bem como avaliar a cobertura destas áreas pelas AP´s. Para a determinação da diversidade e conectividade na Europa, foram realizados modelos de distribuição de espécies (MDE) bem como análises de conectividade. Além disso, análises de sobreposição foram feitas, de modo a determinar a eficácia das AP´s na cobertura das áreas mais relevantes na diversidade e manutenção de conectividade.

Entre todas as espécies europeias, foram selecionadas 26 espécies que eram passiveis de análise. Os dados de presença de morcegos foram obtidos a partir de bases de dados online bem como a partir de colaboradores. MDE´s foram usados de modo a encontrar a distribuição potencial na Europa de cada espécie de morcego. Estes modelos foram calculados no programa MaxEnt. Para isso, selecionei um grupo de variáveis climáticas conhecidas por influenciar a distribuição de morcegos. Ao mesmo tempo, foram realizadas análises de conectividade no programa Conefor, de forma a determinar as regiões europeias que mais contribuem para a manutenção da conectividade ecológica dos morcegos. O Conefor mede a conectividade total através de três métricas: Intra, Flux e Connector. A conectividade Intra (patch) é uma medida

da conectividade intrínseca do fragmento, identificando que fragmentos possuem maior adequabilidade para cada espécie. A conectividade flux provem da conectividade intrínseca traduzida no numero de ligações com outros fragmentos ou seja a importância aumenta com o número de ligações. Por fim, a conectividade connector é uma medida da importância do fragmento para a manutenção da conectividade geral, e provêm da quantidade de fragmentos que ficam isolados entre si. A importância do fragmento em análise é obtida através da remoção do fragmento e da determinação da alteração da conectividade geral, em relação à conectividade antes da remoção deste. Para representar os possíveis corredores de conectividade, calculei uma superfície de conectividade, sob a qual todas as análises do Conefor foram realizadas. Algumas estruturas lineares, tais como rios/cursos de agua ou cumes montanhosos, em conjunto com a quantidade de habitat adequado disponível são conhecidas por promoverem a movimentação de morcegos. Assim sendo, as distâncias aos rios/cursos de água e áreas de declive acentuado foram calculadas para o espaço europeu, e integradas na superfície de conectividade.

Os resultados dos MDE´s identificaram áreas de elevada diversidade no Norte da Península Ibérica, parte Sul da Europa Central e na parte Central da Península itálica. Por outro lado, áreas de baixa diversidade foram identificadas no Norte da Europa e Norte de Itália. As zonas de elevada conectividade intra foram encontrados no Norte da Península Ibérica e na Europa Central. A diversidade da conectividade Intra é também alta na área Central da Península Itálica e no Reino Unido. A conectividade flux é mais elevada no Norte da Península Ibérica bem como na Europa Central. Por outro lado, zonas de baixa diversidade de flux ocorrem principalmente no Norte da Europa e na Europa Oriental, bem como em pequenas ilhas. Apenas duas áreas demonstram elevada conectividade connector. Essas áreas foram a parte Central do Norte da Península Ibérica bem como a região dos Alpes, no Sul da Europa Central. As análises de cobertura sugerem uma baixa eficácia das áreas protegidas na proteção da diversidade de espécies. Por outro lado, as análises de cobertura mostram um incremento na cobertura de AP´s em todas as métricas de conectividade, apesar de a percentagem de cobertura total continuar a ser baixo.

Os resultados enfatizam a importância da expansão da cobertura das AP´s de forma a proteger áreas de elevada diversidade de espécie e de conectividade. Zonas de alta de diversidade de morcegos foram identificados nas penínsulas do Sul da Europa, o que está de acordo com o conhecimento atual. No entanto, as análises de sobreposição indicam baixa cobertura das AP´s na Europa em geral, e nessas áreas em particular. Em relação a conectividade ecológica das populações europeias de morcegos, a cobertura destas pelas AP´s foi maior que a cobertura da alta diversidade de espécies, no entanto os valores de cobertura continuam baixos. Os resultados também indicaram que a parte Central do Norte da Península Ibérica e os Alpes eram as zonas mais relevantes para a manutenção da conectividade – uma provável consequência da sobreposição de áreas de elevada diversidade com áreas de distribuição fragmentada. No geral, este estudo identificou falhas na cobertura das populações de morcegos pelas AP´s, enquanto também chamou a atenção para a necessidade de ser considerada a conectividade dessas áreas para o desenho das AP´s. Através do uso de novas ferramentas tecnológicas e metodológicas, talvez possa ser possível a identificação de áreas para ações de conservação, em que seja considerado também a sua sustentabilidade para toda a distribuição da espécie.

Keywords

Bats, Ecological connectivity, GAP analyses, Species Distribution Modelling, Conefor, MaxEnt, Europe, Conservation, Protected areas, Natura 2000

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Abbreviations and Acronyms

Area protegida- AP

Area Under Curve- AUC

Bio1- Annual Mean Temperature

Bio3 -Isothermality

Bio5 -Max Temperature of Warmest Month

Bio7 -Temperature Annual Range

Bio12 -Annual Precipitation

Bio15 -Precipitation Seasonality

Digital elevation model- DEM

Ecogeographical Variables- EGV

International Union for the Conservation of Biodiversity- IUCN

Modelos de distribuição de espécies- MDE

Protected Area- PA

Receiving Operator Characteristic- ROC

Small sample corrected Akaike’s information criteria- AICc

Species Distribution Models- SDM

Introduction

A brief glimpse on the chiroptera world

First records of chiroptera species dates about 50 Million years ago (Simmons et al. 2008). Among all Mammalia class almost one quarter of the species belongs to chiroptera order (Jones et al. 2002). Bats can be further divided in two suborders Megachiroptera and Microchiroptera (Agnarsson et al. 2011). Microchiroptera are mostly insectivorous, with some exceptions, and use a tonal echolocation system to hunt (Freeman 2000, Denzinger and Schnitzler 2013). On the other hand, Megachiroptera are exclusively phytophagous (Almeida et al. 2011). Chiroptera species are present in all continents but Antarctica (Ruedi et al. 2013). In Europe only species of the subclass Microchiroptera are present (Mickleburgh et al. 1992). On Europe during the 20th century bat populations have severely declined (Walsh and Harris 1996). However, recent data suggests a possible increase on European bat populations though the rate is still very shallow to compensate decades of loss (Van der Meij et al. 2015, Barlow et al. 2015).

Microchiroptera species are small, with body mass usually under 10 grams (Barclay and Brigham 1991). The small size of bats strongly constrains the rate of respiration, wingbeat and the echolocation characteristics. Echolocation energy efficiency is a result of wingbeat cycle in which exhalated air is used to produce the sound pulse (Jones 1994). Nonetheless, due to body/mass relationship bats' flight have a high energy demand. Thus, chiroptera flight efficiency is lower than of birds. However, bats have a greater aerobatic ability (Hunter 2007). Bats flight ability evolved independently from other animals that fly (Shen et al. 2010). To cope with their energy requirements, bats need to have a high intake of preys. A single colony of 150 bats can consume almost a 1 million of arthropod per year (Whitaker 1995). Yet, bats are vulnerable to heat loss, due to their high surface area-volume ratio, and have low capacity to regulate body temperature (Hock 1951). Chiroptera activity is limited by temperature, insect availability and wind speed (Salvarina et al. 2018). Chiroptera can enter in a torpor state daily or seasonally in order to manage energy input shortages (Heldmaier et al. 2004). During the winter in temperate regions bats go into hibernation (Zubaid et al. 2006). In northern Europe the period of hibernation is longer than in southern latitudes due to colder temperatures deploying earlier and ending later (Rodrigues et al. 2003). Yet, a recent study showed that Natterer's bats (*Myotis* *nattereri*) hibernation in Europe is irregular with frequent arousals for feeding during winter, challenging the prevalent idea that hibernation is continuous (Hope et al. 2014).

Bat sexual maturity may be influenced by individual fitness. Spermiogenesis in bats peaks on the period of lower torpor time and leads to a decrease on individual body mass. In addition, spermiogenesis is delayed in unfitted adult males (Entwistle et al. 1998). Reproductive period usually began in autumn and ends on spring. However, in winter reproductive cycle is on hold, with two main patterns occurring in hibernating bats. In the first one, after the copulation sperm is stored in female reproductive tract and the cycle holds until spring. The second one, reproduction holds in a advanced stage, after the initial embryogenesis the process stops and hold until spring (Oxberry 1979). Usually bats are monotocous, and produces low number of descents per year (Crichton and Krutzsch 2000).

Chiroptera provide a useful ecosystem service of pest suppression (Stahlschmidt and Brühl 2012). Ecosystem services can give a contribution to overcome agricultural loses. Kalka (2008) has shown that bats have higher impact than birds in insects' populations suppression and therefore contribute to limit insect herbivory. In addition, Kunz (2011) stated that bats are effective controlling insect populations, among them agricultural pests. In corn plantations bats were shown to provide effective insect herbivory suppression while also promoting indirect fungal and mycotoxin control (Maine and Boyles 2015). Therefore, pest suppression effects may not only concern on direct prey consumption but also by prey avoidance and can cause an underestimation on bats economic value (Russo et al. 2018). Agricultural pest suppression services are estimated over billions of dollars (Boyles et al. 2011, Puig-Montserrat et al. 2015, Taylor et al. 2018).

Notwithstanding, many species of bats are endangered. Urban expansion and agricultural intensification can threat bats, mainly because roost and foraging areas destruction (Park 2015, Russo and Ancillotto 2015). In addition, recent expansion of wind farms increased bat mortality (Rydell et al. 2010) while also, pesticide applications can increase bat mortality asynchronous from pesticide applications. Kunz (1977) published a study where mortality only peaked two years after the pesticide application. In parallel, the white-nose syndrome epidemics merged in 2006. This disease is a fungal infection provoking mass death in North American bat colonies (Turner et al. 2011). However, although the fungus is present in European colonies, European chiroptera seem to show resistance to the fungus (Puechmaille et al. 2011).

Chiroptera may also be used has bioindicators, since they are taxonomic stable, have a wide distribution and their populations trends can be easily monitored. Because insectivorous bats are also top predators, they are expected to show a fast response to changes in prey abundance and pesticide or toxin accumulation (Jones et al. 2009). Moreover, a wide range of stressors affects bats, among them extreme climatic events (e.g., severe droughts and heat waves) and anthropogenic induced stressors such as intensification of agriculture, forest fragmentation and destruction, wind turbines fatalities, bushmeat and abusive pesticide use (Jones et al. 2009). Possible usefulness of bats as bioindicators of riverine ecosystem quality and of agricultural changes has already been proposed (Wickramasinghe et al. 2003, De Conno et al. 2018). Nonetheless, lack of studies at wider scales and deficit on information regarding chiroptera response to environmental changes and relationship with other taxas response are needed (Park 2015).

Biodiversity crisis, Protected areas, Diversity and Connectivity

Nowadays planet Earth is facing a biodiversity crisis, associated to an ongoing mass extinction event (Barnosky et al. 2011, Ceballos et al. 2015). Extinction rate is higher than expected taking into account previous mass extinctions events (Barnosky et al. 2011). Nowadays we are now what is considered by many as the 6th mass extinction event in planetary history. What is striking is that such events may occur in a small time scales considering what has happened in the other mass extinction events (Singh 2002, Barnosky et al. 2011, Toukhsati 2018). Yet, it is expected that by 2050 at least 18% of species may become extinct due to anthropogenic causes, though this value can increase even if climatic warming exceeds predictions of the minimal warming scenario, reaching up to 35% of losses (Cahill et al. 2012). In some regions, extinction rates may even exceed 50% (Thomas et al. 2004). In fact, some currently not threatened taxa may alter its conservation status due to predicted extremely high rate of population loss (Ceballos et al. 2017). Extinctions can occur by both natural or anthropogenic drivers, or an interaction of both (Milberg and Tyrberg 1993, Fox 2013, Harper et al. 2014). Despite human induced climatic change, other anthropogenic induced factors contributes to strongly contribute to increase the extinction threat of species: habitat loss and fragmentation, overexploitation of biological resources, pollution and alien species invasion (Cahill et al. 2012, Toukhsati 2018, Yuan et al. 2018). Biodiversity loss has an impact over mankind wellbeing (Díaz et al. 2006) through direct welfare loses, for example, by destruction of natural resources or indirect impacts by loss of ecosystem services(Yuan et al. 2018).

Since 19th century, international community has been taken measures, to manage environmental problems and challenges (Schofer and Hironaka 2005, Holder and Lee 2007).Early agreements have been primarily focused in the protection of shared living resources, such as birds or fishes (Iriye and Saunier 2016). Some of the earlier ecological approaches were developed in the 1930s, with measures to protect Africa wild fauna and flora and the establishment of the first reserves to protect animals and plants in the western hemisphere. In recent years, several political measures to decrease biodiversity loss and preserve natural resources have been proposed. The bases for these agreements have emerged in the Stockholm conference of 1972 (Weiss 2011). Despite adopted measures as a result of the Stockholm conference, environmental degradation has not stopped or diminished. A more holistic, in global level, approach begins to be adopted in Rio conference in 1992. “As result of Rio conference, a convention on biological diversity was adopted in order to preserve biological diversity, (Kiss and Shelton 2007). Additionally, to the international treaties, several regional agreements to preserve local biodiversity, have been taken. Examples of those agreements are the birds directive, habitats directive or the regulation on invasive species promoted by the European union (Holder and Lee 2007). Examples of regional agreements include national or local legislation to promote biological preservation, species action plans and local protected areas (Queirós 2001, Papageorgiou and Vogiatzakis 2006). In summary, legal instruments that aim natural protection can emanate from a variety of sources from global agreements to national or local legislation.

Among the most successful tools, created by legal means, to tackle biodiversity losses are the protected areas. This success is achieved due to the management of areas for biodiversity conservation assisted by the surveillance provided by legal authorities and supported by a legal framework (Leverington et al. 2010). Historically, many protected areas have not been designed aiming specific biodiversity conservation objectives, but instead to cultural or scenic motives like holiday destinations or hunting reserves. In terms of nature management, a number of those areas are designed towards a few flagship and umbrella species, not necessarily guarantying the conservation of regional biota (Andelman and Fagan 2000). In turn, these areas prioritized mainly the protection of extreme habitats (eg. High mountains, rocky infertile soils) (Possingham et al. 2000). On the other hand, flat fertile soils are rarely conserved. To ensure biodiversity protection, European Union emanated a directive aiming the protection of habitats and wild fauna (European Council 1992). That directive created a legal instrument targeting the creation of a coherent ecological network of special conservation areas, designed as NATURA 2000. The selection of sites to include in Natura 2000 network have been based in several principles: degree of isolation, habitat quality, representativeness of protected species and habitats as also as their density and size (Dimitrakopoulos et al. 2004).

Yet, a number of relevant ecological functions essential for populations sustainability remain disregarded like the lack of protection of populations' connectivity between protected areas (Gurrutxaga et al. 2011, Saura et al. 2018, Schoville et al. 2018). Ecological connectivity (or functional connectivity) is defined, by Taylor (1993) has "the degree to which landscapes actually facilitate or impede the movement of organisms and processes". Connectivity plays a key role in species viability, wherein highly connected landscapes have greater populations size and genetic variability (Bender et al. 1998, Leffler et al. 2012). Low genetic diversity, provoked by endogamy as result of small population size, causes inbreeding depression that can lead to local species extinction (Frankham et al. 2014). . Connectivity also allows movement of the species in response to environmental disturbances or climatic changes (McRae et al. 2012). Frey-Ehrenbold (2013) has shown that several bat species have their activity increased in well-connected landscapes. Furthermore, fragmentation can lead up to 75% reduction in biodiversity, with losses higher in smaller and most isolated patches, which highlight the importance of connectivity to maintain species diversity(Haddad et al. 2015). To tackle biodiversity loss two main strategies were proposed: expand PA´s and increase connectivity between them (Heller and Zavaleta 2009).

Connectivity can be measured by a wide range of methods that may be based on direct/individual, genetic or biogeochemical observations (Moilanen and Nieminen 2002, Luque et al. 2012). The direct approaches to measure connectivity include morphological analyses, individual marking or biologging (Jacobson and Peres-Neto 2010, McKinnon and Love 2018). The genetic methods require population specific genetic markers to identify which populations are connected as assessed by the measurement of gene flow levels between populations (Razgour et al. 2013). Alternatively, biogeochemical methods rely their analyses in the geographical variance of natural stable isotopes (Webster et al. 2002). Connectivity can also be accessed by simple ecological analyses of the spatial patterns of habitat or resources requirements of targeted species (Moilanen and Nieminen 2002).

In this study I aimed to evaluate the coverage of European protected areas (PA) for bat populations. During the 20th century several European bat species had their distribution and population size contracted (Walsh and Harris 1996). Climate has a major impact in bat ecology by influencing biogeography, access to food and water resources, hibernation, development and reproduction, rate of energy expenditure and duration and frequency of the torpor. The most affected Chiroptera species are associated to small range size, restricted to regions that may become water stressed, and species with limited dispersal (Sherwin et al. 2013). Ecosystem equilibrium rest on prey-predator balanced interactions and changes in this balance can lead to ecosystemic degradation with negative consequences to the environment and human activities, such as agriculture. Bats can also be used has bioindicators, since they are taxonomic stable, have a wide distribution and their populations trends can be easily monitored. Because insectivorous bats are also top predators, they are expected to show a fast response to changes in prey abundance and pesticide or toxin accumulation (Jones et al. 2009). Moreover, a wide range of stressors affect bats, among them extreme climatic events (e.g., severe droughts and heat waves) and anthropogenic induced stressors such as intensification of agriculture, forest fragmentation and destruction, wind turbines fatalities, bushmeat and abusive pesticide use (Jones et al. 2009). These threat factors can be further exacerbated when interacting with each other, resulting in population decreases, contractions and eventually population isolation from the species' core distribution.

Bats are among the most threatened mammals of Europe and consequently all of their species suffer from some level of legal protection (Battersby 2010). In parallel, a number of European PAs include bats as one their conservation priorities (e.g., Parque Natural da Serra d'Aire e Candeeiros). The effectiveness of PAs for bat conservation has seldom been discussed but some studies report that Natura 2000 network may be providing insufficient coverage to protect bat populations (Lisón et al. 2013). Yet, connectivity is rarely considered in the analyses of PAs coverage, especially at larger scales. In here, I propose to determine the spatial patterns of European bat diversity and evaluate the coverage of PAs over the diversity hotspots. In parallel, a connectivity analyses will be carried to identify which European regions are most relevant for the maintenance of connectivity and also evaluate the PA coverage of those areas. Specifically, I aim to tackle the following objectives:

1) Are European protected areas covering areas with high bat species richness?

2) Which European areas are most relevant for the connectivity of bat populations?

3) What areas are in need of protection to cover connectivity areas for bats?

Material and methods

Study area

Study area comprised mainland of Western and Central European countries. These included the following countries: Portugal, Spain, France, Andorra, Monaco, Switzerland, Italy, Luxemburg, Belgium, Germany, Netherlands and United Kingdom (2,478,238 km2). Latitudes higher than 60ºN, due the lack of bat fauna, as also as digital elevation model data limitation, are not included (Rabus et al. 2003). Due to the lack of spatial coverage of bat occurrence data in the free online databases, I opted to exclude all countries east of Germany and Austria in the distribution models. The inclusion of these countries would likely produce severe model's underpredictions, especially for eastern Europe (Vale et al. 2014).

Species data

To obtain the European chiroptera species list, a query in International Union for Conservation of Nature (IUCN) website (https://www.iucn.org) was performed. As a result, 46 species were found. Then species were selected following two criteria: their distribution had to be mostly European (this excludes species with marginal distribution in Europe), endemic species with small distribution range are not included (this excludes island endemic species). Endemic species are associated to narrow and restricted distributions, therefore large-scale connectivity analyses would produce non-significant results (Stockwell and Peterson 2002).

Criteria application excluded 19 species, resulting in a total of 26 study species. The species included in this study were: *Barbatella barbastellus, Eptesicus isabellinus, Eptesicus nilssonii, Eptesicus serotinus, Hypsugo savii, Miniopterus schreibersii, Myotis bechsteinii, Myotis brandtii, Myotis capaccinii, Myotis dasycneme, Myotis daubentonii, Myotis emarginatus, Myotis myotis, Myotis mystacinus, Nyctalus leisleri, Nyctalus noctula, Pipistrellus kuhlii, Pipistrellus nathusii, Pipistrellus pipistrellus, Plecotus austriacus, Rhinolophus Euryale, Rhinolophus ferrumequinum, Rhinolophus hipposideros, Rhinolophus mehelyi, Tadarida teniotis* and *Vespertilio murinus.* Presence data for all species were obtained from Global Biodiversity Information

Facility (https://www.gbif.org)database, personal data and from collaborators. Species occurrence was checked for errors, taxonomic inconsistencies and unreliable data (data distant from real known distribution) was deleted.

In order to remove environmental biased occurrence data, spatial autocorrelation (SAC) was analysed prior to spatial analyses by SDMtoolbox 2.0 (Brown 2017). Spatial biased data filtering improves model quality in uneven sampled data (Kramer-Schadt et al. 2013). This tool removes presence points within a certain Euclidian distance from each other's. This distance depends on climatic heterogeneity matrix that is calculated considering the local environmental variables (e.g., climatic variables) rate of change.

Environmental data

To represent predictors related to bat occurrence three classes of ecogeographical variables were used. Bioclimatic variables were associated with species physiology and energy demands, as also as water availability (Racey et al. 1987, Webb et al. 1995, Adams and Hayes 2008, Frick et al. 2010). Land use and distance to habitat classes were related to potential foraging areas and roosts for tree-dwelling bats (Russo and Jones 2003, Russo et al. 2005). Finally, topographic variables are linked with the presence of roosts to crevice and cave-dwelling bats (Jaberg and Guisan 2001, Georgiakakis et al. 2010, Rainho and Palmeirim 2011).

Bioclimatic variables were obtained in Worldclim website (http://www.worldclim.org ; Fick and Hijmans 2017) with a 30 arcseconds resolution. Treecover has been downloaded from Copernicus website (http://www.copernicus.eu ; Copernicus Land Monitoring service 2015) with a 20 meters resolution. Land use were downloaded from United States Geographical Survey website (https://www.usgs.gov) with 1 kilometer resolution, and then reclassified, following criteria presented in table 1. Digital elevation model (DEM) were obtained from Shuttle Radar Topography Mission (https://www.usgs.gov) with 1 arcsecond resolution. Northness, eastness slope, broadleaf distance, coniferous distance, crops distance, shrubs distance and urban distance were calculated in ArcGis 10.2.2 (Environmental Systems Research Institute 2011). The final layers and data have been resampled to five kilometers resolution.

Enviromental variables were checked for covariance and multicollinearity in R 3.4.3 (R Core Team 2013) by packages raster (Hijmans and van Etten 2014) and usdm (Naimi 2015). The selection of variables within a group of correlated variables was done considering their ecological relevance for bats and their distribution (Ulrich et al. 2007). As a result, the following ecogeographical variables (EGV´s) have been used as model variables: Bio1, Bio3, Bio5, Bio7, Bio12, Bio15, northness, eastness, slope, broadleaf distance, coniferous distance, crops distance, shrubs distance and urban distance, DEM, land use and tree cover (see table 2).

Table 1- Land Use Reclassification

Original classification	**New classification**
Evergreen Needleleaf Forest	Coniferous
Evergreen Broadleaf Forest	Broadleaf
Deciduous Needleleaf Forest	Coniferous
Deciduous Broadleaf Forest	Broadleaf
Mixed Forest	Broadleaf
Closed Shrublands	Shrubland
Open Shrublands	Shrubland
Woody Savannas	Broadleaf
Savannas	Broadleaf
Grasslands	Shrubland
Permanent Wetlands	Wetlands
Croplands	Croplands
Urban and Built-Up	Urban
Cropland/Natural Vegetation Mosaic	Broadleaf
Snow and Ice	Bareground
Barren or Sparsely Vegetated	Bareground
Water Bodies	Water

Table 2- Description of EGV´s and their acronyms

Code	Type	Description
Bio1	Climatic	Annual Mean Temperature
Bio3	Climatic	Isothermality
Bio5	Climatic	Max Temperature of Warmest Month
Bio7	Climatic	Temperature Annual Range
Bio12	Climatic	Annual Precipitation
Bio15	Climatic	Precipitation Seasonality
Northness	Topographical	Orientation declination relative to North
Eastness	Topographical	Orientation declination relative to East
DEM	Topographical	Surface elevation
Slope	Topographical	Surface inclination
Broadleaf distance	Habitat	Distance to broadleaf trees habitats
Coniferous distance	Habitat	Distance to coniferous trees habitats
Crops distance	Habitat	Distance to crops habitats
Shrubs distance	Habitat	Distance to shrubs habitats
Urban distance	Habitat	Distance to urban habitats
Land use	Habitat	Habitat type
Treecover	Habitat	Percentage of treecover

Protected areas data

Natura 2000 areas shapefiles were obtained in European Environment Agency website (https://www.eea.europa.eu/ ; European Environment Agency 2017) of which marine PA´s were excluded. Natura 2000 areas of special conservation interest were then selected and used for gap analyses to assess their coverage over bat diversity and connectivity hotspots. These areas have a total of 12126 sites and cover about 9,20% of total study area (225,302 km2).

Species distribution model

Species distribution models were performed with MaxEnt modeling software (Phillips et al. 2017). Maxent returns habitat suitability index indicating which areas have higher carrying capacity for a species (Elith et al. 2010). Also, MaxEnt achieved a good predictive performance when compared with other algorithms (Elith et al. 2006, Wisz et al. 2008). Bats have low detection probability due to their nocturnal and elusive behavior, together with several biases in species identification through ultrasounds detection (Ahlén and Baagoe 1999, Tillon et al. 2018). As a result of their low detectability, false absences are likely to occur in bat occurrence datasets. Therefore, presence-only algorithms like MaxEnt are the most adequate to avoid the inclusion of false absences in the models (Elith et al. 2010).

To evaluate model fitness, MaxEnt models were performed with regularization multipliers of 1,2, 4 and 6, and then best models were selected by small sample size corrected Akaike information criterion (AICc). AICc have been calculated in ENMTools 1.4.4 (Warren et al. 2010 ; http://enmtools.blogspot.com/). Regularization multipliers used for each species were selected according to AICc results (Akaike 1998, Murtaugh 2009). After, 20 cross-validated replicates were used to calculate the predictive performance of the final models. The cross-validation approach allows to use all data in turns to validate models. Cross-validation method splits the dataset into random equal sized subdatasets and use them to calculate replicates (Phillips 2008). Final model’s fitness was measured according to Area Under Curve (AUC) of receiving operating characteristics (ROC). Overprediction correction have been performed restraining model predictions to 100km buffer of minimum convex polygon from presence data.

Binary presence/absence maps were calculated using the Maximum training sensitivity plus specificity threshold, as recommend by Liu (2016). Afterwards, binary results were stacked to produce bat diversity hotspot maps.

Connectivity analyses

Resistance rasters were calculated using distances to slope higher than 5% and large rivers with a basin above 5000km2 (Navarra and Tubiana 2013, Santos et al. 2014, Skoulikidis et al. 2018). Resistance describes the degree of impedance to species movement exerted by landscape. High slope areas and rivers facilitates dispersal movement of bats (Russo and Jones 2003, Parmesan 2006, Roscioni et al. 2014). Consequently, the degree of resistance to the movement increase with the distance to this habitat features.

Distances to habitat features that facilitate dispersal have been normalized to integer values between 1 and 101. Habitat patches were obtained by binary presence raster polygonalisation. Intrinsic habitat value has been calculated by multiplying habitat area and average MaxEnt coglog value for the patch. Coglog value can be used as indicator of habitat suitability which is related to population size while patch size is related to number of individuals as also as migration probability (Elith et al. 2011, Mortelliti et al. 2014, Unglaub et al. 2018) – the product of both should be proportional to population size. Cost-weighted distances calculation where performed in ArcGis 10.2.2 using Linkagemapper 1.1.0 toolbox (McRae and Kavanagh 2011). Least-cost path showed better performance than distances because the former had a strongest correlation with true connectivity (Simpkins et al. 2018). The production of resistance distance layers requires a high computational power, making it non-viable for large study areas (Pelletier et al. 2014). Calabrese (2004) have suggested that graph based metrics have the best effort ratio to large landscape connectivity.

Connectivity analyses were performed in Conefor Sensinode 2.6 software (Saura and Torne 2009). This software bases their calculations in graph theory and returns individual patch importance to overall connectivity. To access connectivity between patches a probabilistic metric has been used. The distance to a 0.5 probability of connection depends on bat dispersal ecology (see table 3 for further details; Hutterer 2005). Overall connectivity can be divided into 3 metrics reflecting on different ways that a patch can be contribute to landscape connectivity. Intrapach connectivity is a measure of connectivity within the patch. It is calculated as the product of patch area and mean suitability as calculated by MaxEnt. This result should be a proxy of population size and indicates which patches contribute more to overall population size. Flux connectivity is the number of connections from analyzed patch to the other patches. This metric simply identifies which patches are more connected to others while weighing this results by the patch area. Finally, connector connectivity is the contribution of analyzed patch to maintain the other patches connectivity. This metric identifies which patch or patches are stopping the isolation of another patches. In other words, this metric evaluates if the removal of a specific patch implies that other patches are no longer connected to the overall connectivity network.

Finally, the last set of analyses aimed to evaluate the coverage of the PAas over bat diversity and relevant connectivity metrics. For the gap analyses, all connectivity polygons with a positive connectivity value were considered. Nonetheless, a more conservative approach has been considered for the geographical analyses where all polygons considered had to at least contribute 1% for each metric of connectivity. If this later threshold was not employed the distribution and connectivity over Europe Was almost continuous. Rather than representing reality, this approach is a probable results of a large pixel size (5 km) that does not represent the fragmented distribution within the pixel.

Table 3- Migration distances used in connectivity analyses

Species	Distance
Barbatella barbastellus	5km
Eptesicus isabellinus	10km
Eptesicus nilssonii	15km
Eptesicus serotinus	40km
Hypsugo savii	50km
Miniopterus schreibersii	50km
Myotis bechsteinii	20km
Myotis brandtii	25km
Myotis capaccinii	45km
Myotis dasycneme	150km
Myotis daubentonii	5km
Myotis emarginatus	40km
Myotis myotis	30km
Myotis mystacinus	5km
Nyctalus leisleri	200km
Nyctalus noctula	500km
Pipistrellus kuhlii	5km
Pipistrellus nathusii	1300km
Pipistrellus pipistrellus	15km
Plecotus austriacus	10km
Rhinolophus euryale	10km
Rhinolophus ferrumequinum	15km
Rhinolophus hipposideros	10km
Rhinolophus mehelyi	20km
Tadarida teniotis-	100km
Vespertilio murinus	400km

Gap analysis

To access PA´s protection effectiveness on species diversity a gap analyses were performed by overlapping the polygons of bat species richness and protected areas location. The amount of PA overlapping bat diversity hotspots will provide the measure of Natura 2000 effectiveness for bat protection. Similarly, to access PA´s effectiveness on conservation of connectivity areas, gap analyses have been performed by overlapping the extent of the layers representing connectivity diversity and protected areas. This approach was used for each connectivity metric (intra, flux and connector).

Results

Species diversity

In Figure 1 it is represented the spatial distribution of bat species richness in Europe. The three identified main areas of diversity were, the north of the Iberian Peninsula, southern France and central part of Italian peninsula. On other hand, low diversity areas were identified in northern Europe and in the Po Valley, northern Italy.

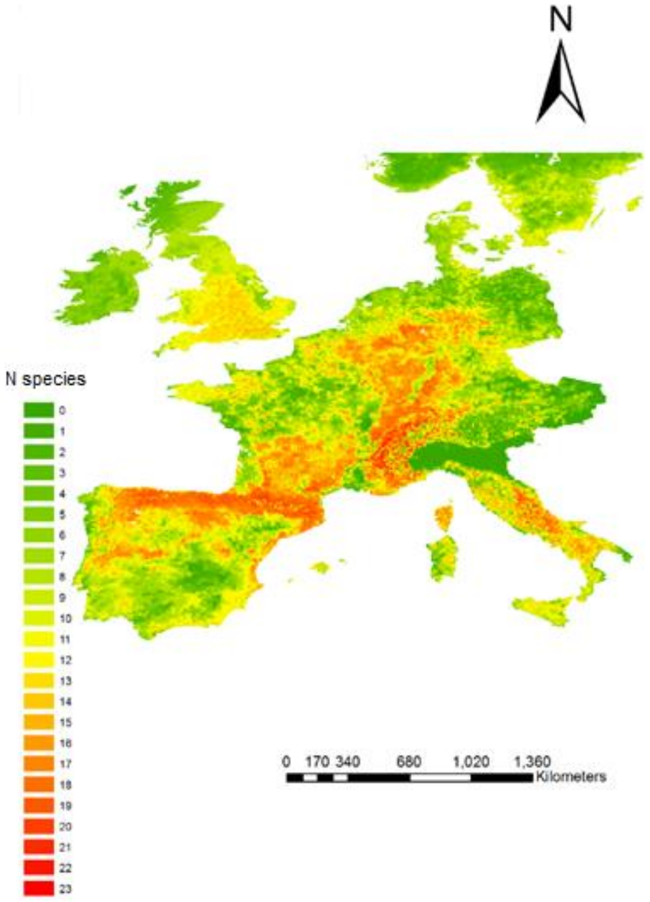

Figure 1- Representation of bat species richness where warmer colours indicate the presence of a higher number of species.

The following figures (Fig. 2-3) clearly show that vast majority of the high diversity areas remains unprotected. Most notably, the northern Iberian Peninsula and the Alps seem to harbour the highest levels of unprotected high species richness areas.

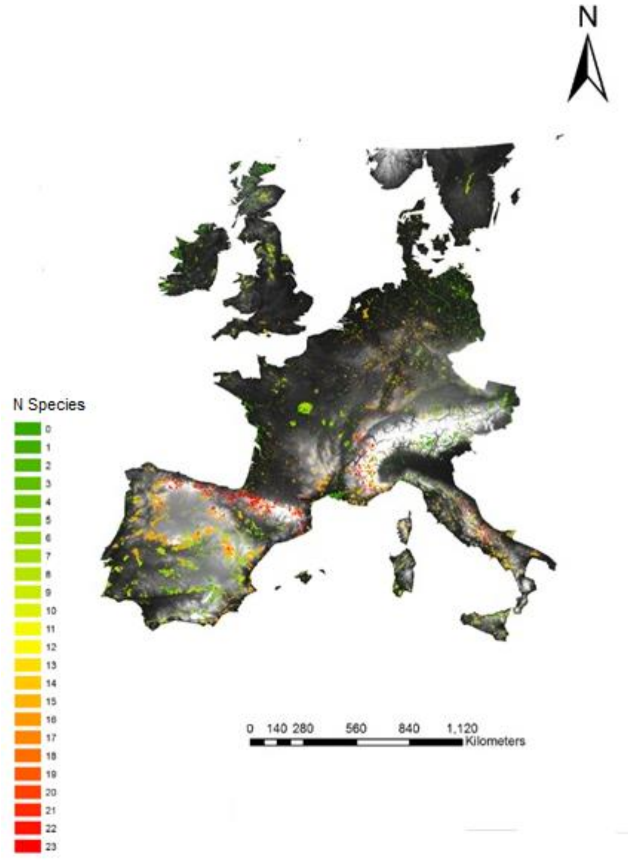

Figure 2- Bat species richness present in European protected areas network

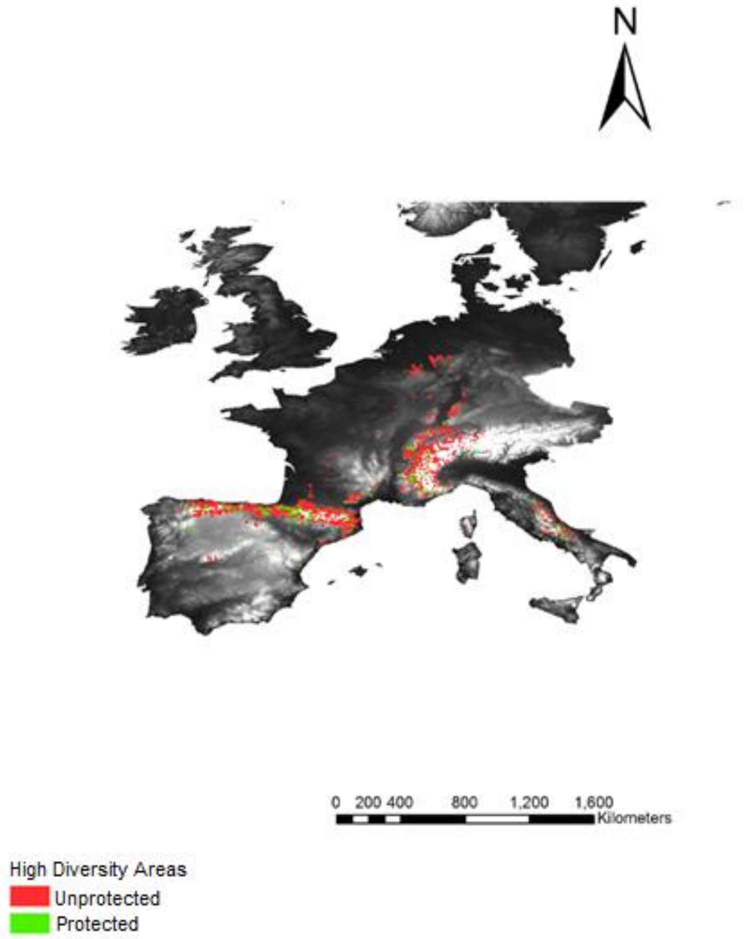

Figure 3- Map of the protected areas coverage over the hotspots of bat diversity

Low diversity areas (0-5) covered more than 20% of study area and in turn these areas had 6% of low diversity were covered by protected areas (Fig. 4). Medium diversity areas (6-11) composed more than 40% of study area and nearly 8% of medium diversity areas were covered by protected areas. Medium-high diversity areas (12-17) covered almost 30% of study area. For those 11% were covered by protected areas. High diversity areas (18-23) represented less than 5% of study area but despite its smaller area less than 30% of high diversity areas were covered by protected areas. In summary, gap between diversity groups and protected area shows a clear lack of coverage of the protected areas

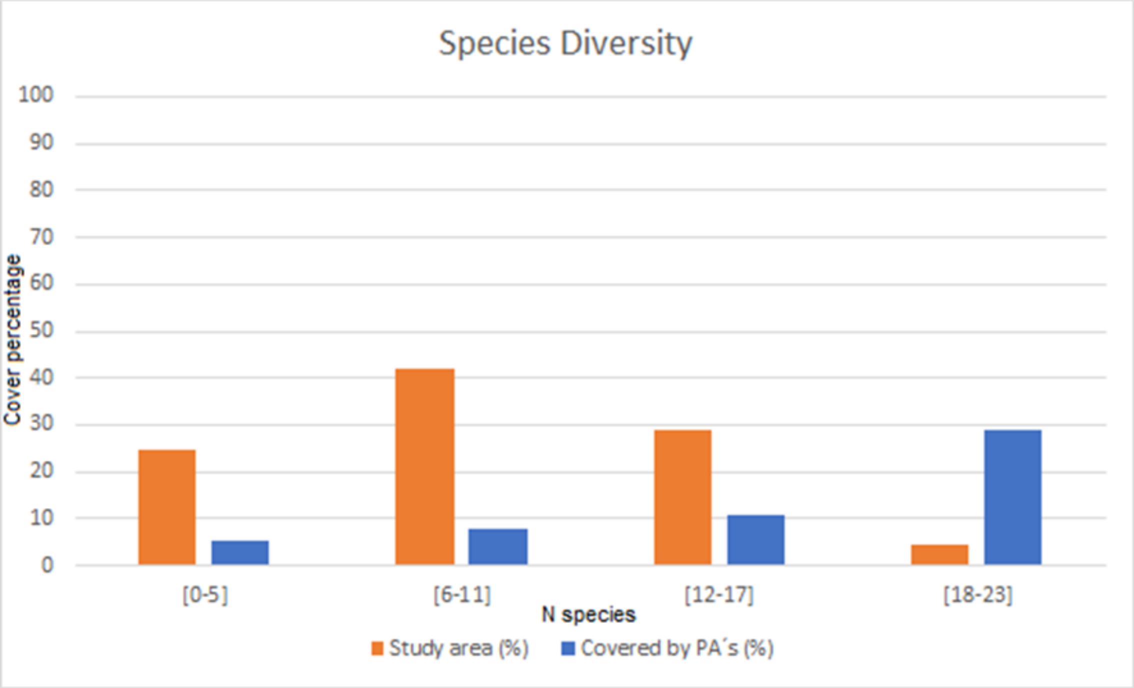

Figure 4-Percentage of cover of bat species richness and GAP analyses of the protected areas

Intra diversity

The main hotspots of intra connectivity in Europe (Fig. 5) were located in the north Iberian Peninsula and central Europe. Diversity in central Italian Peninsula and United Kingdom also showed some relevance. on the other hand, low diversity intra connectivity occurs mainly in distribution edges and also in small islands

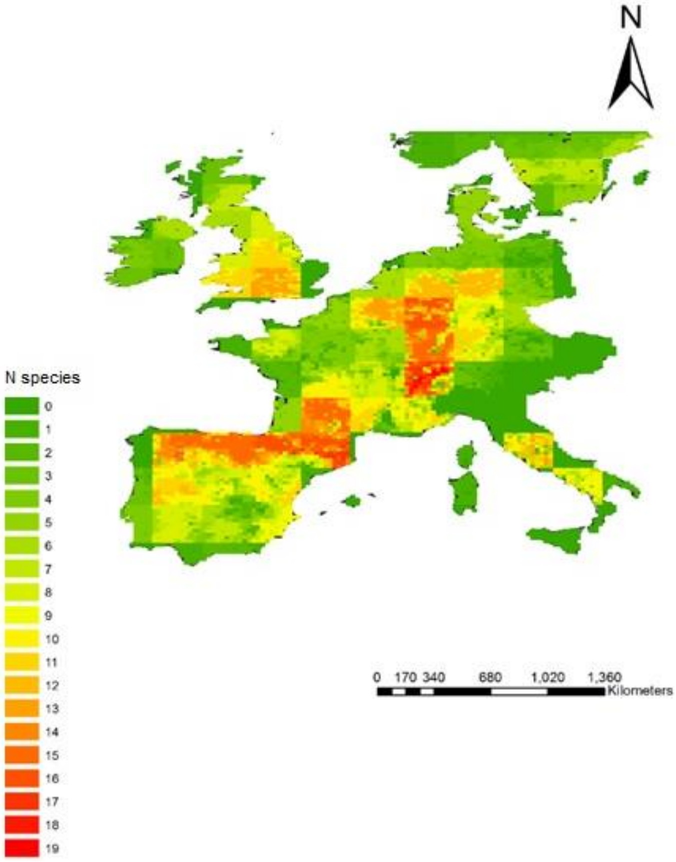

Figure 5- Map representing the richness of intra patches with relevance higher than 1%. Warmer colours indicates the number of bat species with high Intra value for a specific pixel.

Similarly to the results obtained for the distribution of bat species richness, the majority of high intra connectivity areas were not covered by protected areas (Fig. 6-7) with major gaps identified in northern Iberia and central Europe.

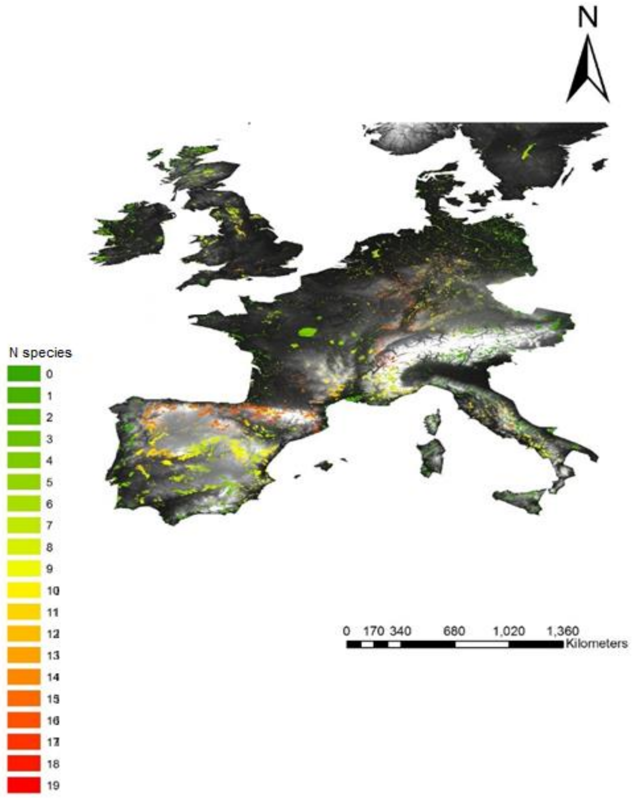

Figure 6- Bat intra richness present in European protected areas network

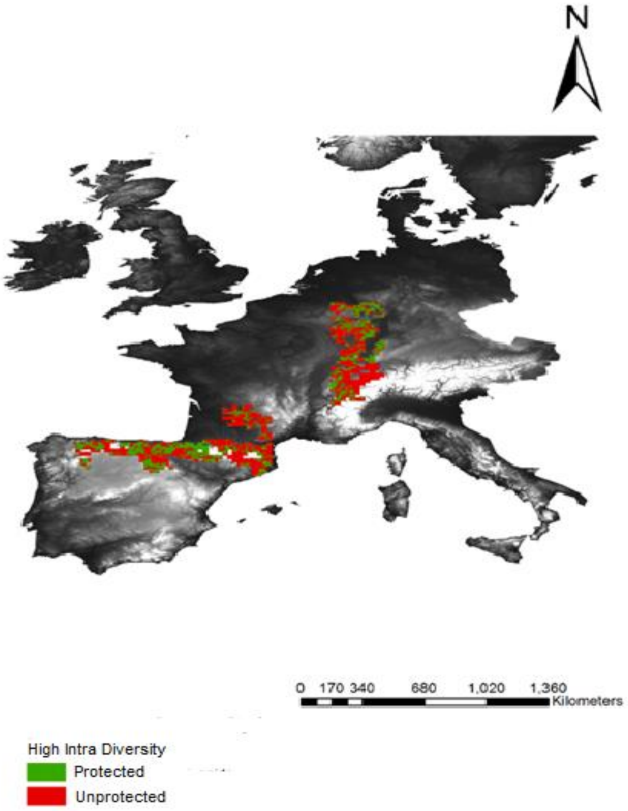

Figure 7- Map of the protected areas coverage over the hotspots of bat intra diversity

Low diversity intrapatch connectivity (0-5) covered about 25% of study area (Fig. 8). From those 25% about 7% were protected by protected areas. Medium diversity intrapatch connectivity areas (6-11) composed about 41% of study area. Protected areas covered almost 8% of medium diversity areas. Medium-high intrapatch connectivity diversity (12-17) areas represented almost 30% of study area of which about 11% were covered by protected areas. Finally, high diversity intrapatch connectivity (18-23) areas represented almost 4% of study area. More than 15% of High intrapatch connectivity areas were covered by protected areas. In summary, gap increases when intrapatch connectivity increases, although gap values remain low.

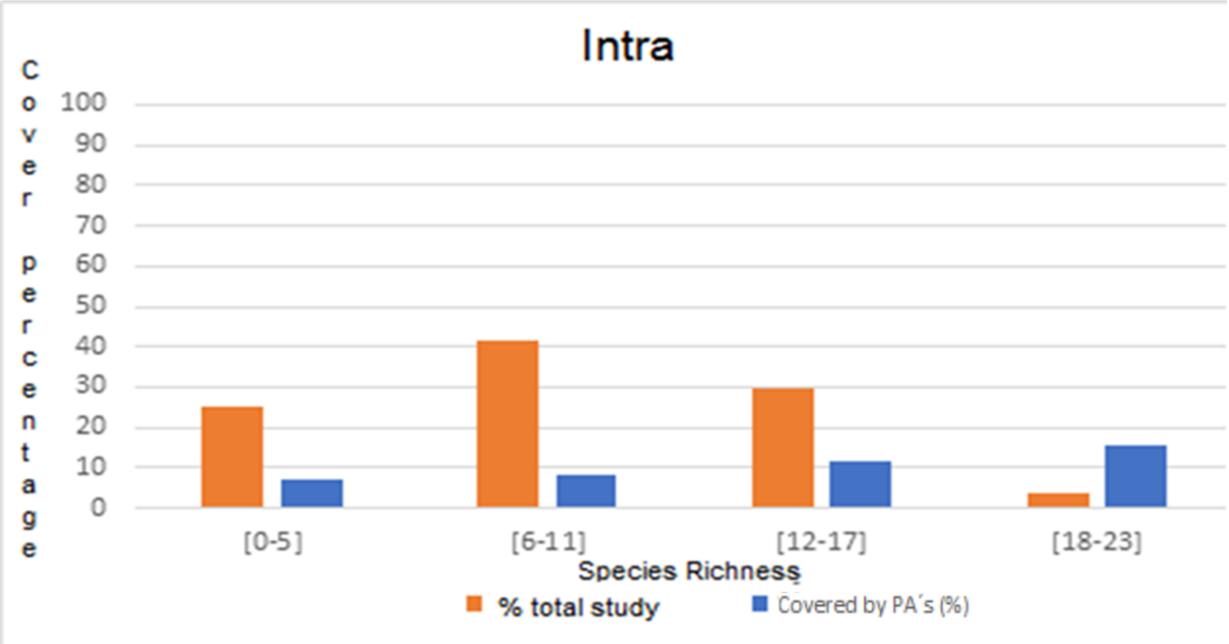

Figure 8- Percentage of cover of bat intra richness and GAP analyses of the protected areas

Flux diversity

Flux connectivity showed higher diversity in northern Iberian Peninsula and central Europe (Fig. 9). On other hand, lower diversity flux areas occur principally in northern as eastern Europe as also as in smaller islands.

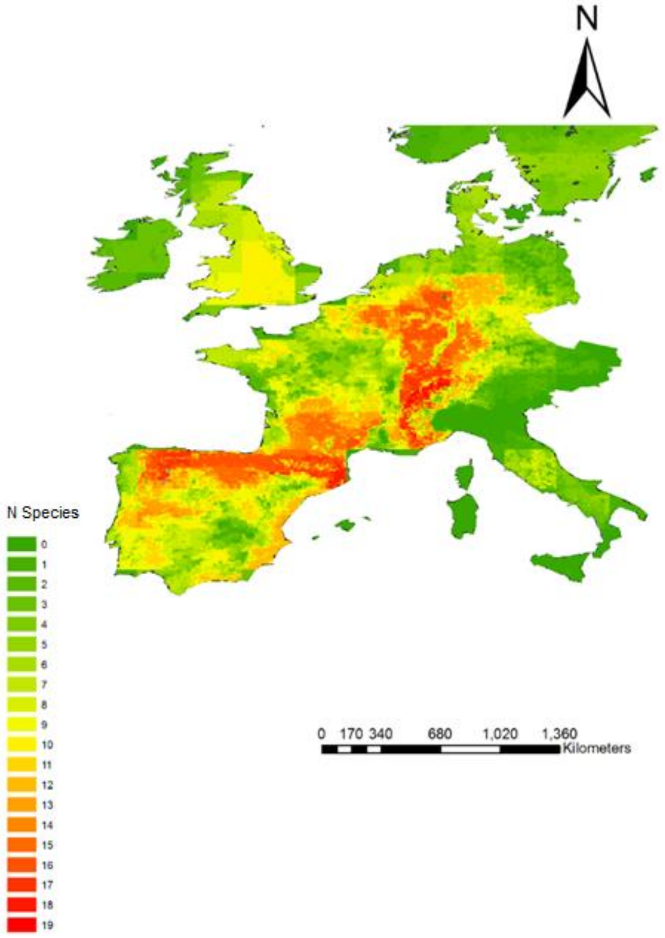

Figure 9- Map representing the richness of flux patches with relevance higher than 1%. Warmer colours indicates the number of bat species with high Intra value for a specific pixel

Similarly to the previous GAP results, the majority of high flux connectivity areas were not covered by protected areas (Fig. 10-11), especially in northern Iberia and central Europe.

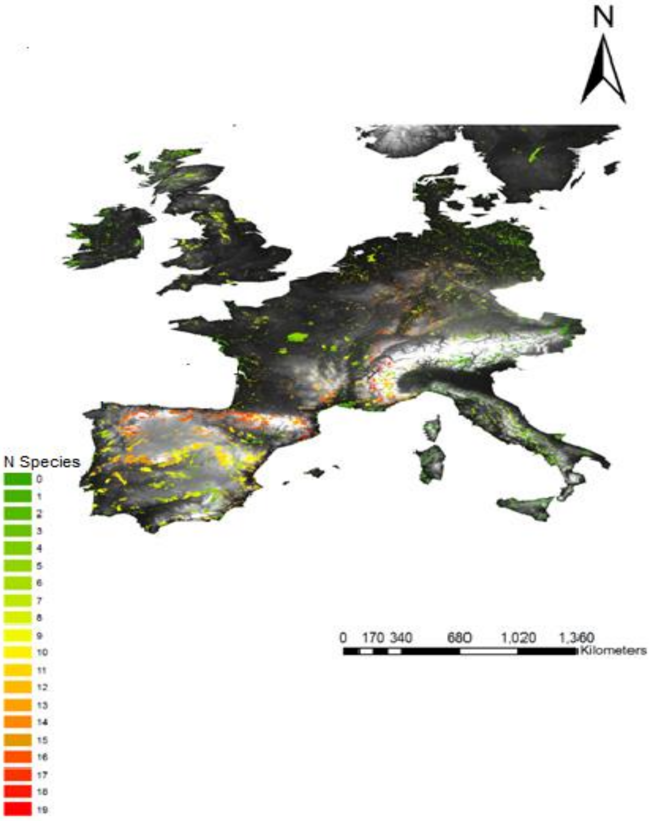

Figure 10- Bat flux richness present in European protected areas network

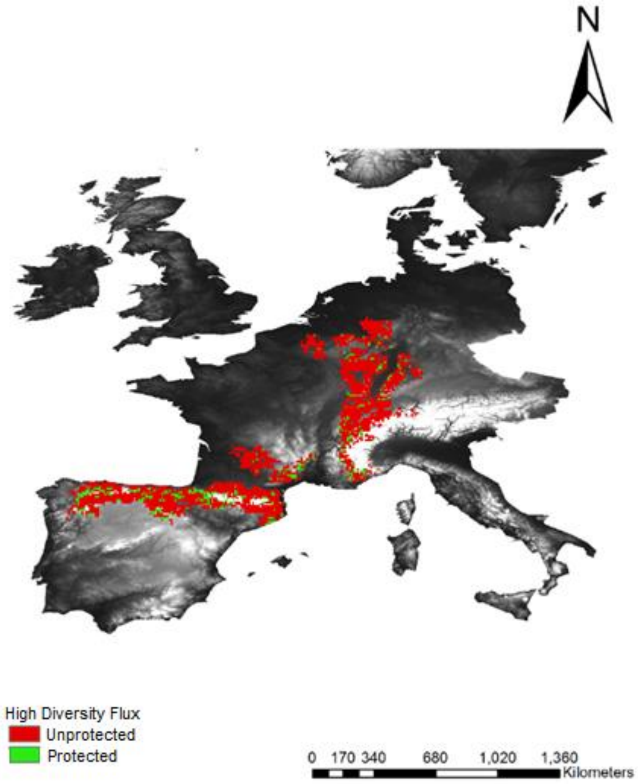

Figure 11- Map of the protected areas coverage over the hotspots of bat flux

Low diversity flux connectivity (0-5) covered about 25% of study area (Fig. 12). From those 25% about 7% were covered by protected areas. Medium diversity flux connectivity areas (6-11) composed about 41% of study area with protected areas covering almost 8% of medium diversity areas. Medium-high flux connectivity diversity (12-17) areas represent almost 30% of study area with about 11% covered by protected areas. Finally, high diversity flux connectivity (18-23) areas represented almost 4% of study area and more than 15% of high flux connectivity areas were covered by protected areas. In summary, gap increases when flux connectivity increases, although gap values remain always low.

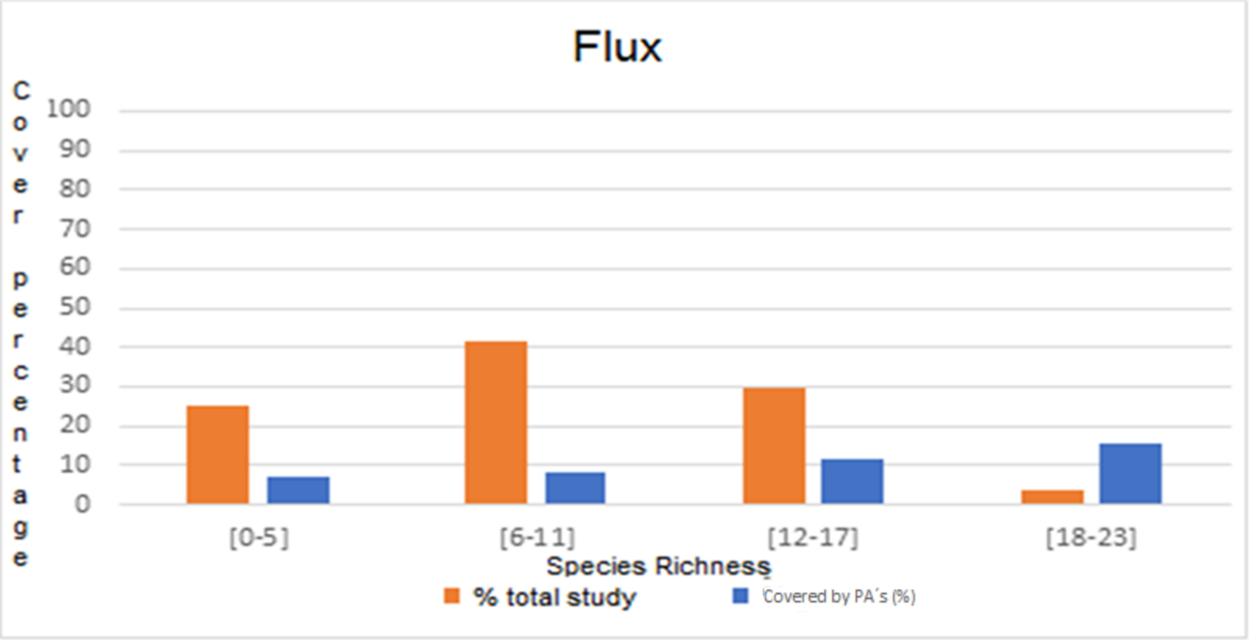

Figure 12- Percentage of cover of bat flux richness and GAP analyses of the protected areas

Connector diversity

Regarding which areas are relevant to hamper population isolation, only two areas have shown high diversity in connector connectivity (Fig. 13). These areas are the central northern part of Iberian Peninsula and the alps area in southern central Europe. Peripheral areas of study areas have lower connector diversity. The gradient between high diversity connector areas and low diversity areas were high, which means that the diversity decreases rapidly nearby high diversity areas. To sum up, two small areas comprise the majority of connector diversity.

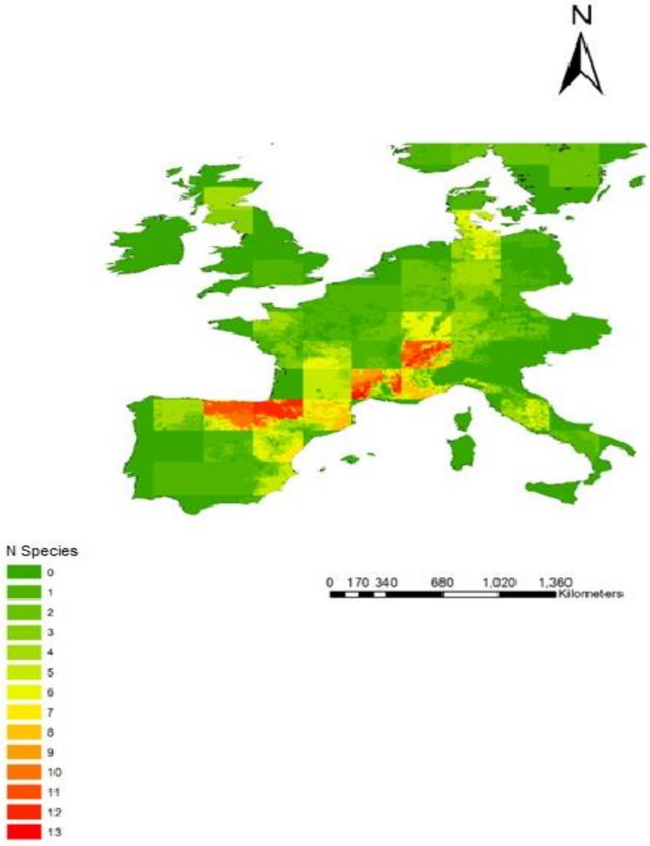

Figure 13- Map representing the richness of Connector patches with relevance higher than 1%. Warmer colours indicates the number of bat species with high Intra value for a specific pixel

Regarding PA coverage of relevant connectivity areas for bats (Fig. 14-15), the majority of high connector connectivity areas were not covered by protected areas.

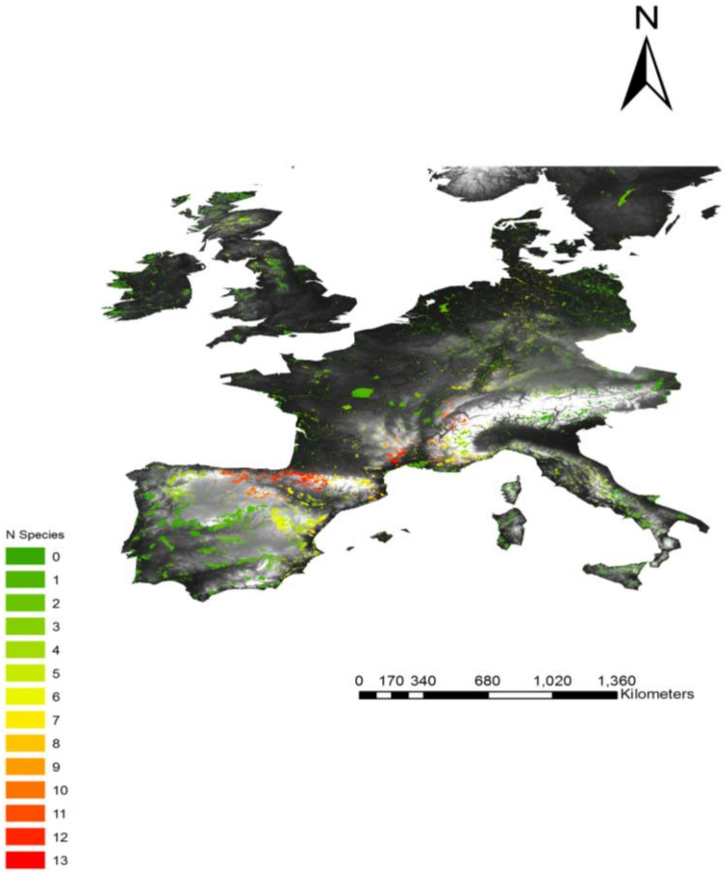

Figure 14- Bat connector richness present in European protected areas network

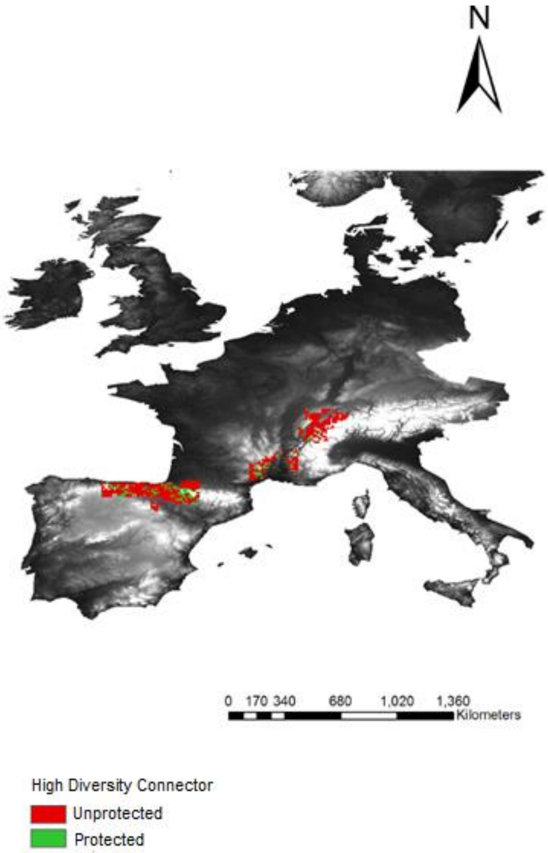

Figure 15- Map of the protected areas coverage over the hotspots of Connector diversity

Regarding gap analyses of bat connectivity (Fig. 16), low diversity connector connectivity (0-5) covered about 27% of study area. From those 27% about 7% were protected by protected areas, Medium diversity connector connectivity areas (6-11) composed about 41% of study area. Protected areas covered about 8% of medium diversity areas. Medium-high connector connectivity diversity (12-17) areas represent almost 28% of study area. From medium-high diversity areas about 11% were protected by protected areas. Finally, high diversity connector connectivity (18-23) areas represented about 3% of study area. More than 15% of High connector connectivity areas were covered by protected areas. In summary, gap increases when connector connectivity increases, although gap values remain low

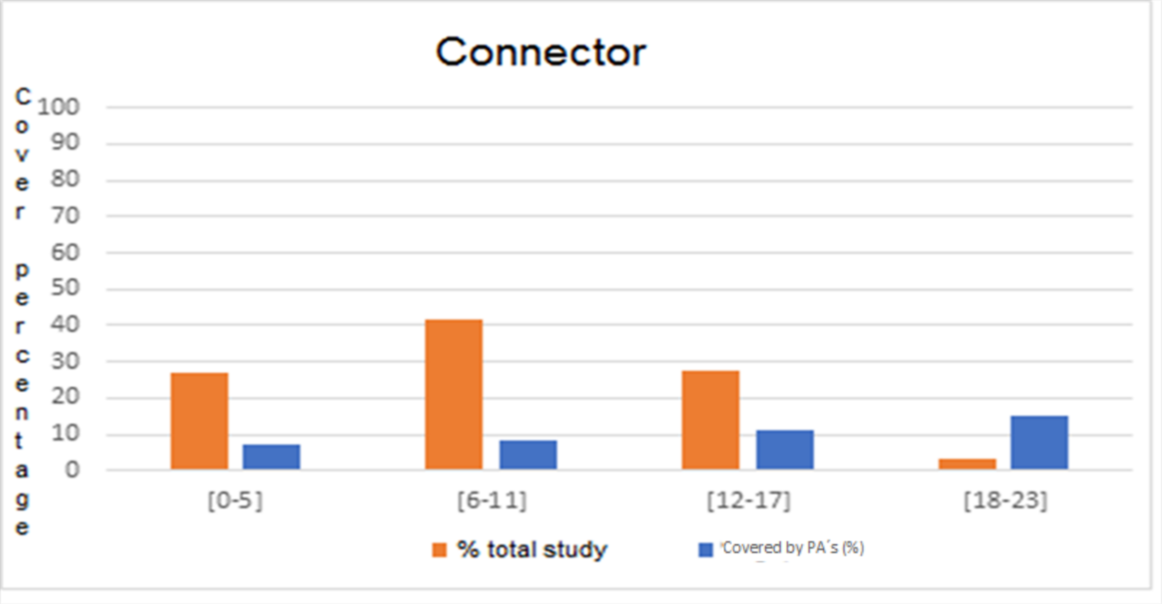

Figure 16- Percentage of cover of bat connector richness and GAP analyses of the protected areas

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Discussion

My findings revealed a low effectiveness of PA to cover the diversity of European chiroptera species. This low coverage was also observed regarding the PA coverage on high connectivity areas. Bats are legally protected by a series of agreements and measures. Yet, one of the most effective tools for conservation has been the establishment of PAs. This study highlights that for European bat fauna this conservation tool is clearly insufficient to cover most relevant areas. This is in line with previous regional studies evaluating Natura 2000 effectiveness for conservation (Lisón et al. 2013). Besides this flaw, I also detected a poor coverage for bat connectivity, further stressing the inadequacy of the design of Natura 2000 for bat conservation.

Caveats and limitations

My results need to be critically analyzed considering some caveats. First, the available species distribution modeling techniques have some limitations and can induce errors in the results. These errors may be a result of model limitations or biased data. Maxent assumes that effort samples are unbiased, however this was not observed in my data (Merow et al. 2013). Spatial biased data falsely inflates model performance (Veloz 2009). To minimize errors related to uneven sampling, spatial rarefication of occurrence data have been performed (Boria et al. 2014, Brown 2014). To overcome model´s overpredictions, the minimum convex polygon technique have been applied to restrict the predictive area to the regions where observations area present. This technique is the standard method recommended by IUCN (Standards and Petitions Working Group 2006). Nevertheless, maximum entropy model technique has a good performance to overcome these limitations (Graham et al. 2008). EGV´s may also lack some ecologically significant variables, with possible effect in the final results (Velez–Liendo et al. 2013, Porfirio et al. 2014). However, this should not be a limitation of my study considering that several studies used similar sets of EGV´s to model chiroptera species. Chosen variables are acknowledged to exert a strong influence on chiroptera physiology, ecology, and behavior (Rebelo and Jones 2010, Santos et al. 2014, Razgour et al. 2016).

In addition, errors and limitations related to connectivity analysis are conceivable. The inaccuracy of mean dispersal distance, together with some level of subjectivity of chosen landscape elements for dispersal, may be the main error sources in this work. (Beier et al. 2008). Nevertheless, most dispersal distances used in this study were supported by previous studies (Hutterer 2005). When several distinct dispersal distances where available for the same species, a conservative approach was performed. The use of linear landscape features as connecting elements for bats in the landscape is arguable. Yet, several studies have shown the importance of these landscape elements by demonstrating that several bat species use these linear features as fly routes, either to commute between roost and foraging or for migration (Limpens and Kapteyn 1991, Serra-Cobo et al. 2000, Lentini et al. 2012).

On the chiroptera diversity

The spatial patterns of bat diversity in Europe can be explained by a wide-range of factors. At a global level, species diversity peaks in equator and decreases along latitudinal gradient (Willig and Presley 2013). This gradient is explained due to lower energy input and increased climatic instability at higher latitudes (Gaston 2000, Charbonnier et al. 2016). The richness in European species of chiroptera peaks in Mediterranean countries and decreases towards northern Europe, probably as a result of the latitudinal gradient. Notwithstanding, southern Europe species' richness is also greater due to the last glaciation effects (Provan and Bennett 2008, Salicini et al. 2013). The Mediterranean region was a glacial refugia where large areas remained suitable for a vast array of wildlife (Clark and Mix 2002, Araújo et al. 2007). Although, bats have some particular distribution in the palearctic region, where chiroptera diversity peaks between 40 to 50Nº (Horáček et al. 2000, Ulrich et al. 2007). These previous studies support my results, where bat species richness is higher in the Mediterranean region. Nevertheless, diversity was uneven distributed across this region. The diversity hotspots were found particularly in mountainous regions. Climatic heterogeneity of topographical diverse regions and their high temperature range can explain this results (Moreno-Rueda and Pizarro 2007, Ulrich et al. 2007, Ford et al. 2013, López-González et al. 2015). Climatic heterogeneity leads to a wider range of habitats, which supports higher species diversity (Kerr and Packer 1997, López-González et al. 2015, Kim et al. 2018). Furthermore, Ulrich (2007) found that wide temperature range increases species richness. In addition, due to anthropogenic activities occurring at plains and valleys, such as agriculture and pastorage, the highest altitudes and slopes of southern Europe mountains still harbour large extents of autochthonous forests and habitats (Chauchard et al. 2007, Benayas and Bullock 2015). My results can also be supported by previous studies that showed high diversity in the Alps, Apennines and Iberian Peninsula (Maiorano et al. 2006; Ulrich et al. 2007; Rebelo et al. 2010; Lisón et al. 2013).

On the connectivity diversity

Intrapatch connectivity relies on patch area together with the habitat suitability within (Saura and Rubio 2010). Intra diversity have two main hotspots located in Northern Iberian Peninsula and central Europe in the Alps region. Nevertheless, intra diversity is also high in British islands and central Italian peninsula. Areas of high intra diversity were located on areas where several species have a large continuous distribution, thus coinciding with the larger suitable areas along the species distribution.

Flux diversity results were similar to the species diversity results. Flux results can be explained by the number of links to other patches on the region (Saura and Rubio 2010). Flux (and connector metric below) high connectivity areas were mainly located in mountainous areas where species' distribution is marginal or becomes more fragmented. Connectivity is therefore an issue under fragmentation scenarios, as opposite to areas where distribution of a species is continuous (Saura & Rubio 2010).For the majority of bat species, there was a considerably more fragmented distribution at the edge of the distribution rather that at its core in central Europe

Connector diversity results from whether the removal of a patch isolates other patches. Those areas act like stepping stones connecting patches that in other way were unconnected (Rubio and Saura 2012). High connector diversity areas may result from central location in patches on species distribution ranges. If connectivity in central areas disappear, peripheral species distribution sites may become unconnected leading to higher number of patches becoming unconnected. Therefore, the most relevant identified connector areas were located in the northern mountains of the Iberian Peninsula and in central Europe.

The (un)protection of diversity

The coverage of PA over bat species diversity was low, although increased in areas with higher diversity. To justify this, several factors need to be taken in account. First of all, protected areas design results of several ad-hoc and political factors that can be not favorable to protect chiroptera species (Araújo et al. 2007). Several protected areas have been created considering flagship or umbrella species (Cabeza and Moilanen 2001). In fact, umbrella species where usually large-bodied wide-range Mammalia which excludes bats (Caro et al. 2004). Protected area design based in umbrella species can under protect bat suitable habitats (Johnson et al. 2017). Furthermore, bat species usually have a wide-range distribution, thus with requirements over large geographical areas covering several countries which further hampers the establishment of international protection for bats (Razgour et al. 2016). Furthermore, anthropogenic occupation and disturbance in many landscapes leads to protected areas size restriction and fragmentation (Mcdonald et al. 2009, Angulo et al. 2016). Maiorano (2006) has shown that diversity inside and outside protected areas where similar, thus raising the challenge of developing large scale measures for bat conservation.

Should protected areas range be expanded?

Despite the issues related to the creation of wide-range protected areas, I recommend the expansion of current protected sites in order to archive better chiroptera diversity protection. Wider-range protected areas could preserve important ecossystemic linkages and processes not present in small ones (Hansen and DeFries 2007). Furthermore, larger protected areas can protect a higher number of species and habitats (Honkanen et al. 2010, Storch 2016). Some species occupy a heterogenous range of habitats that can be not totally covered in small protected areas. This is particularly true in bats that occupy a wide-range of habitats (Wermundsen and Siivonen 2008). In addition, climatic conditions are dynamic, hence species range can change along time. This change can be seasonal or permanent. Climatic change induced range changes can lead to species future habitat become unprotected (Araújo et al. 2004, Monzón et al. 2011). As such, larger protected areas can reduce these effects due to a wide coverage of various climatic conditions. That said, small protected areas are also useful to nature protection. As an example, larger reserve size does not inevitably mean better habitat quality, population size or higher species diversity (Schwartz 1999, Thomas et al. 2012, Häkkilä et al. 2018). Furthermore, increases in protected area size could lead to minor enforcement efficiency (Kuempel et al. 2018). Additionally, there are some cases where protected area size is limited by spatial limiting factors (e.g. Islands).

On the connectivity protection

The results concerning connectivity diversity protection on protected areas must be analyzed with some caution. Coarse pixel analyses can influence the results by overlooking relevant ecological features. Minimum area to represent all species increases with the increase of pixel size (Schwartz 1999). This can lead to a bias due to underrepresentation of smaller protected areas. Those factors can be special exacerbated due to the high number of small protected areas in Europe (Oldfield et al. 2004, Maiorano et al. 2006).

The overlap between protected areas and connectivity diversity increases with the increase of diversity, although is lower than the species diversity protection. This can be explained by several factors. First of all, Natura 2000 network was as targeted to achieve an ecological coherent network. Additionally, protected areas habitat quality is usually higher and land-use changes have a lower rate (Nagendra 2008, Sallustio et al. 2017). Habitat quality can be used as an proxy to population size (Stephens et al. 2015). Higher population size increases connectivity probability (Roland et al. 2000, Franzén and Nilsson 2010, Robles and Ciudad 2012) due to a higher production of dispersal individuals. Nevertheless, bat high mobility may lead to overlooking connectivity issues, which can explain the difference between species diversity and connectivity diversity protection. Mazaris (2013) stated that the number of graph components in protected areas decreases as species dispersal distances increases. Nonetheless, a species with long distance dispersal abilities can reach distant patches and eventually overcome topographical barriers like mountains. My results can highlight the protection areas where effort should be directed to protect connectivity. However, the coverage of PA over important connectivity areas was low. Due to analyses limitations', my outcomes need to be careful accounted. The ad-hoc choice of dispersal variables can lead to a bias on dispersal routes. Furthermore, ocean and seas have been defined as infinite resistance barriers to dispersal, however there are cases of dispersal from continental Europe to islands (Debrot et al. 2014). Moreover, oceanic dispersal barriers have different effects on bats species. There are cases where genetic differentiation is relevant and others where population genetic structure is similar between mainland and islands (Atterby et al. 2010, Razgour et al. 2014).

Moreover, due to graph method limitations important dispersal routes may be ignored. The Fenno-scandinavian peninsula connectivity routes can be underestimated due to lack of eastern Europe route analyses. Additionally, coarse pixel size may lead to an underestimation of the importance of small protected areas. However, my results are useful to get a general picture of European chiroptera connectivity and to identify areas in need of protection to connectivity conservation.

What to do next?

Future studies should increase study area to overcome errors related to unaccounted migration routes. Furthermore, species distribution is changing due to climatic alterations. Future climate SDM and connectivity analyses should be performed o get an accurate picture of protected areas effectiveness on maintaining future connectivity. In addition, circuit theory-based connectivity analyses could reveal several new connection pathways. Only through preemptive measures can we safeguard tomorrow biodiversity and at much lower costs.

References

Adams, R. A., and M. A. Hayes. 2008. Water availability and successful lactation by bats as related to climate change in arid regions of western North America. Journal of Animal Ecology 77:1115–1121.

Agnarsson, I., C. M. Zambrana-Torrelio, N. P. Flores-Saldana, and L. J. May-Collado. 2011. A time-calibrated species-level phylogeny of bats (Chiroptera, Mammalia). PLoS Currents 3:RRN1212.

Ahlén, I., and H. J. Baagoe. 1999. Use of ultrasound detectors for bat studies in Europe: experiences from field identification, surveys, and monitoring. Acta Chiropterologica 1:137–150.

Akaike, H. 1998. Selected Papers of Hirotugu Akaike. Page (E. Parzen, K. Tanabe, and G. Kitagawa, Eds.) Springer-Verlag New York. Springer New York, New York, NY.

Almeida, F. C., N. P. Giannini, R. DeSalle, and N. B. Simmons. 2011. Evolutionary relationships of the old world fruit bats (Chiroptera, Pteropodidae): Another star phylogeny? BMC Evolutionary Biology 11:281.

Andelman, S. J., and W. F. Fagan. 2000. Umbrellas and flagships: Efficient conservation surrogates or expensive mistakes? Proceedings of the National Academy of Sciences 97:5954–5959.

Angulo, E., R. Boulay, F. Ruano, A. Tinaut, and X. Cerdá. 2016. Anthropogenic impacts in protected areas: assessing the efficiency of conservation efforts using Mediterranean ant communities. PeerJ 4:e2773.

Araújo, M. B., M. Cabeza, W. Thuiller, L. Hannah, and P. H. Williams. 2004. Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. Global Change Biology 10:1618–1626.

Araújo, M. B., J. M. Lobo, and J. C. Moreno. 2007. The effectiveness of Iberian protected areas in conserving terrestrial biodiversity. Conservation Biology 21:1423–1432.

Atterby, H., J. N. Aegerter, G. C. Smith, C. M. Conyers, T. R. Allnutt, M. Ruedi, and A. D. MacNicoll. 2010. Population genetic structure of the Daubenton's bat (Myotis daubentonii) in western Europe and the associated occurrence of rabies. European Journal of Wildlife Research 56:67–81.

Barclay, R. M. R., and R. M. Brigham. 1991. Prey Detection, Dietary Niche Breadth, and Body Size in Bats: Why are Aerial Insectivorous Bats so Small? The American Naturalist 137:693–703.

Barlow, K. E., P. A. Briggs, K. A. Haysom, A. M. Hutson, N. L. Lechiara, P. A. Racey, A. L. Walsh, and S. D. Langton. 2015. Citizen science reveals trends in bat populations: The National Bat Monitoring Programme in Great Britain. Biological Conservation 182:14–26.

Barnosky, A. D., N. Matzke, S. Tomiya, G. O. U. Wogan, B. Swartz, T. B. Quental, C. Marshall, J. L. McGuire, E. L. Lindsey, K. C. Maguire, B. Mersey, and E. A. Ferrer. 2011. Has the Earth’s sixth mass extinction already arrived? Nature 471:51–57.

Battersby, J. 2010. Guidelines for Surveillance and Monitoring of European Bats.

Beier, P., D. R. Majka, and W. D. Spencer. 2008. Forks in the road: Choices in procedures for designing wildland linkages. Conservation Biology 22:836–851.

Benayas, J. M. R., and J. M. Bullock. 2015. Vegetation restoration and other actions to enhance wildlife in European agricultural landscapes. Page Rewilding European Landscapes.

Bender, D. J., T. A. Contreras, and L. Fahrig. 1998. Habitat Loss and Population Decline : A Meta-Analysis of the Patch Size Effect. Ecology 79:517–533.

Boria, R. A., L. E. Olson, S. M. Goodman, and R. P. Anderson. 2014. Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. Ecological Modelling 275:73–77.

Boyles, J. G., P. M. Cryan, G. F. McCracken, and T. H. Kunz. 2011. Economic Importance of Bats in Agriculture. Science 332:41–42.

Brown, J. L. 2014. SDMtoolbox: A python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. Methods in Ecology and Evolution 5:694–700.

Brown, J. L. 2017. SDMtoolbox 2.0 User Guide.

Cabeza, M., and A. Moilanen. 2001. Design of reserve networks and the persistence of biodiversity. Trends in Ecology and Evolution 16:242–248.

Cahill, A. E., M. E. Aiello-Lammens, M. C. Fisher-Reid, X. Hua, C. J. Karanewsky, H. Yeong Ryu, G. C. Sbeglia, F. Spagnolo, J. B. Waldron, O. Warsi, and J. J. Wiens. 2012. How does climate change cause extinction? Proceedings of the Royal Society B: Biological Sciences 280:1–10.

Calabrese, J. M., and W. F. Fagan. 2004. A comparison-shopper's guide to connectivity metrics. Frontiers in Ecology and the Environment 2:529–536.

Caro, T., J. M. Roberge, and P. Angelstam. 2004. Conservation by proxy: Indicator, Umbrella, Keystone, Flagship and other surrogate species. Page Conservation Biology.

Ceballos, G., P. R. Ehrlich, A. D. Barnosky, A. Garcia, R. M. Pringle, and T. M. Palmer. 2015. Accelerated modern human-induced species losses: Entering the sixth mass extinction. Science Advances 1:1–5.

Ceballos, G., P. R. Ehrlich, and R. Dirzo. 2017. Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. Proceedings of the National Academy of Sciences of the United States of America 114:6089–6096.

Charbonnier, Y. M., L. Barbaro, J. Y. Barnagaud, E. Ampoorter, J. Nezan, K. Verheyen, and H. Jactel. 2016. Bat and bird diversity along independent gradients of latitude and tree composition in European forests. Oecologia 182:529–537.

Chauchard, S., C. Carcaillet, and F. Guibal. 2007. Patterns of land-use abandonment control tree-recruitment and forest dynamics in mediterranean mountains. Ecosystems 10:936–948.

Clark, P. U., and a. C. Mix. 2002. Ice sheets and sea level of the Last Glacial Maximum. Quaternary Science Reviews 21:1–7.

De Conno, C., V. Nardone, L. Ancillotto, S. De Bonis, M. Guida, I. Jorge, U. Scarpa, and D. Russo. 2018. Testing the performance of bats as indicators of riverine ecosystem quality. Ecological Indicators 95:741–750.

Copernicus Land Monitoring Service. 2015. Tree Cover Density 2015. https://land.copernicus.eu/pan-european/high-resolution-layers/forests/tree-cover-density/status-maps/2015?tab=download.

Crichton, E. G., and P. H. Krutzsch, editors. 2000. Reproductive Biology of the Bats. 1st edition. Academic Press.

Debrot, A. O., M. Ruijter, W. Endarwin, P. Van, G. Van Buurt, J. A. De Freitas, and P. O. Box. 2014. Wageningen UR 011:1–109.

Denzinger, A., and H.-U. Schnitzler. 2013. Bat guilds, a concept to classify the highly diverse foraging and echolocation behaviors of microchiropteran bats. Frontiers in Physiology 4:1–15.

Díaz, S., J. Fargione, F. S. Chapin, and D. Tilman. 2006. Biodiversity loss threatens human well-being. PLoS Biology 4:1300–1305.

Dimitrakopoulos, P. G., D. Memtsas, and a Y. Troumbis. 2004. Questioning the effectiveness of the Natura 2000 species areas for conservation strategy: the case of Crete. Global Ecology and Biogeography 13:199–207.

Elith, J., C. H. Graham, R. P. Anderson, M. Dudik, S. Ferrier, A. Guisan, R. J. Hijmans, F. Huettmann, J. R. Leathwick, A. Lehmann, J. Li, L. G. Lohmann, B. A. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. M. Overton, A. T. Peterson, S. J. Phillips, K. Richardson, R. Scachetti-Pereira, R. E. Schapire, J. Soberon, S. Williams, M. S. Wisz, and N. E. Zimmermann. 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29:129–151.

Elith, J., M. Kearney, and S. Phillips. 2010. The art of modelling range-shifting species. Methods in Ecology and Evolution 1:330–342.

Elith, J., S. J. Phillips, T. Hastie, M. Dudík, Y. E. Chee, and C. J. Yates. 2011. A statistical explanation of MaxEnt for ecologists. Diversity and Distributions 17:43–57.

Entwistle, A. C., P. A. Racey, and J. R. Speakman. 1998. The reproductive cycle and determination of sexual maturity in male brown long-eared bats, Plecotus auritus (Chiroptera: Vespertilionidae). Journal of Zoology 244:63–70.

Environmental Systems Research Institute. 2011. ArcGIS desktop: release 10.

European Council. 1992. Council Directive 92/43/EEC.

European Environment Agency. 2017. Natura 2000 End 2017. https://www.eea.europa.eu/data-and-maps/data/natura-9/natura-2000-spatial-data/natura-2000-shapefile-1.

Fick, S. E., and R. J. Hijmans. 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37:4302–4315.

Ford, K. R., A. K. Ettinger, J. D. Lundquist, M. S. Raleigh, and J. Hille Ris Lambers.

2013. Spatial Heterogeneity in Ecologically Important Climate Variables at Coarse and Fine Scales in a High-Snow Mountain Landscape. PLoS ONE 8.

Fox, R. 2013. The decline of moths in Great Britain: A review of possible causes. Insect Conservation and Diversity 6:5–19.

Frankham, R., C. J. A. Bradshaw, and B. W. Brook. 2014. Genetics in conservation management: Revised recommendations for the 50/500 rules, Red List criteria and population viability analyses. Biological Conservation 170:56–63.

Franzén, M., and S. G. Nilsson. 2010. Both population size and patch quality affect local extinctions and colonizations. Proceedings of the Royal Society B: Biological Sciences 277:79–85.

Freeman, P. W. 2000. Macroevolution in Microchiropteria: Recoupling morphology and ecology with phylogeny. Evolutionary Ecology Research 2:317–335.

Frey-Ehrenbold, A., F. Bontadina, R. Arlettaz, and M. K. Obrist. 2013. Landscape connectivity, habitat structure and activity of bat guilds in farmland-dominated matrices. Journal of Applied Ecology 50:252–261.

Frick, W. F., D. S. Reynolds, and T. H. Kunz. 2010. Influence of climate and reproductive timing on demography of little brown myotis Myotis lucifugus. Journal of Animal Ecology 79:128–136.

Gaston, K. J. 2000. Global patterns in biodiversity. Nature 405:220–227.

Georgiakakis, Vasilakopoulos, Mylonas, and Russo. 2010. Bat Species Richness and Activity over an Elevation Gradient in Mediterranean Shrublands of Crete. Hystrix It. J. Mammalogy 21:43–56.

Graham, C. H., J. Elith, R. J. Hijmans, A. Guisan, A. Townsend Peterson, B. A. Loiselle, R. P. Anderson, M. Dudk, S. Ferrier, F. Huettmann, J. Leathwick, A. Lehmann, J. Li, L. Lohmann, B. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. Overton, S. Phillips, K. Richardson, R. S. Pereira, R. Schapire, J. Soberón, S. Williams, M. Wisz, and N. Zimmermann. 2008. The influence of spatial errors in species occurrence data used in distribution models. Journal of Applied Ecology 45:239–247.

Gurrutxaga, M., L. Rubio, and S. Saura. 2011. Key connectors in protected forest area networks and the impact of highways: A transnational case study from the Cantabrian Range to the Western Alps (SW Europe). Landscape and Urban

Planning 101:310–320.

Haddad, N. M., L. A. Brudvig, J. Clobert, K. F. Davies, A. Gonzalez, R. D. Holt, T. E. Lovejoy, J. O. Sexton, M. P. Austin, C. D. Collins, W. M. Cook, E. I. Damschen, R. M. Ewers, B. L. Foster, C. N. Jenkins, A. J. King, W. F. Laurance, D. J. Levey, C. R. Margules, B. A. Melbourne, A. O. Nicholls, J. L. Orrock, D.-X. Song, and J. R. Townshend. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Science Advances 1:1–9.

Häkkilä, M., N. Abrego, O. Ovaskainen, and M. Mönkkönen. 2018. Habitat quality is more important than matrix quality for bird communities in protected areas. Ecology and Evolution 8:4019–4030.

Hansen, A. J., and R. DeFries. 2007. Ecological mechanisms linking protected areas to surrounding lands. Ecological Applications 17:974–988.

Harper, D. A. T., E. U. Hammarlund, and C. M. Ø. Rasmussen. 2014. End Ordovician extinctions: A coincidence of causes. Gondwana Research 25:1294–1307.

Heldmaier, G., S. Ortmann, and R. Elvert. 2004. Natural hypometabolism during hibernation and daily torpor in mammals. Respiratory Physiology & Neurobiology 141:317–329.

Heller, N. E., and E. S. Zavaleta. 2009. Biodiversity management in the face of climate change: A review of 22 years of recommendations. Biological Conservation 142:14–32.

Hijmans, R. J., and J. van Etten. 2014. raster: Geographic data analysis and modeling. R package version 2.

Hock, R. J. 1951. The metabolic rates and body temperature of bats. The Biological Bulletin 101:289–299.

Holder, J., and M. Lee. 2007. Environmental Protection, Law and Policy. 2nd edition. Cambridge University Press, Cambridge.

Honkanen, M., J.-M. Roberge, A. Rajasärkkä, and M. Mönkkönen. 2010. Disentangling the effects of area, energy and habitat heterogeneity on boreal forest bird species richness in protected areas. Global Ecology and Biogeography 19:61–71.

Hope, P. R., K. Bohmann, M. T. P. Gilbert, M. L. Zepeda-Mendoza, O. Razgour, and G. Jones. 2014. Second generation sequencing and morphological faecal analysis reveal unexpected foraging behaviour by Myotis nattereri (Chiroptera, Vespertilionidae) in winter. Frontiers in Zoology 11:1–15.

Horáček, I., V. Hanák, and J. Gaisler. 2000. Bats of the Palearctic region: a taxonomic and biogeographic review. Pages 11–157 Proceedings of the VIIIth European bat research symposium. CIC ISEZ PAN Kraków.

Hunter, P. 2007. The nature of flight. The molecules and mechanics of flight in animals. EMBO reports 8:811–813.

Hutterer, R. 2005. Bat migrations in Europe: a review of banding data and literature. Federal Agency for Nature Conservation.

Iriye, A., and P. Saunier. 2016. Environmental diplomacy. Page The Palgrave Dictionary of Transnational History: From the mid-19th century to the present day. Springer.

Jaberg, C., and A. Guisan. 2001. Modelling the distribution of bats in relation to landscape structure in a temperate mountain environment. Journal of Applied Ecology 38:1169–1181.

Jacobson, B., and P. R. Peres-Neto. 2010. Quantifying and disentangling dispersal in metacommunities: How close have we come? How far is there to go? Landscape Ecology 25:495–507.

Johnson, S. A., H. K. Ober, and D. C. Adams. 2017. Are keystone species effective umbrellas for habitat conservation? A spatially explicit approach. Journal for Nature Conservation 37:47–55.

Jones, G. 1994. Scaling of Wingbeat and Echolocation Pulse Emission Rates in Bats: Why are Aerial Insectivorous Bats so Small? Functional Ecology 8:450.

Jones, G., D. S. Jacobs, T. H. Kunz, M. R. Wilig, and P. A. Racey. 2009. Carpe noctem: The importance of bats as bioindicators. Endangered Species Research 8:93–115.

Jones, K. E., A. Purvis, A. Maclarnon, O. R. P. Bininda-Emonds, and N. B. Simmons. 2002. A phylogenetic supertree of the bats (Mammalia: Chiroptera). Biological Reviews of the Cambridge Philosophical Society 77:S1464793101005899.

Kalka, M. B., A. R. Smith, and E. K. V. Kalko. 2008. Bats limit arthropods and herbivory in a tropical forest. Science 320:71.

Kerr, J. T., and L. Packer. 1997. Habitat heterogeneity as a determinant of mammal species richness in high-energy regions.

Kim, J. Y., S. Lee, M. S. Shin, C. H. Lee, C. Seo, and S. H. Eo. 2018. Altitudinal patterns in breeding bird species richness and density in relation to climate, habitat heterogeneity, and migration influence in a temperate montane forest (South Korea). PeerJ 6:e4857.

Kiss, A. C., and D. Shelton. 2007. Guide To International Environmental Law. 1st edition. Martinus Nijhoff Publishers.

Kramer-Schadt, S., J. Niedballa, J. D. Pilgrim, B. Schröder, J. Lindenborn, V. Reinfelder, M. Stillfried, I. Heckmann, A. K. Scharf, D. M. Augeri, S. M. Cheyne, A. J. Hearn, J. Ross, D. W. Macdonald, J. Mathai, J. Eaton, A. J. Marshall, G. Semiadi, R. Rustam, H. Bernard, R. Alfred, H. Samejima, J. W. Duckworth, C. Breitenmoser-Wuersten, J. L. Belant, H. Hofer, and A. Wilting. 2013. The importance of correcting for sampling bias in MaxEnt species distribution models. Diversity and Distributions 19:1366–1379.

Kuempel, C. D., V. M. Adams, H. P. Possingham, and M. Bode. 2018. Bigger or better: The relative benefits of protected area network expansion and enforcement for the conservation of an exploited species. Conservation Letters 11:1–8.

Kunz, T. H. 1977. Mortality of Little Brown Bats Following Multiple Pesticide Applications. The Journal of Wildlife Management 41:476–483.

Kunz, T. H., E. B. de Torrez, D. Bauer, T. Lobova, and T. H. Fleming. 2011. Ecosystem services provided by bats. Annals of the New York Academy of Sciences 1223:1–38.

Leffler, E. M., K. Bullaughey, D. R. Matute, W. K. Meyer, L. Ségurel, A. Venkat, P. Andolfatto, and M. Przeworski. 2012. Revisiting an Old Riddle: What Determines Genetic Diversity Levels within Species? PLoS Biology 10.

Lentini, P. E., P. Gibbons, J. Fischer, B. Law, J. Hanspach, and T. G. Martin. 2012. Bats in a Farming Landscape Benefit from Linear Remnants and Unimproved Pastures. PLoS ONE 7.

Leverington, F., K. L. Costa, H. Pavese, A. Lisle, and M. Hockings. 2010. A global analysis of protected area management effectiveness. Environmental Management 46:685–698.

Limpens, H. J. G. A., and K. Kapteyn. 1991. Bats, their behavior and linear landscape elements. Myotis 29:39–48.

Lisón, F., J. A. Palazón, and J. F. Calvo. 2013. Effectiveness of the Natura 2000 Network for the conservation of cave-dwelling bats in a Mediterranean region. Animal Conservation 16:528–537.

Liu, C., G. Newell, and M. White. 2016. On the selection of thresholds for predicting species occurrence with presence-only data. Ecology and Evolution 6:337–348.

López-González, C., S. J. Presley, A. Lozano, R. D. Stevens, and C. L. Higgins. 2015. Ecological biogeography of Mexican bats: The relative contributions of habitat heterogeneity, beta diversity, and environmental gradients to species richness and composition patterns. Ecography 38:261–272.

Luque, S., S. Saura, and M. J. Fortin. 2012. Landscape connectivity analysis for conservation: Insights from combining new methods with ecological and genetic data. Landscape Ecology 27:153–157.

Maine, J. J., and J. G. Boyles. 2015. Bats initiate vital agroecological interactions in corn. Proceedings of the National Academy of Sciences 112:12438–12443.

Maiorano, L., A. Falcucci, and L. Boitani. 2006. Gap analysis of terrestrial vertebrates in Italy: Priorities for conservation planning in a human dominated landscape. Biological Conservation 133:455–473.

Mazaris, A. D., A. D. Papanikolaou, M. Barbet-Massin, A. S. Kallimanis, F. Jiguet, D. S. Schmeller, and J. D. Pantis. 2013. Evaluating the Connectivity of a Protected Areas' Network under the Prism of Global Change: The Efficiency of the European Natura 2000 Network for Four Birds of Prey. PLoS ONE 8.

Mcdonald, R. I., R. T. T. Forman, P. Kareiva, R. Neugarten, D. Salzer, and J. Fisher. 2009. Urban effects, distance, and protected areas in an urbanizing world. Landscape and Urban Planning 93:63–75.

McKinnon, E. A., and O. P. Love. 2018. Ten years tracking the migrations of small landbirds: Lessons learned in the golden age of bio-logging. The Auk 135:834–856.

McRae, B. H., S. A. Hall, P. Beier, and D. M. Theobald. 2012. Where to Restore Ecological Connectivity? Detecting Barriers and Quantifying Restoration Benefits. PLoS ONE 7.

McRae, B. H., and D. M. Kavanagh. 2011. Linkage mapper connectivity analysis software. The Nature Conservancy.

Van der Meij, T., A. J. Van Strien, K. A. Haysom, J. Dekker, J. Russ, K. Biala, Z. Bihari, E. Jansen, S. Langton, A. Kurali, H. Limpens, A. Meschede, G. Petersons, P. Presetnik, J. Prüger, G. Reiter, L. Rodrigues, W. Schorcht, M. Uhrin, and V. Vintulis. 2015. Return of the bats? A prototype indicator of trends in European bat populations in underground hibernacula. Mammalian Biology 80:170–177.

Merow, C., M. J. Smith, and J. A. Silander. 2013. A practical guide to MaxEnt for modeling species' distributions: What it does, and why inputs and settings matter. Ecography 36:1058–1069.

Mickleburgh, S. P., A. M. Hutson, and P. A. Racey. 1992. Old world fruit bats: an action plan for their conservation. Page International Union for Conservation of Nature and Natural Resources. IUCN.

Milberg, P., and T. Tyrberg. 1993. Naïve birds and noble savages - a review of man-caused prehistoric extinctions of island birds. Ecography 16:229–250.

Moilanen, A., and M. Nieminen. 2002. Simple connectivity measure in spatial ecology. Ecology 83:1131–1145.

Monzón, J., L. Moyer-Horner, and M. B. Palamar. 2011. Climate Change and Species Range Dynamics in Protected Areas. BioScience 61:752–761.

Moreno-Rueda, G., and M. Pizarro. 2007. The relative influence of climate, environmental heterogeneity, and human population on the distribution of vertebrate species richness in south-eastern Spain. Acta Oecologica 32:50–58.

Mortelliti, A., G. Sozio, D. A. Driscoll, L. Bani, L. Boitani, and D. B. Lindenmayer. 2014. Population and individual-scale responses to patch size, isolation and quality in the hazel dormouse. Ecosphere 5:1–21.

Murtaugh, P. A. 2009. Performance of several variable-selection methods applied to real ecological data. Ecology Letters 12:1061–1068.

Nagendra, H. 2008. Do Parks Work? Impact of Protected Areas on Land Cover Clearing. AMBIO: A Journal of the Human Environment 37:330–337.

Naimi, B. 2015. usdm: Uncertainty analysis for species distribution models. R package version:1.

Navarra, A., and L. Tubiana. 2013. Regional assessment of climate change in the Mediterranean. Springer.

Oldfield, T. E. E., R. J. Smith, S. R. Harrop, and N. Leader-Williams. 2004. A gap analysis of terrestrial protected areas in England and its implications for conservation policy. Biological Conservation 120:307–313.

Oxberry, B. A. 1979. Female reproductive patterns in hibernating bats. Journal of reproduction and fertility 56:359–367.

Papageorgiou, K., and I. N. Vogiatzakis. 2006. Nature protection in Greece: an appraisal of the factors shaping integrative conservation and policy effectiveness. Environmental Science and Policy 9:476–486.

Park, K. J. 2015. Mitigating the impacts of agriculture on biodiversity: bats and their potential role as bioindicators. Mammalian Biology 80:191–204.

Parmesan, C. 2006. Ecological and Evolutionary Responses to Recent Climate Change. Annual Review of Ecology, Evolution, and Systematics 37:637–669.

Pelletier, D., M. Clark, M. G. Anderson, B. Rayfield, M. A. Wulder, and J. A. Cardille. 2014. Applying circuit theory for corridor expansion and management at regional scales: Tiling, pinch points, and omnidirectional connectivity. PLoS ONE 9:1–11.

Phillips, S. 2008. A Brief Tutorial on Maxent. AT&T Research:1–38.

Phillips, S. J., M. Dudík, and R. E. Schapire. 2017. Maxent software for modeling species niches and distributions.

Porfirio, L. L., R. M. B. Harris, E. C. Lefroy, S. Hugh, S. F. Gould, G. Lee, N. L. Bindoff, and B. Mackey. 2014. Improving the Use of Species Distribution Models in Conservation Planning and Management under Climate Change. PLoS ONE 9:e113749.

Possingham, H., I. H. Ball, and S. Andelman. 2000. Mathematical methods for identifying representative reserve networks. Pages 291–305 in S. Ferson and M. Burgman, editors. Quantitative Methods for Conservation Biology. Springer-Verlag.

Provan, J., and K. D. Bennett. 2008. Phylogeographic insights into cryptic glacial refugia. Trends in Ecology and Evolution 23:564–571.

Puechmaille, S. J., G. Wibbelt, V. Korn, H. Fuller, F. Forget, K. Mühldorfer, A. Kurth, W. Bogdanowicz, C. Borel, T. Bosch, T. Cherezy, M. Drebet, T. Görföl, A.-J. Haarsma, F. Herhaus, G. Hallart, M. Hammer, C. Jungmann, Y. Le Bris, L. Lutsar, M. Masing, B. Mulkens, K. Passior, M. Starrach, A. Wojtaszewski, U. Zöphel, and E. C. Teeling. 2011. Pan-European Distribution of White-Nose Syndrome Fungus

(Geomyces destructans) Not Associated with Mass Mortality. PLoS ONE 6:e19167.

Puig-Montserrat, X., I. Torre, A. López-Baucells, E. Guerrieri, M. M. Monti, R. Ràfols-García, X. Ferrer, D. Gisbert, and C. Flaquer. 2015. Pest control service provided by bats in Mediterranean rice paddies: linking agroecosystems structure to ecological functions. Mammalian Biology 80:237–245.

Queirós, M. 2001. Os parques naturais e o ordenamento do território em portugal. Inforgeo 16/17:141–150.

R Core Team. 2013. R: A language and environment for statistical computing.

Rabus, B., M. Eineder, A. Roth, and R. Bamler. 2003. The shuttle radar topography mission - A new class of digital elevation models acquired by spaceborne radar. ISPRS Journal of Photogrammetry and Remote Sensing 57:241–262.

Racey, P. A., J. R. Speakman, and S. M. Swift. 1987. Reproductive adaptations of heterothermic bats at the northern borders of their distribution. South African Journal of Science 83:635–638.

Rainho, A., and J. M. Palmeirim. 2011. The Importance of Distance to Resources in the Spatial Modelling of Bat Foraging Habitat. PLoS ONE 6:e19227.

Razgour, O., J. Juste, C. Ibáñez, A. Kiefer, H. Rebelo, S. J. Puechmaille, R. Arlettaz, T. Burke, D. A. Dawson, M. Beaumont, and G. Jones. 2013. The shaping of genetic variation in edge-of-range populations under past and future climate change. Ecology Letters 16:1258–1266.

Razgour, O., H. Rebelo, M. Di Febbraro, and D. Russo. 2016. Painting maps with bats: Species distribution modelling in bat research and conservation. Hystrix 27.

Razgour, O., H. Rebelo, S. J. Puechmaille, J. Juste, C. Ibáñez, A. Kiefer, T. Burke, D. A. Dawson, and G. Jones. 2014. Scale-dependent effects of landscape variables on gene flow and population structure in bats. Diversity and Distributions 20:1173–1185.

Rebelo, H., and G. Jones. 2010. Ground validation of presence-only modelling with rare species: A case study on barbastelles Barbastella barbastellus (Chiroptera: Vespertilionidae). Journal of Applied Ecology 47:410–420.

Robles, H., and C. Ciudad. 2012. Influence of Habitat Quality, Population Size, Patch Size, and Connectivity on Patch-Occupancy Dynamics of the Middle Spotted

Woodpecker. Conservation Biology 26:284–293.

Rodrigues, L., A. Zahn, A. Rainho, and J. M. Palmeirim. 2003. Contrasting the roosting behaviour and phenology of an insectivorous bat (Myotis myotis) in its southern and northern distribution ranges. Mammalia 67.

Roland, J., N. Keyghobadi, and S. Fownes. 2000. Alpine Parnassius Butterfly Dispersal : Effects of Landscape and Population Size. Ecology 81:1642–1653.

Roscioni, F., H. Rebelo, D. Russo, M. L. Carranza, M. Di Febbraro, and A. Loy. 2014. A modelling approach to infer the effects of wind farms on landscape connectivity for bats. Landscape Ecology 29:891–903.

Rubio, L., and S. Saura. 2012. Assessing the importance of individual habitat patches as irreplaceable connecting elements: An analysis of simulated and real landscape data. Ecological Complexity 11:28–37.

Ruedi, M., B. Stadelmann, Y. Gager, E. J. P. Douzery, C. M. Francis, L.-K. Lin, A. Guillén-Servent, and A. Cibois. 2013. Molecular phylogenetic reconstructions identify East Asia as the cradle for the evolution of the cosmopolitan genus Myotis (Mammalia, Chiroptera). Molecular Phylogenetics and Evolution 69:437–449.

Russo, D., D. Almenar, J. Aihartza, U. Goiti, E. Salsamendi, and I. Garin. 2005. Habitat selection in sympatric Rhinolophus mehelyi and R. euryale (Mammalia: Chiroptera). Journal of Zoology 266:327–332.

Russo, D., and L. Ancillotto. 2015. Sensitivity of bats to urbanization: a review. Mammalian Biology 80:205–212.

Russo, D., L. Bosso, and L. Ancillotto. 2018. Novel perspectives on bat insectivory highlight the value of this ecosystem service in farmland: Research frontiers and management implications. Agriculture, Ecosystems & Environment 266:31–38.

Russo, D., and G. Jones. 2003. Use of foraging habitats by bats (Mammalia : Chiroptera) in a Mediterranean area determined by acoustic surveys : conservation implications Use of foraging habitats by bats in a Mediterranean area determined by acoustic surveys : conservation implicatio. Ecography 26:197–209.

Rydell, J., L. Bach, M.-J. Dubourg-Savage, M. Green, L. Rodrigues, and A. Hedenström. 2010. Bat Mortality at Wind Turbines in Northwestern Europe. Acta Chiropterologica 12:261–274.

Salicini, I., C. Ibáñez, and J. Juste. 2013. Deep differentiation between and within

Mediterranean glacial refugia in a flying mammal, the Myotis nattereri bat complex. Journal of Biogeography 40:1182–1193.

Sallustio, L., A. De Toni, A. Strollo, M. Di Febbraro, E. Gissi, L. Casella, D. Geneletti, M. Munafò, M. Vizzarri, and M. Marchetti. 2017. Assessing habitat quality in relation to the spatial distribution of protected areas in Italy. Journal of Environmental Management 201:129–137.

Salvarina, I., D. Gravier, and K.-O. Rothhaupt. 2018. Seasonal bat activity related to insect emergence at three temperate lakes. Ecology and Evolution 8:3738–3750.

Santos, H., J. Juste, C. Ibáñez, J. M. Palmeirim, R. Godinho, F. Amorim, P. Alves, H. Costa, O. de Paz, G. Pérez-Suarez, S. Martínez-Alos, G. Jones, and H. Rebelo. 2014. Influences of ecology and biogeography on shaping the distributions of cryptic species: Three bat tales in Iberia. Biological Journal of the Linnean Society 112:150–162.

Saura, S., B. Bertzky, L. Bastin, L. Battistella, A. Mandrici, and G. Dubois. 2018. Protected area connectivity: Shortfalls in global targets and country-level priorities. Biological Conservation 219:53–67.

Saura, S., and L. Rubio. 2010. A common currency for the different ways in which patches and links can contribute to habitat availability and connectivity in the landscape. Ecography 33:523–537.

Saura, S., and J. Torne. 2009. Conefor Sensinode 2.2: a software package for quantifying the importance of habitat patches for landscape connectivity. Environmental Modelling & Software 24:135–139.

Schofer, E., and A. Hironaka. 2005. The Effects of World Society on Environmental Protection Outcomes. Social Forces 84:25–47.

Schoville, S. D., A. Dalongeville, G. Viennois, F. Gugerli, P. Taberlet, B. Lequette, N. Alvarez, and S. Manel. 2018. Preserving genetic connectivity in the European Alps protected area network. Biological Conservation 218:99–109.

Schwartz, M. W. 1999. CHOOSING THE APPROPRIATE SCALE OF RESERVES FOR CONSERVATION:83–108.

Serra-Cobo, J., M. López-Roig, T. Marquès-Bonet, and E. Lahuerta. 2000. Rivers as possible landmarks in the orientation flight of Miniopterus schreibersii. Acta Theriologica 45:347–352.

Shen, Y. Y., L. Liang, Z. H. Zhu, W. P. Zhou, D. M. Irwin, and Y. P. Zhang. 2010. Adaptive evolution of energy metabolism genes and the origin of flight in bats. Proceedings of the National Academy of Sciences 107:8666–8671.

Sherwin, H. A., W. I. Montgomery, and M. G. Lundy. 2013. The impact and implications of climate change for bats. Mammal Review 43:171–182.

Simmons, N. B., K. L. Seymour, J. Habersetzer, and G. F. Gunnell. 2008. Primitive Early Eocene bat from Wyoming and the evolution of flight and echolocation. Nature 451:818–821.

Simpkins, C. E., T. E. Dennis, T. R. Etherington, and G. L. W. Perry. 2018. Assessing the performance of common landscape connectivity metrics using a virtual ecologist approach. Ecological Modelling 367:13–23.

Singh, J. S. 2002. The biodiversity crisis: A multifaceted review. Current science 82:638–647.

Skoulikidis, N., E. Dimitriou, and I. Karaouzas. 2018. The Rivers of Greece. Springer.

Stahlschmidt, P., and C. A. Brühl. 2012. Bats as bioindicators - the need of a standardized method for acoustic bat activity surveys. Methods in Ecology and Evolution 3:503–508.

Standards and Petitions Working Group. 2006. Guidelines for Using the IUCN Red List Categories and Criteria.

Stephens, P. A., N. Pettorelli, J. Barlow, M. J. Whittingham, and M. W. Cadotte. 2015. Management by proxy? The use of indices in applied ecology. Journal of Applied Ecology 52:1–6.

Stockwell, D. R. B., and A. T. Peterson. 2002. Effects of sample size on accuracy of species distribution models. Ecological Modelling 148:1–13.

Storch, D. 2016. The theory of the nested species–area relationship: geometric foundations of biodiversity scaling. Journal of Vegetation Science 27:880–891.

Taylor, P. D., L. Fahrig, K. Henein, and G. Merriam. 1993. Connectivity Is a Vital Element of Landscape Structure. Oikos 68:571–573.

Taylor, P. J., I. Grass, A. J. Alberts, E. Joubert, and T. Tscharntke. 2018. Economic value of bat predation services – A review and new estimates from macadamia orchards. Ecosystem Services 30:372–381.

Thomas, C. D., P. K. Gillingham, R. B. Bradbury, D. B. Roy, B. J. Anderson, J. M. Baxter, N. A. D. Bourn, H. Q. P. Crick, R. A. Findon, R. Fox, J. A. Hodgson, A. R. Holt, M. D. Morecroft, N. J. O'Hanlon, T. H. Oliver, J. W. Pearce-Higgins, D. A. Procter, J. A. Thomas, K. J. Walker, C. A. Walmsley, R. J. Wilson, and J. K. Hill. 2012. Protected areas facilitate species' range expansions. Proceedings of the National Academy of Sciences 109:14063–14068.

Thomas, C. D., C. D. Thomas, A. Cameron, A. Cameron, R. E. Green, R. E. Green, M. Bakkenes, M. Bakkenes, L. J. Beaumont, L. J. Beaumont, Y. C. Collingham, Y. C. Collingham, B. F. N. Erasmus, B. F. N. Erasmus, M. F. De Siqueira, M. F. De Siqueira, A. Grainger, A. Grainger, L. Hannah, L. Hannah, L. Hughes, L. Hughes, B. Huntley, B. Huntley, A. S. Van Jaarsveld, A. S. Van Jaarsveld, G. F. Midgley, G. F. Midgley, L. Miles, L. Miles, M. a Ortega-Huerta, M. a Ortega-Huerta, a T. Peterson, a T. Peterson, O. L. Phillips, O. L. Phillips, S. E. Williams, and S. E. Williams. 2004. Extinction risk from climate change. Nature 427:145–148.

Tillon, L., M. Barataud, S. Giosa, and S. Aulagnier. 2018. Acoustic detection of radiotracked foraging bats in temperate lowland forests. Mammalian Biology:6–10.

Toukhsati, S. R. 2018. Animal Extinctions. Pages 499–518 Animals and Human Society. Elsevier.

Turner, G. G., D. Reeder, and J. T. H. Coleman. 2011. A Five-year Assessment of Mortality and Geographic Spread of White-Nose Syndrome in North American Bats, with a look to the future. Update of White-Nose Syndrome in bats. Bat Research News 52:13–27.

Ulrich, W., K. Sachanowicz, and M. Michalak. 2007. Environmental correlates of species richness of European bats (Mammalia: Chiroptera). Acta Chiropterologica 9:347–360.

Unglaub, B., S. Steinfartz, D. Kühne, A. Haas, and B. R. Schmidt. 2018. The relationships between habitat suitability, population size and body condition in a pond-breeding amphibian. Basic and Applied Ecology 27:20–29.

Vale, C. G., P. Tarroso, and J. C. Brito. 2014. Predicting species distribution at range margins: Testing the effects of study area extent, resolution and threshold selection in the Sahara-Sahel transition zone. Diversity and Distributions 20:20–33.

Velez–Liendo, X., D. Strubbe, and E. Matthysen. 2013. Effects of variable selection on modelling habitat and potential distribution of the Andean bear in Bolivia. Ursus 24:127–138.

Veloz, S. D. 2009. Spatially autocorrelated sampling falsely inflates measures of accuracy for presence-only niche models. Journal of Biogeography 36:2290–2299.

Walsh, A. L., and S. Harris. 1996. Factors determing the abundance of vespertillionid bats in Britain: geographical. Land classes and local habitat relationships. Journal of Applied Ecology 33:519–529.

Warren, D. L., R. E. Glor, and M. Turelli. 2010. ENMTools: a toolbox for comparative studies of environmental niche models. Ecography 33:607–611.

Webb, P. I., J. R. Speakman, and P. A. Racey. 1995. Evaporative Water-Loss in 2 Sympatric Species of Vespertilionid Bat, Plecotus-Auritus and Myotis-Daubentoni - Relation to Foraging Mode and Implications for Roost Site Selection. Journal of Zoology 235:269–278.

Webster, M. S., P. P. Marra, S. M. Haig, S. Bensch, and R. T. Holmes. 2002. Links between worlds: Unraveling migratory connectivity. Trends in Ecology and Evolution 17:76–83.

Weiss, E. B. 2011. The Evolution of International Environmental Law. Japanese Y.B. Intl. Law 54:1–27.

Wermundsen, T., and Y. Siivonen. 2008. Foraging habitats of bats in southern Finland. Acta Theriologica 53:229–240.

Whitaker, J. O. 1995. Food of the Big Brown Bat Eptesicus fuscus from Maternity Colonies in Indiana and Illinois Food of the Big Brown Bat Eptesicus fuscus from Maternity Colonies in Indiana and Illinois. American Midland Naturalist 134:346–360.

Wickramasinghe, L. P., S. Harris, G. Jones, and N. Vaughan. 2003. Bat activity and species richness on organic and conventional farms: impact of agricultural intensification. Journal of applied ecology 40:984–993.

Willig, M. R., and S. J. Presley. 2013. Latitudinal Gradients of Biodiversity. Encyclopedia of Biodiversity: Second Edition:612–626.

Wisz, M. S., R. J. Hijmans, J. Li, A. T. Peterson, C. H. Graham, A. Guisan, J. Elith, M. Dudík, S. Ferrier, F. Huettmann, J. R. Leathwick, A. Lehmann, L. Lohmann, B. A.

Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. M. C. Overton, S. J. Phillips, K. S. Richardson, R. Scachetti-Pereira, R. E. Schapire, J. Soberón, S. E. Williams, and N. E. Zimmermann. 2008. Effects of sample size on the performance of species distribution models. Diversity and Distributions 14:763–773.

Yuan, X., Y. Jiang, and Z. Yan. 2018. On the Causes of the Decrease of Biodiversity and the Countermeasures. Natural Resources Conservation and Research:15–21.

Zubaid, A., G. M. McCracken, G. F. McCracken, and T. Kunz. 2006. Functional and evolutionary ecology of bats. Page (A. Zubaid and E. Gary F. McCracken Thomas H. Kunz, Eds.). Oxford University Press.

Annex

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SDM´s and Connectivity results

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Barbatella barbastellus

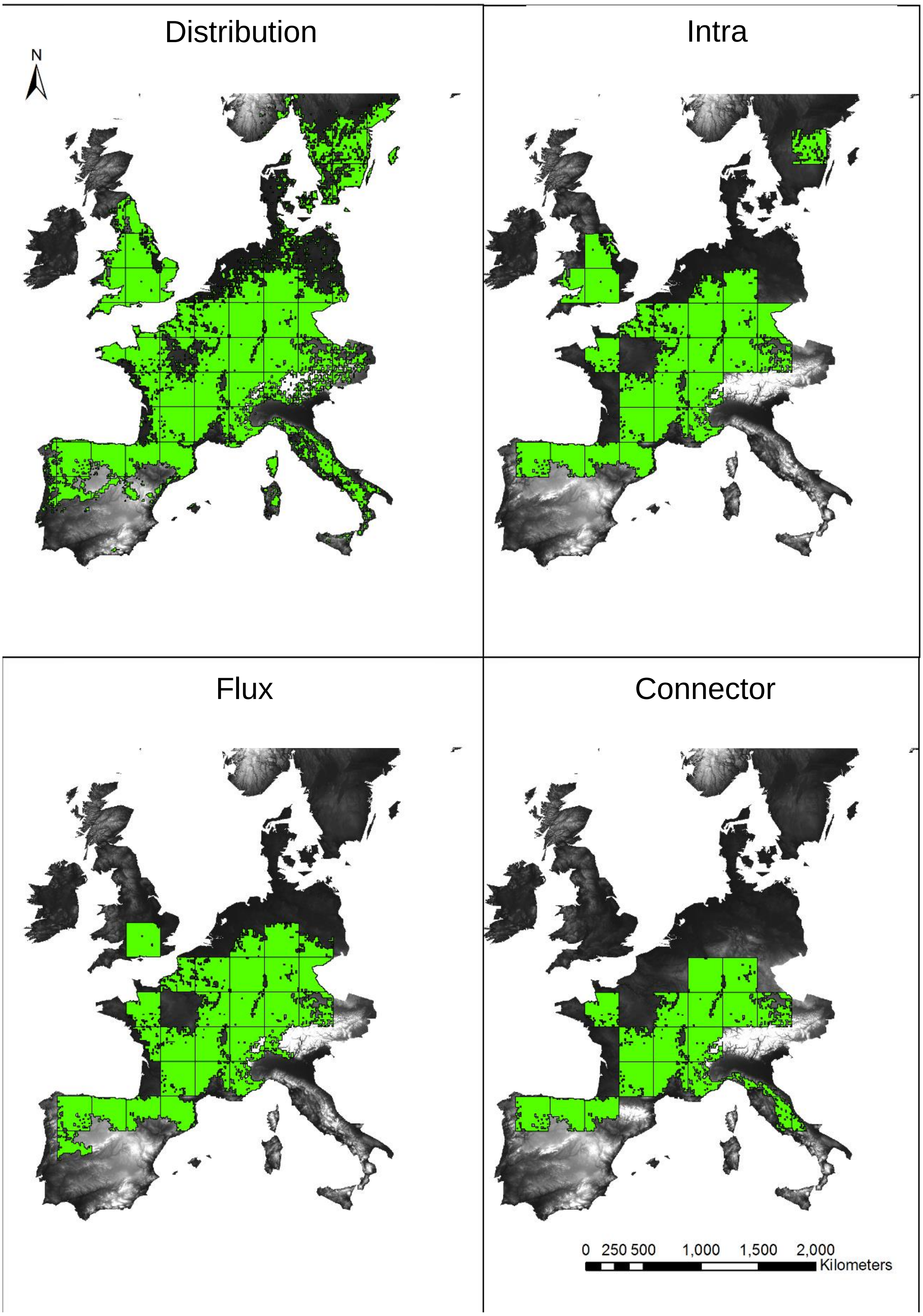


Figure 17- Barbatella barbastellus results regarding species distribution and patches with connectivity importance higher or equal to 1%

Eptesicus isabellinus

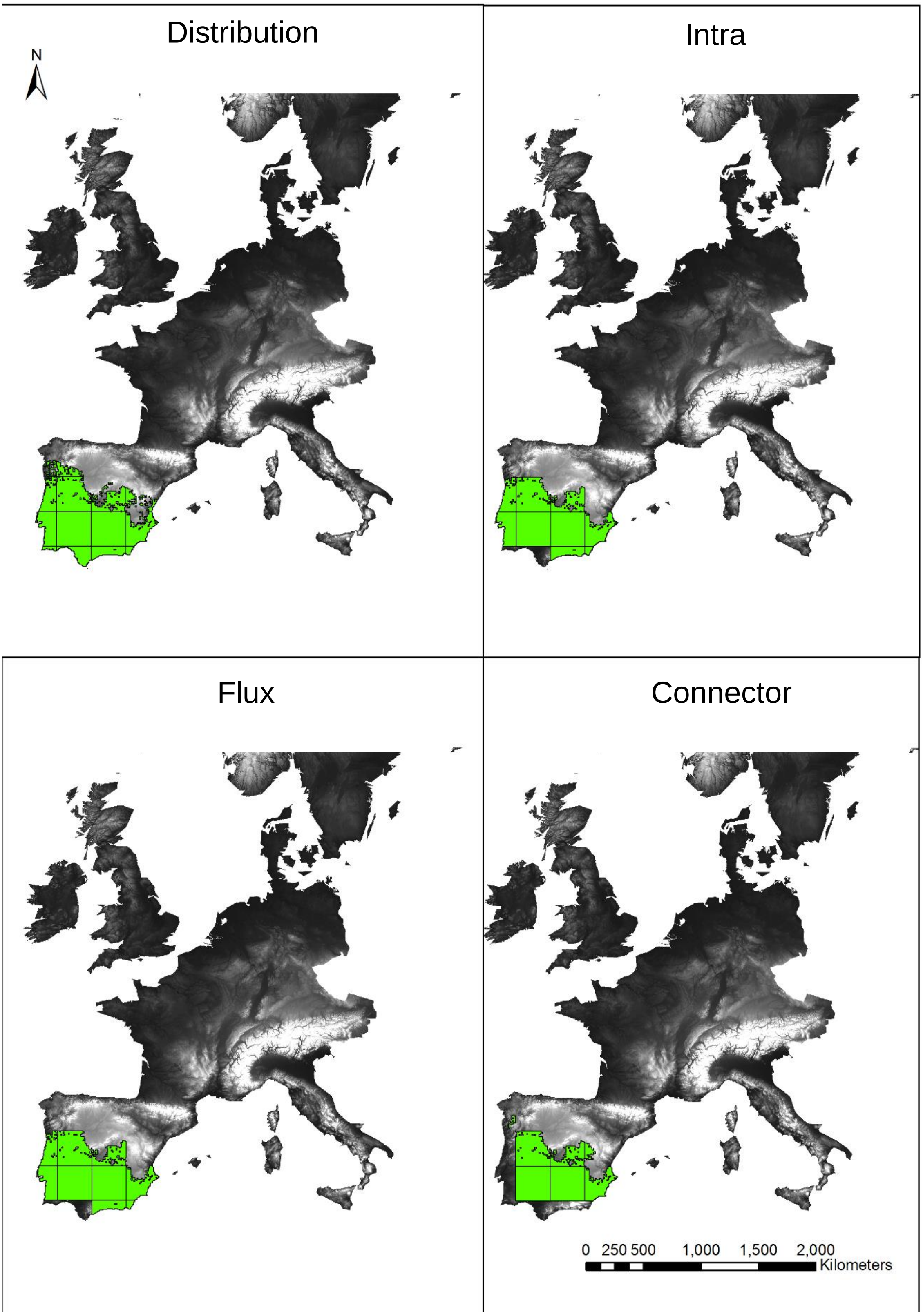


Figure 18- Eptesicus isabellinus results regarding species distribution and patches with connectivity importance higher or equal to 1%

Eptesicus nilssonii

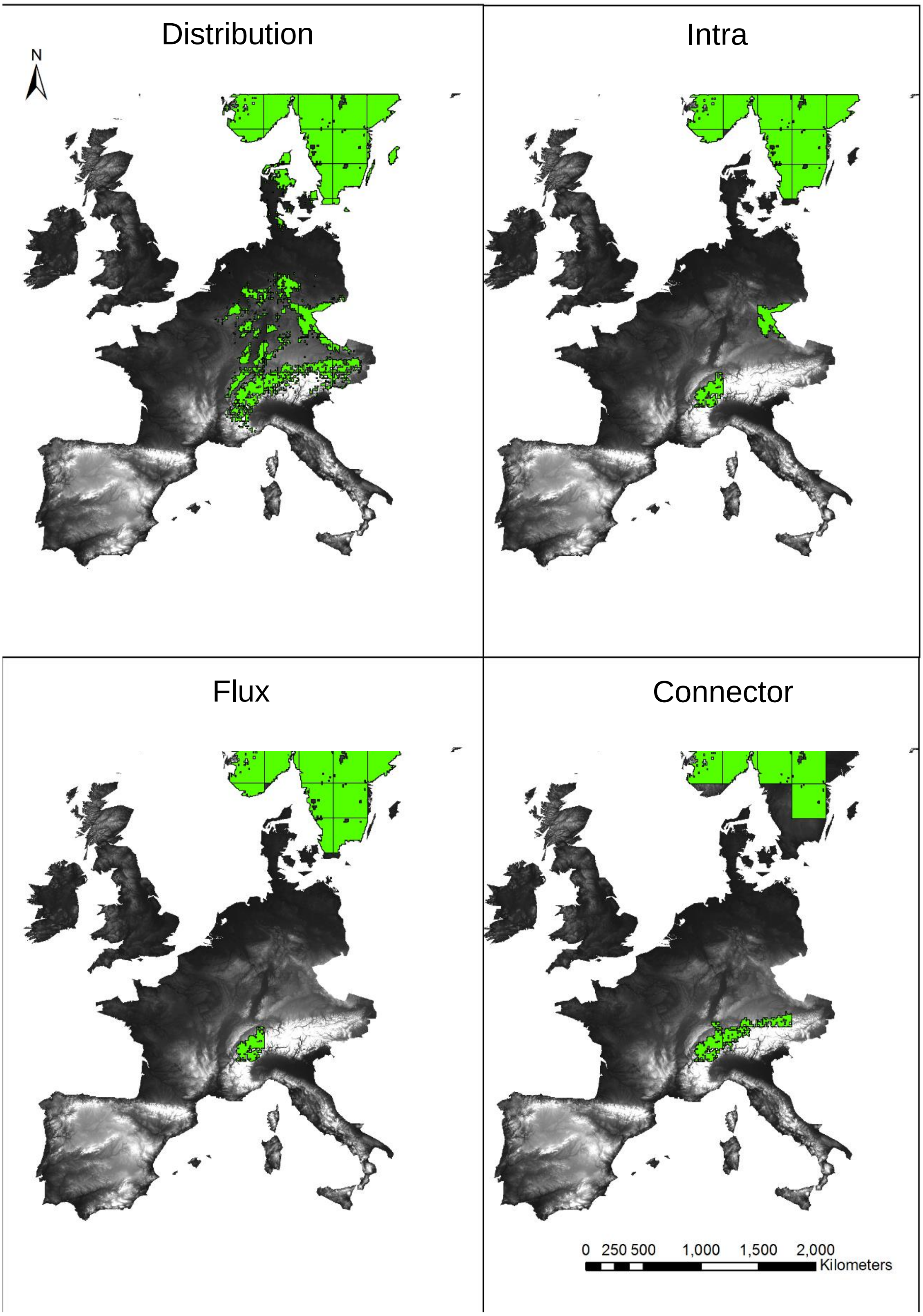


Figure 19- Eptesicus nilssonii results regarding species distribution and patches with connectivity importance higher or equal to 1%

Eptesicus serotinus

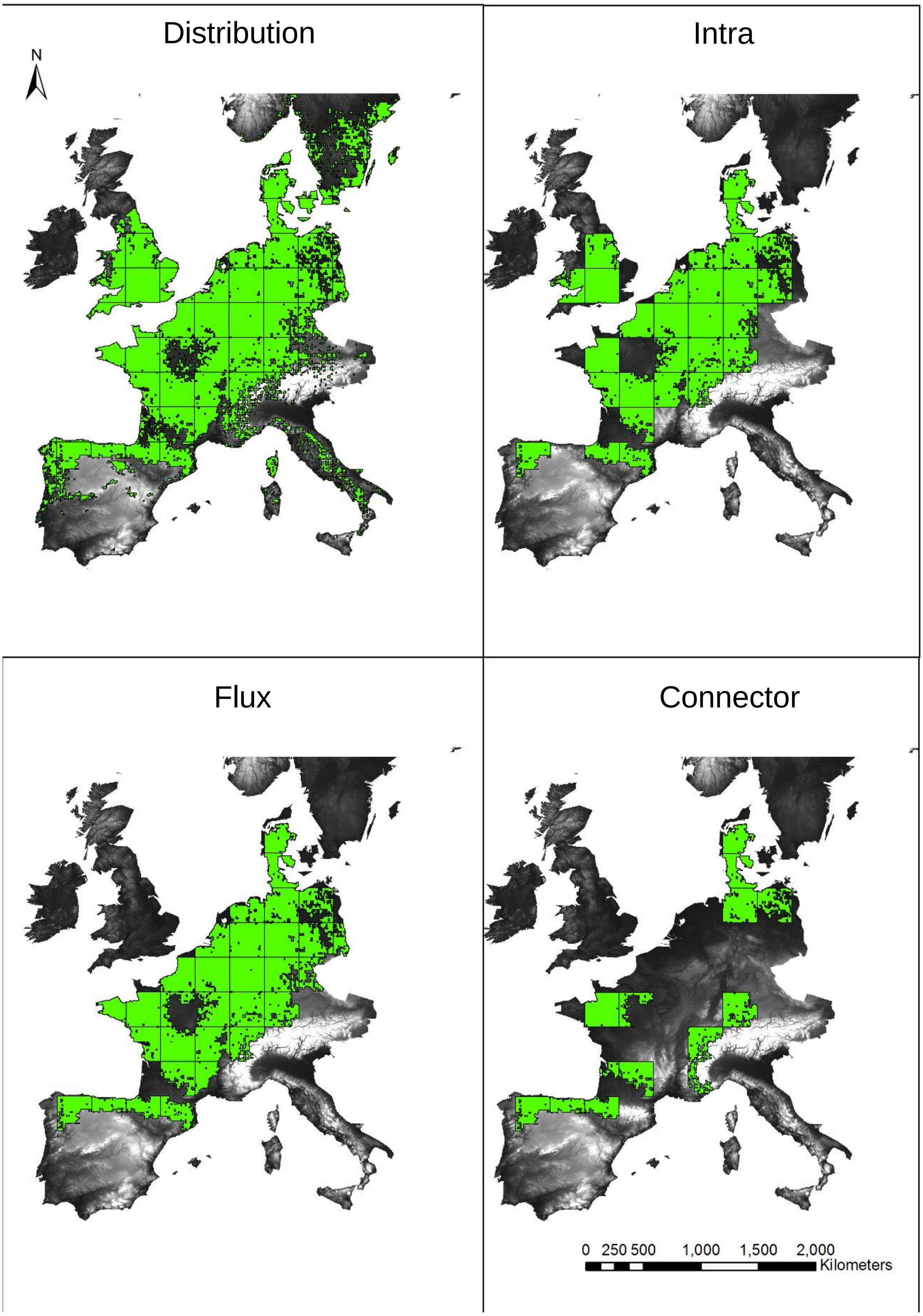


Figure 20- Eptesicus serotinus results regarding species distribution and patches with connectivity importance higher or equal to 1%

Hypsugo savii

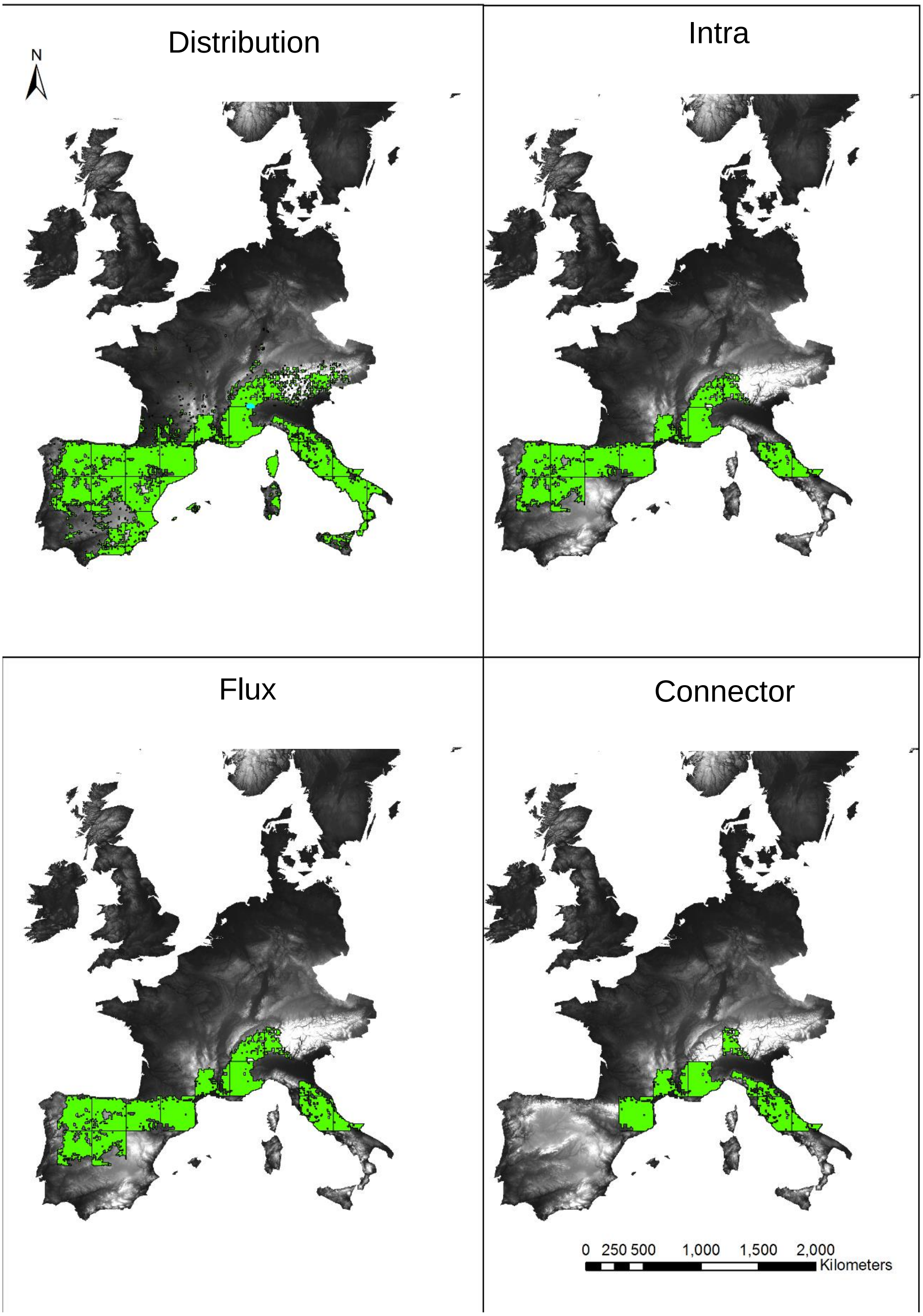


Figure 21- Hypsugo savii results regarding species distribution and patches with connectivity importance higher or equal to 1%

Miniopterus schreibersii

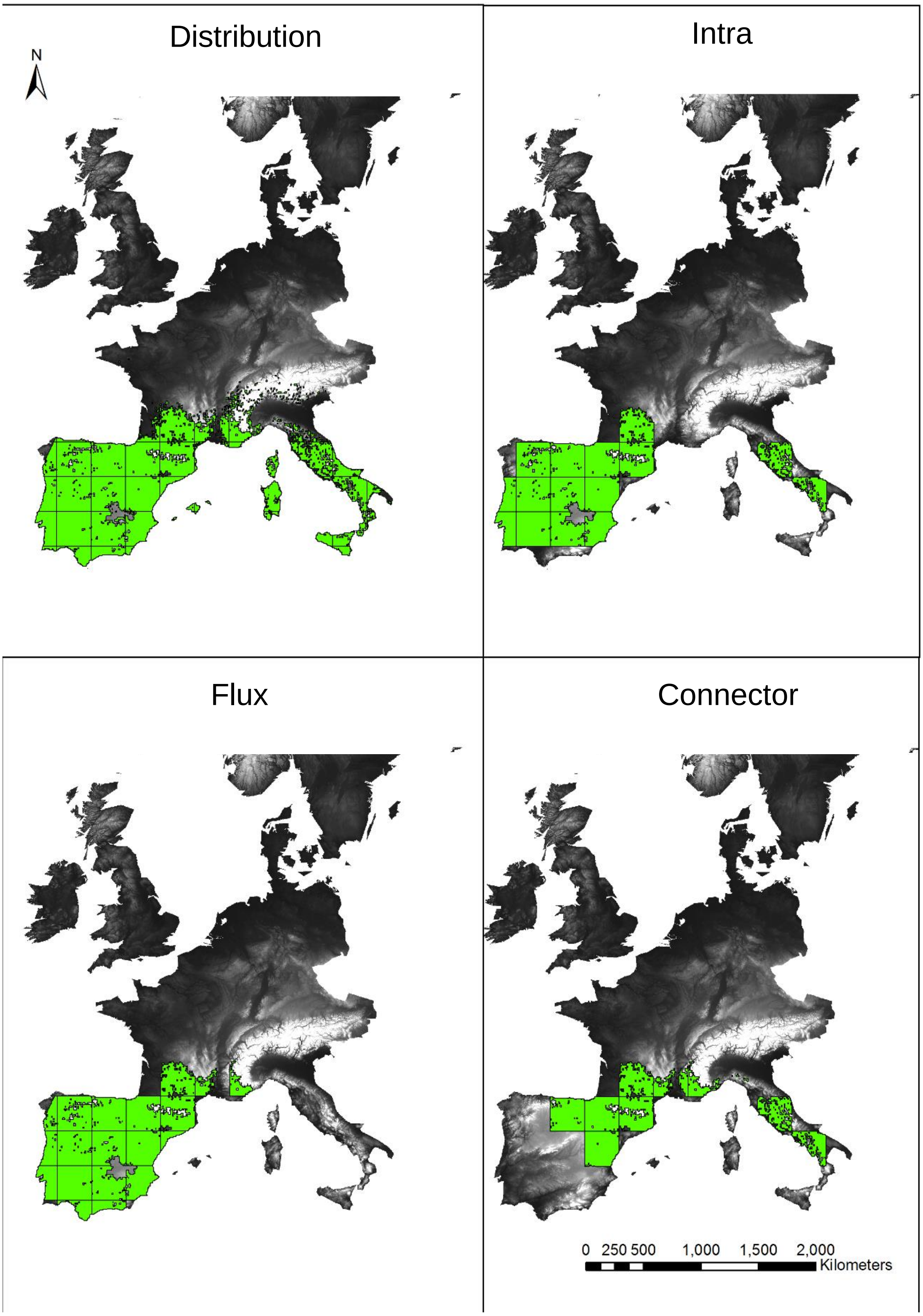


Figure 22- Miniopterus schreibersii results regarding species distribution and patches with connectivity importance higher or equal to 1%

Myotis bechsteinii

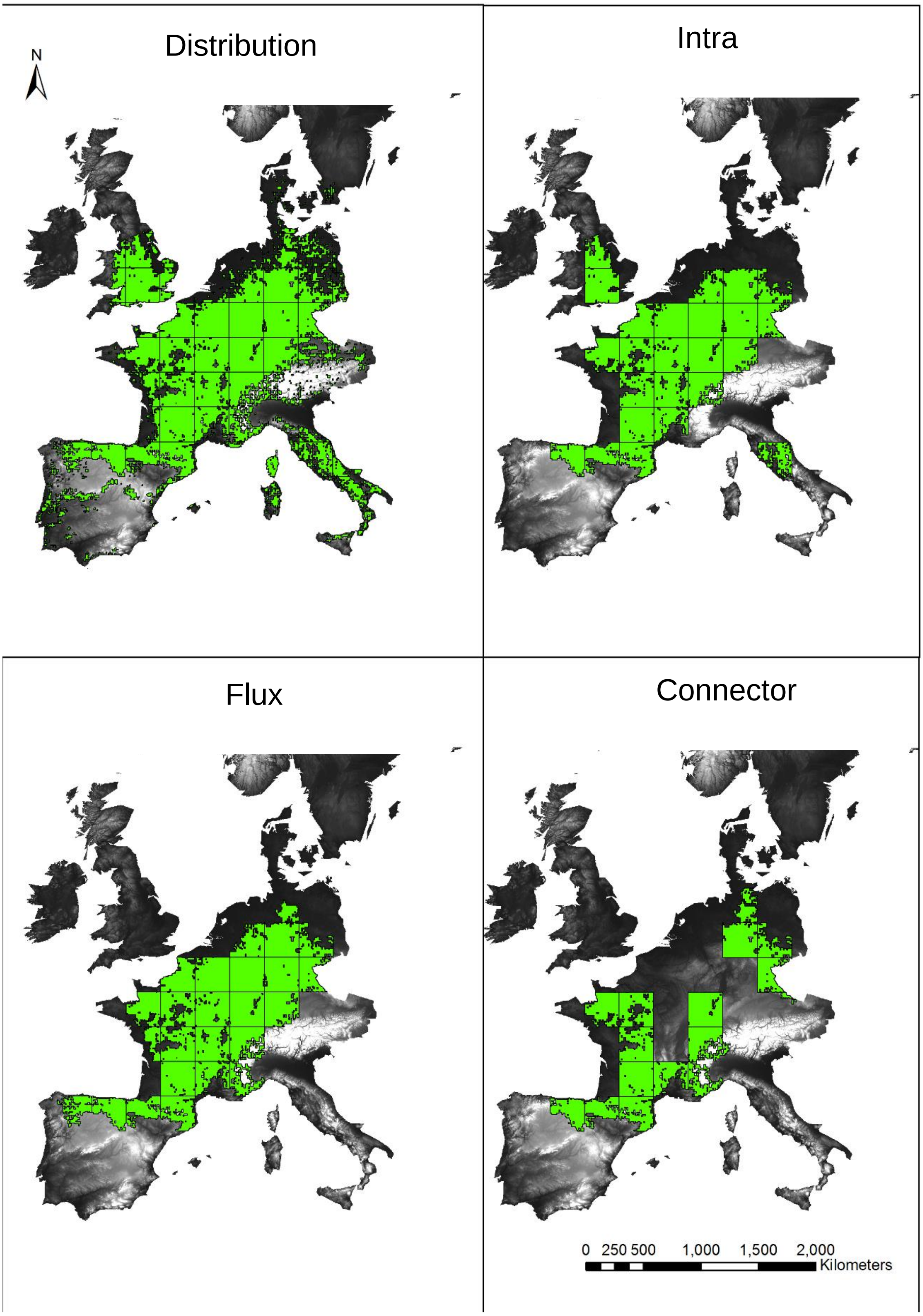


Figure 23 - Myotis bechsteinii results regarding species distribution and patches with connectivity importance higher or equal to 1%

Myotis brandtii

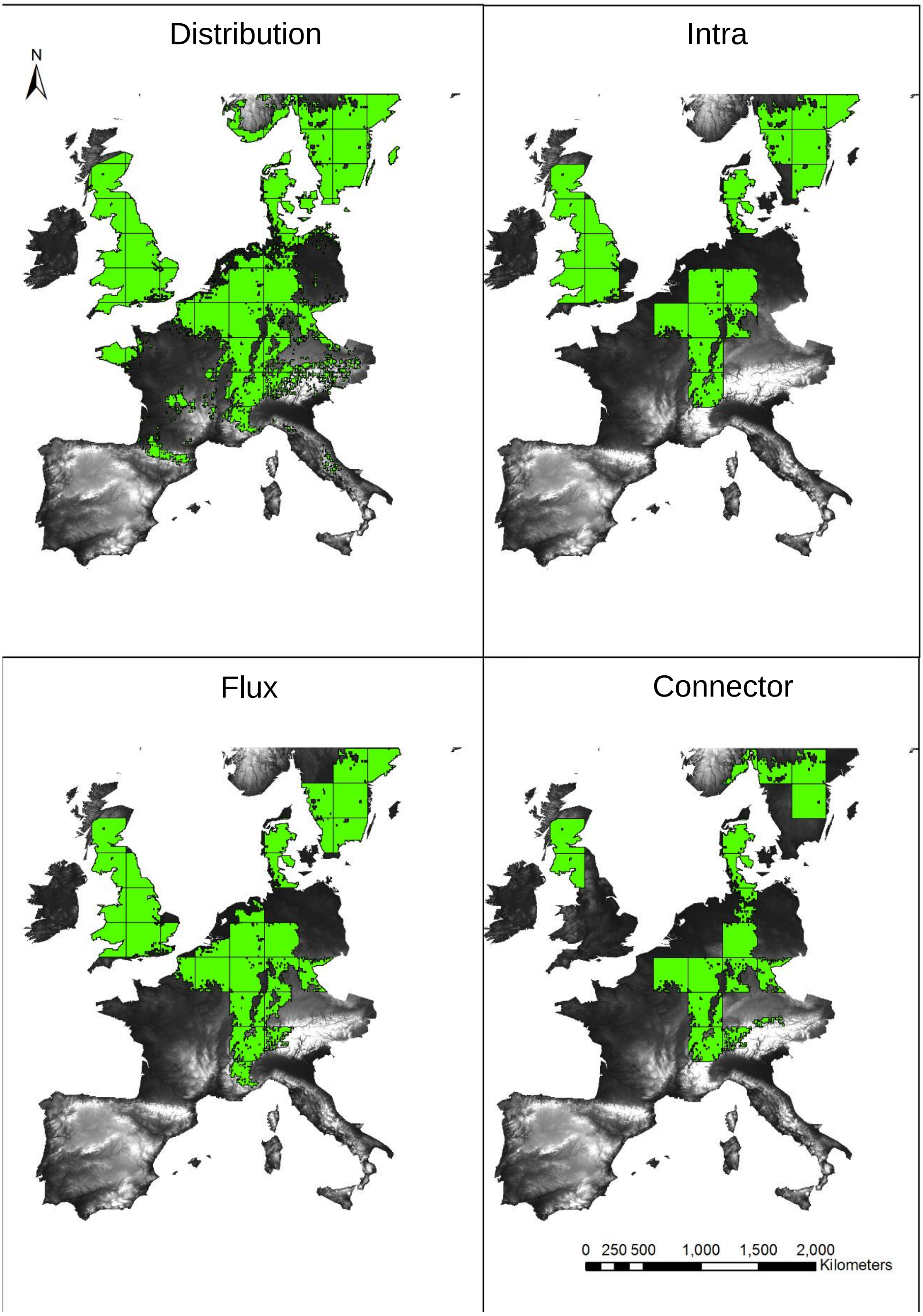


Figure 24 - Myotis brandtii results regarding species distribution and patches with connectivity importance higher or equal to 1%

Myotis capaccinii

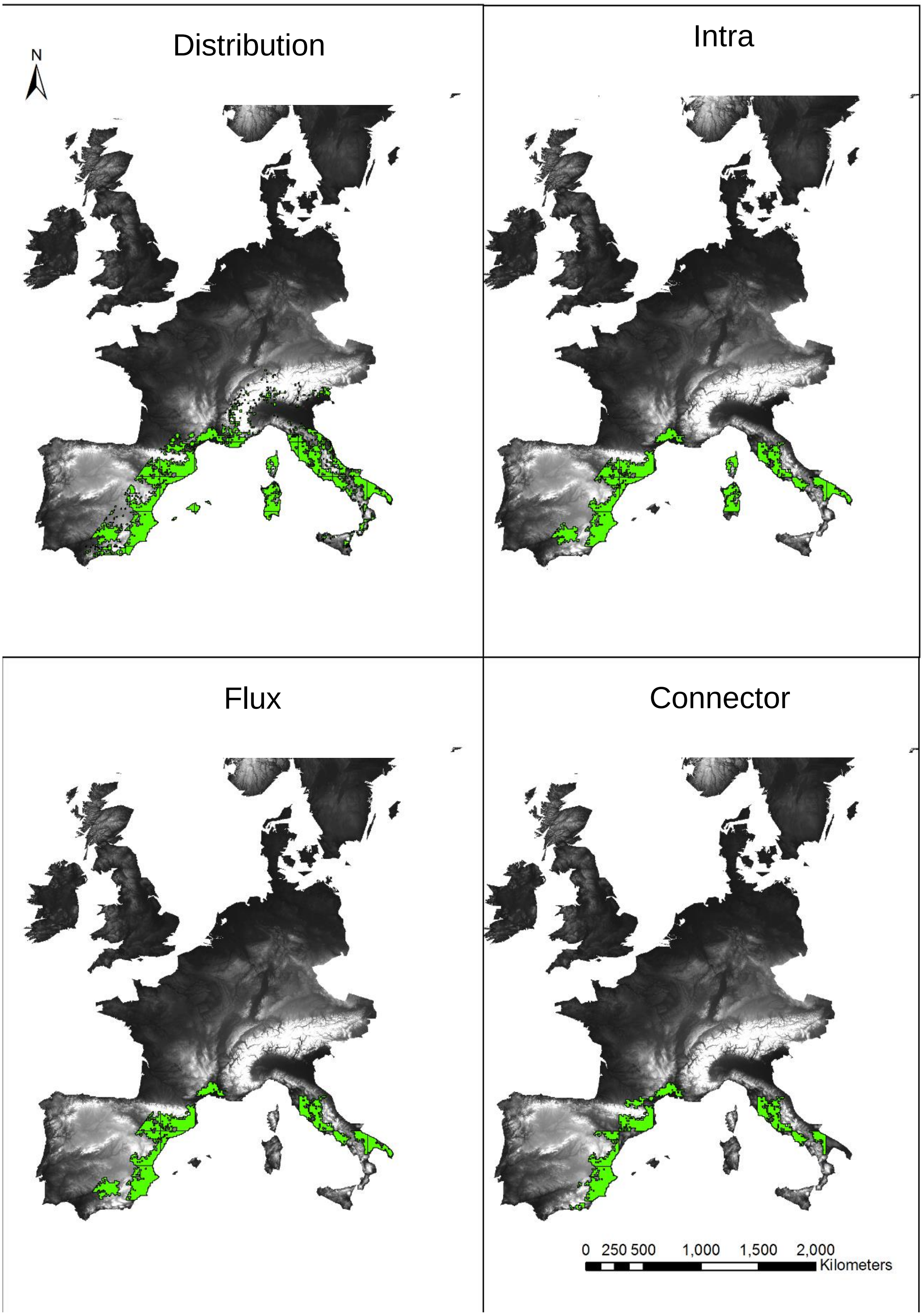


Figure 25- Myotis capaccinii results regarding species distribution and patches with connectivity importance higher or equal to 1%

Myotis dasycneme

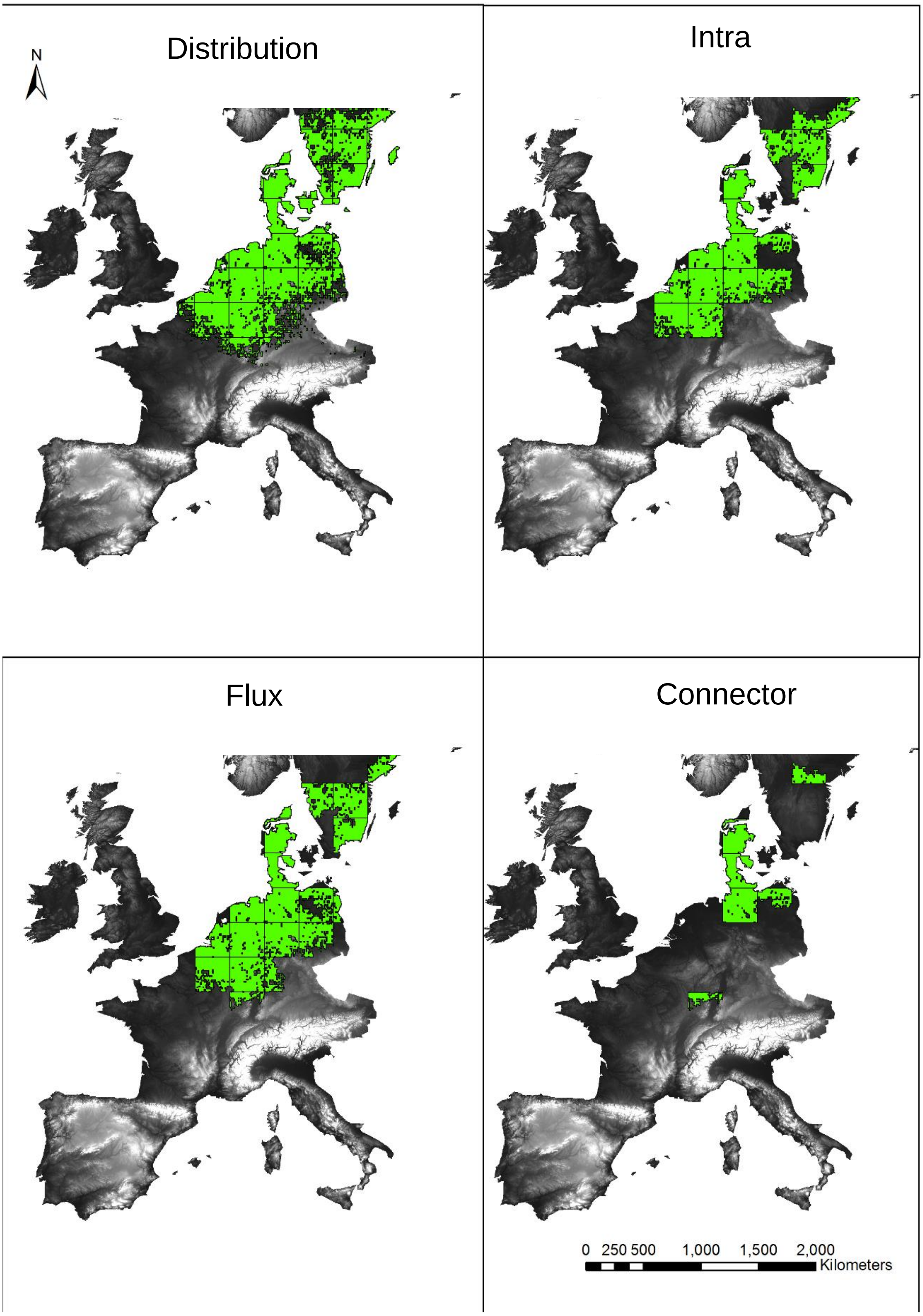


Figure 26- Myotis dasycneme results regarding species distribution and patches with connectivity importance higher or equal to 1%

Myotis daubentonii

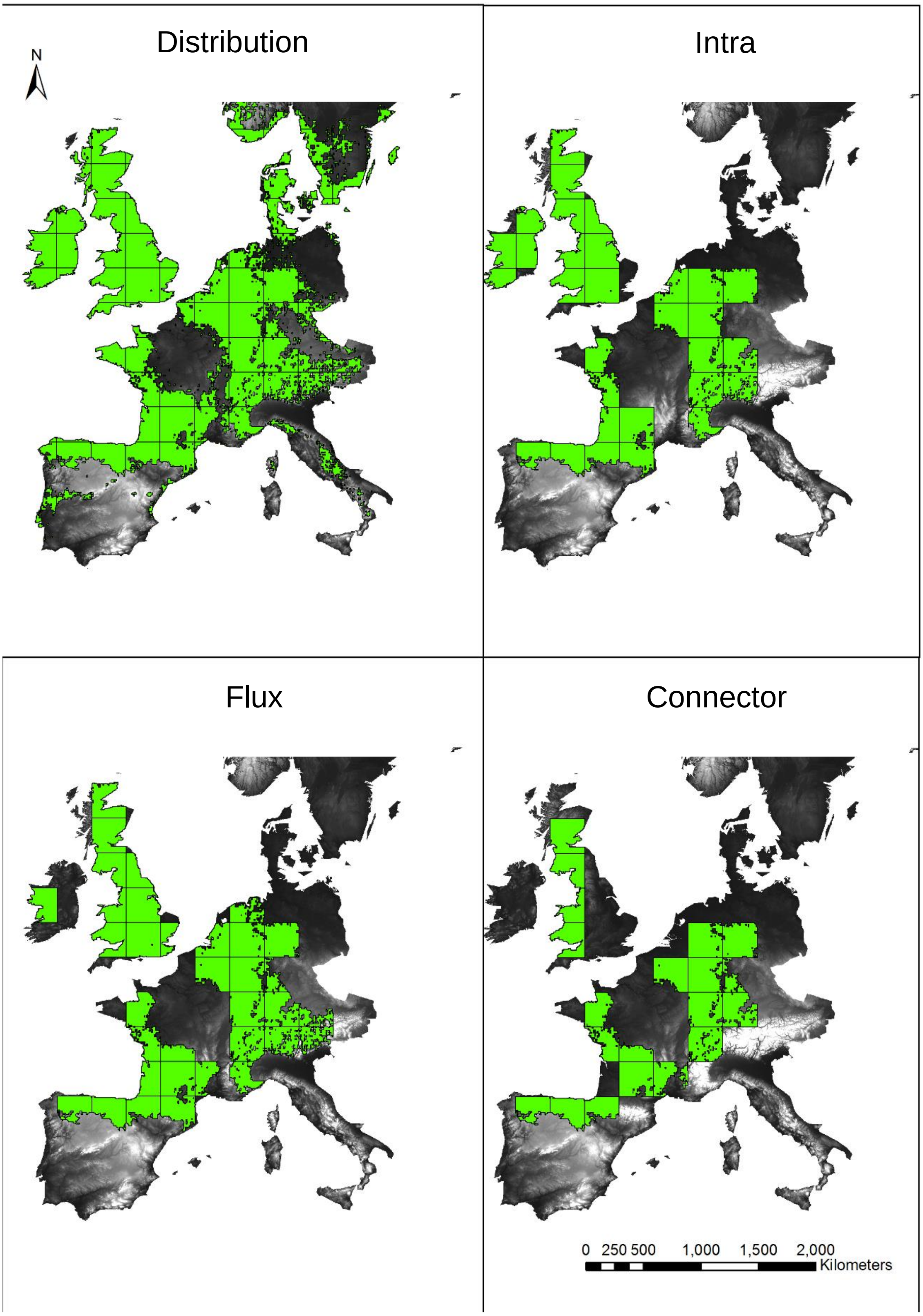


Figure 27- Myotis daubentonii results regarding species distribution and patches with connectivity importance higher or equal to 1%

Myotis emarginatus

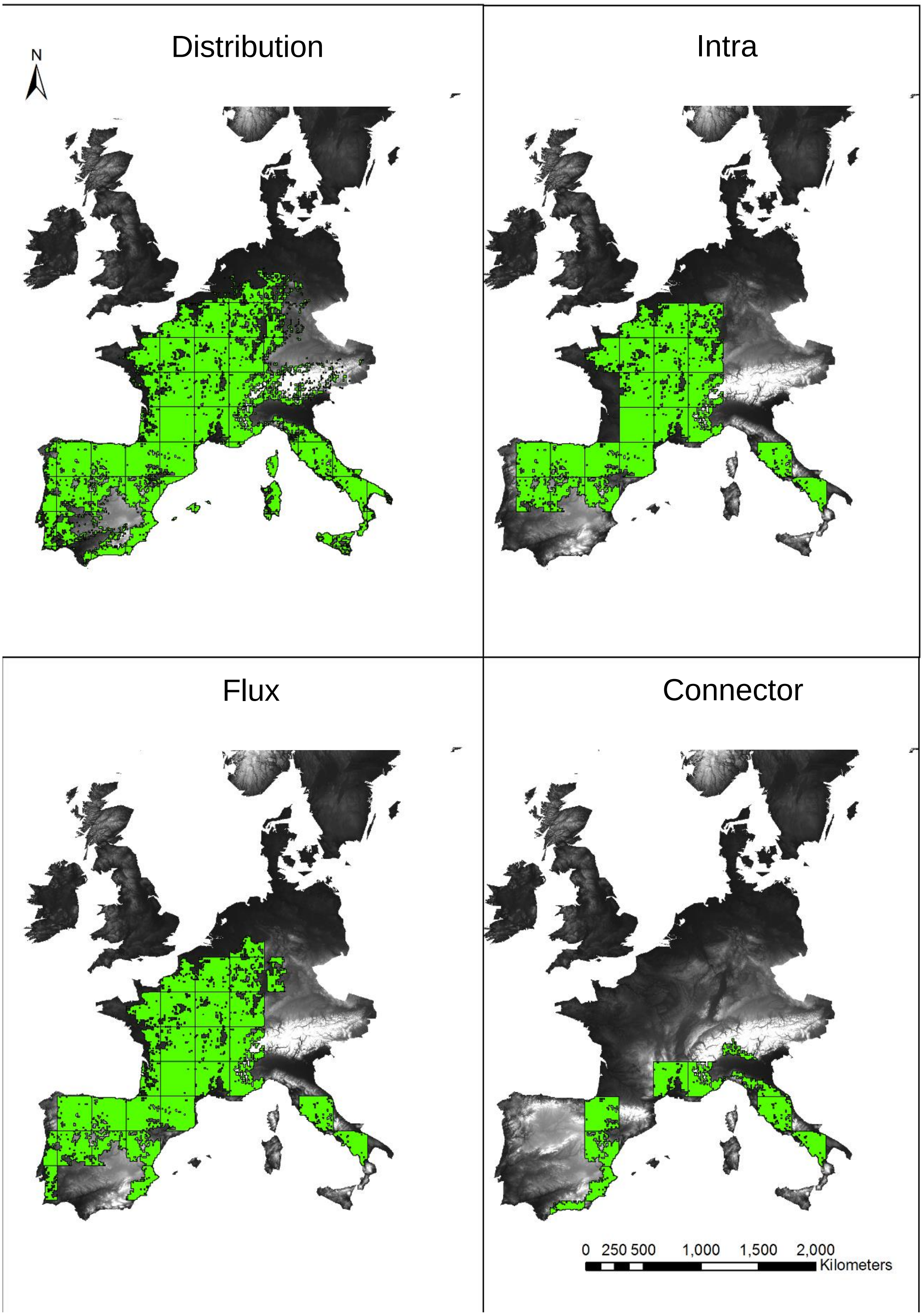


Figure 28- Myotis emarginatus results regarding species distribution and patches with connectivity importance higher or equal to 1%

Myotis myotis

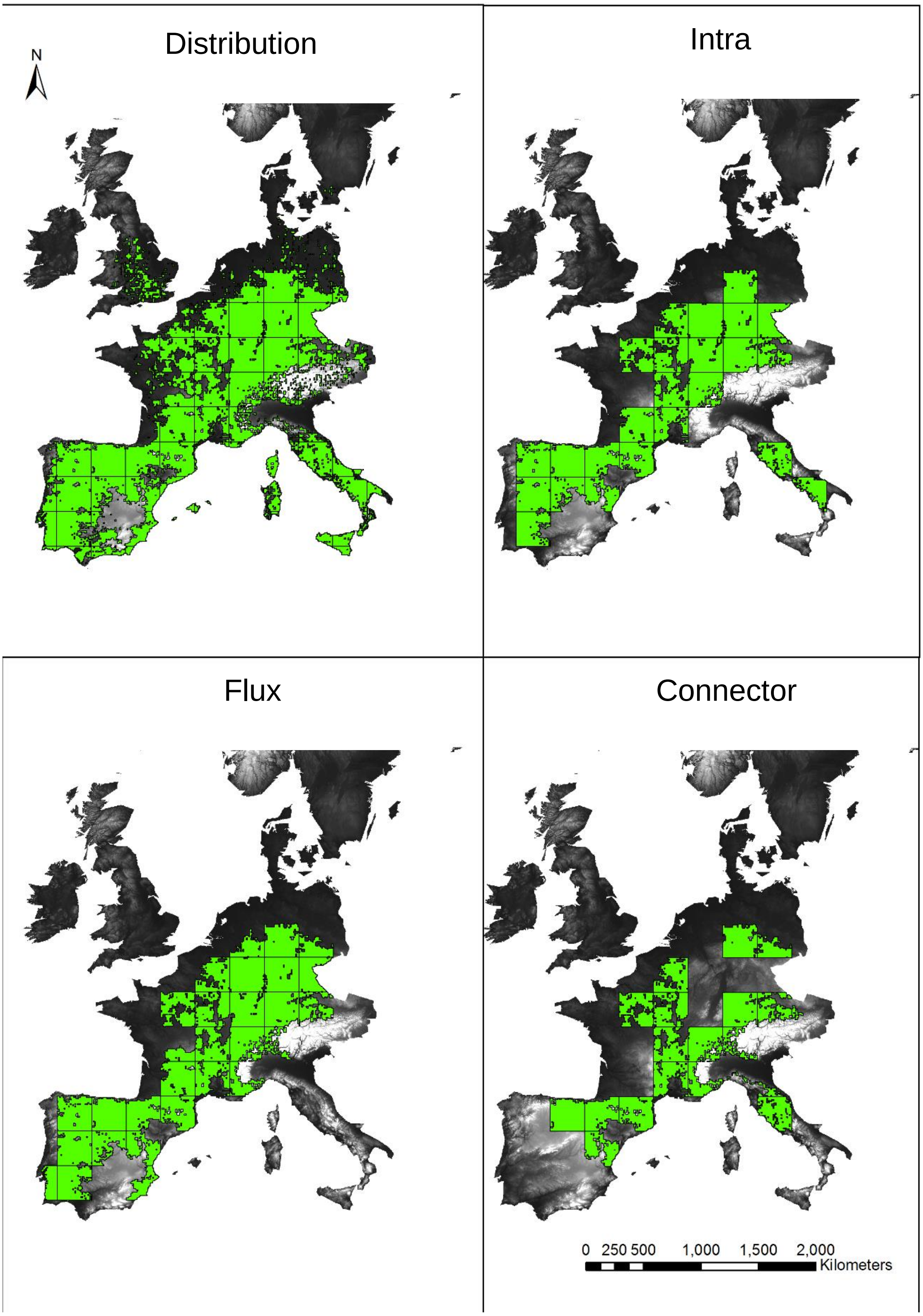


Figure 29- Myotis myotis results regarding species distribution and patches with connectivity importance higher or equal to 1%

Myotis mystacinus

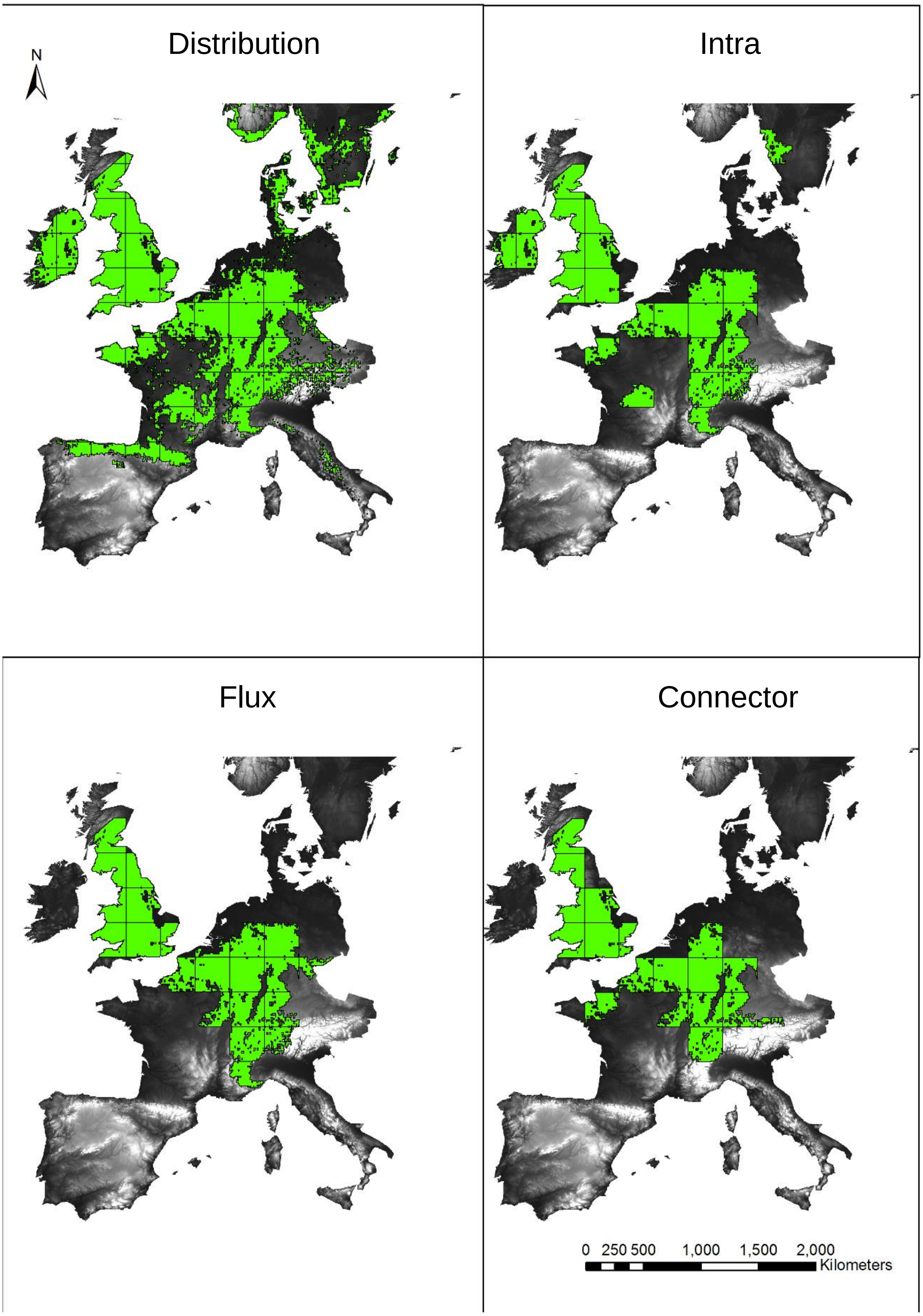


Figure 30- Myotis mystacinus results regarding species distribution and patches with connectivity importance higher or equal to 1%

Nyctalus leisleri

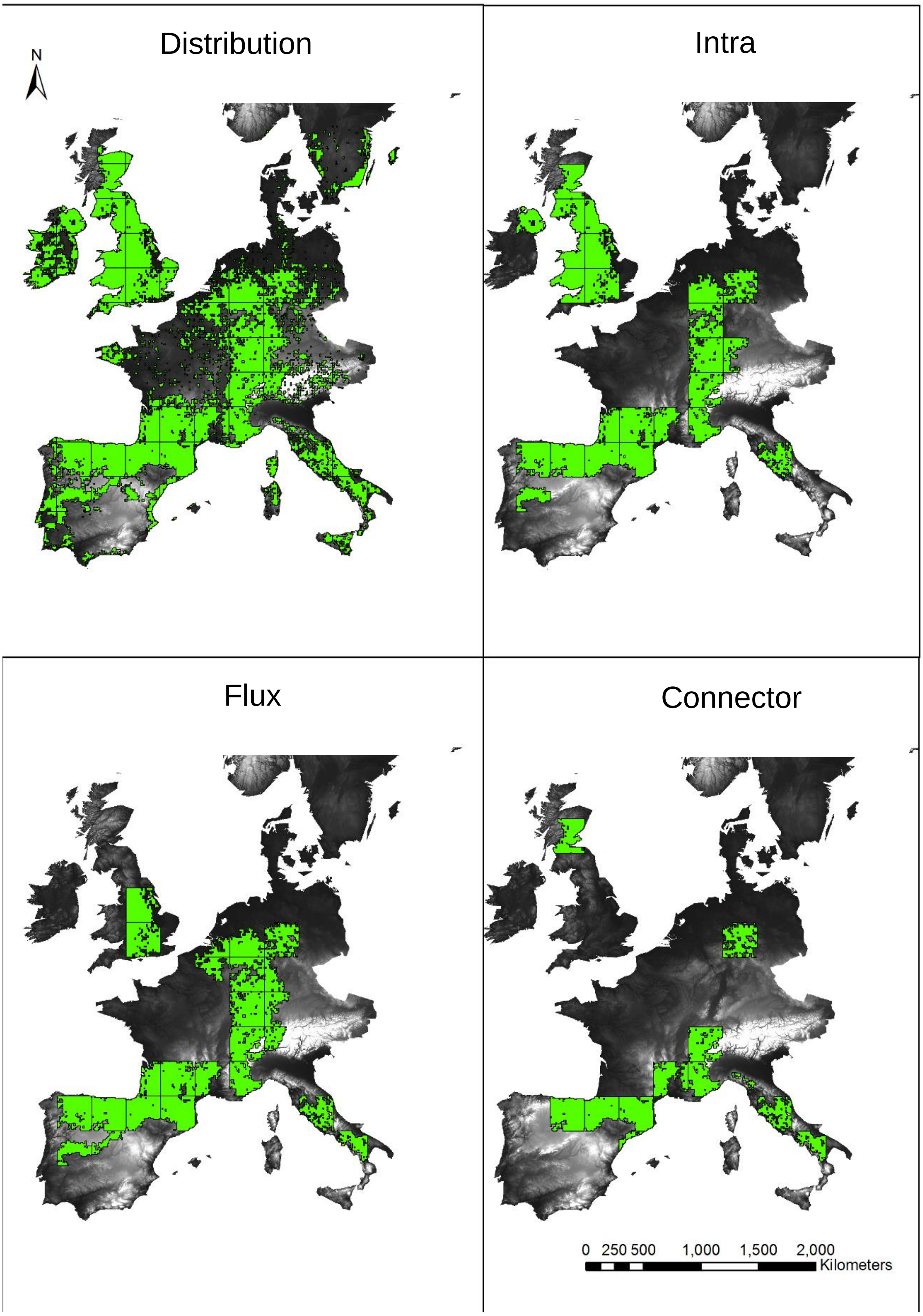


Figure 31- Nyctalus leisleri results regarding species distribution and patches with connectivity importance higher or equal to 1%

Nyctalus noctula

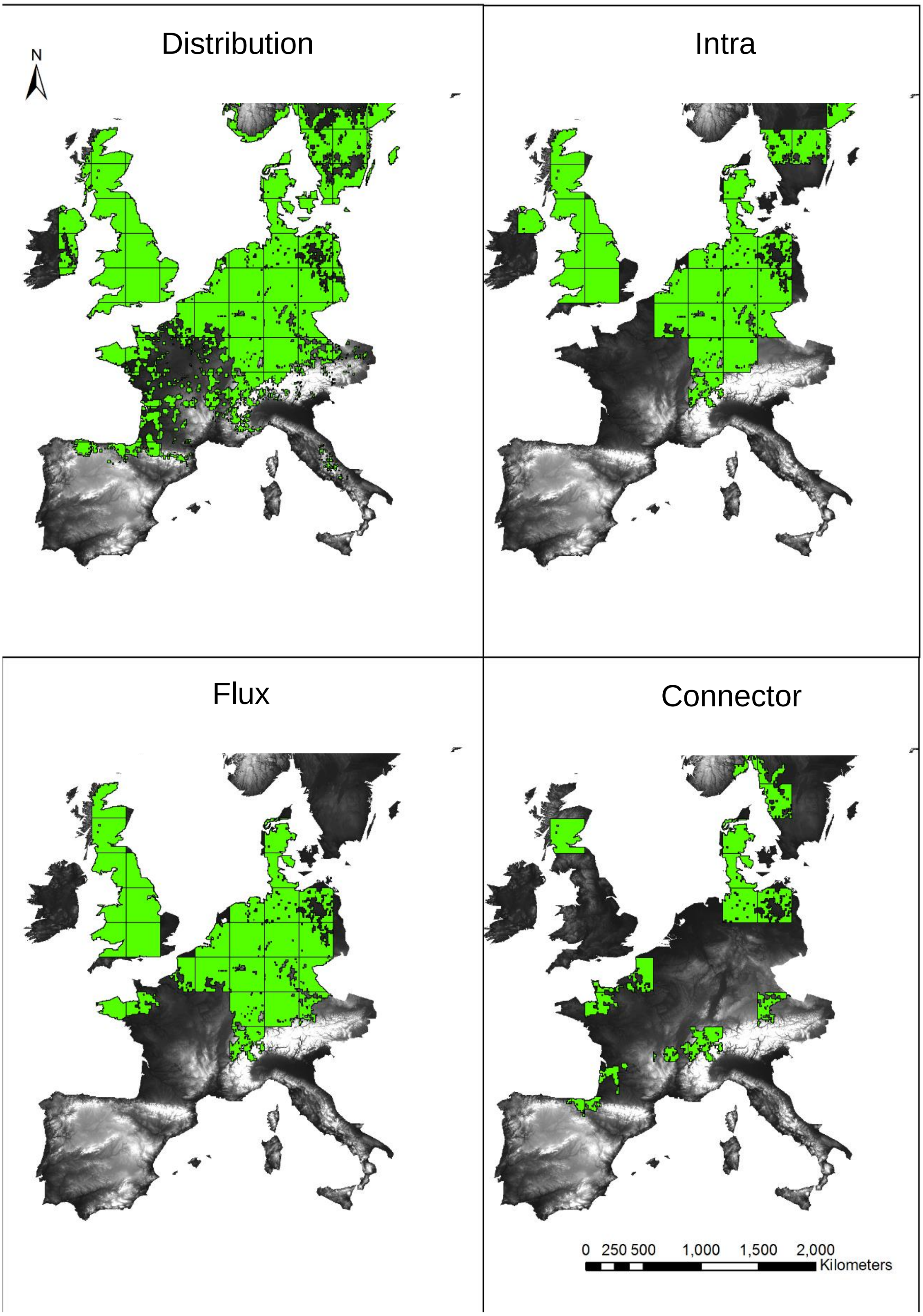


Figure 32- Nyctalus noctula results regarding species distribution and patches with connectivity importance higher or equal to 1%

Pipistrellus kuhlii

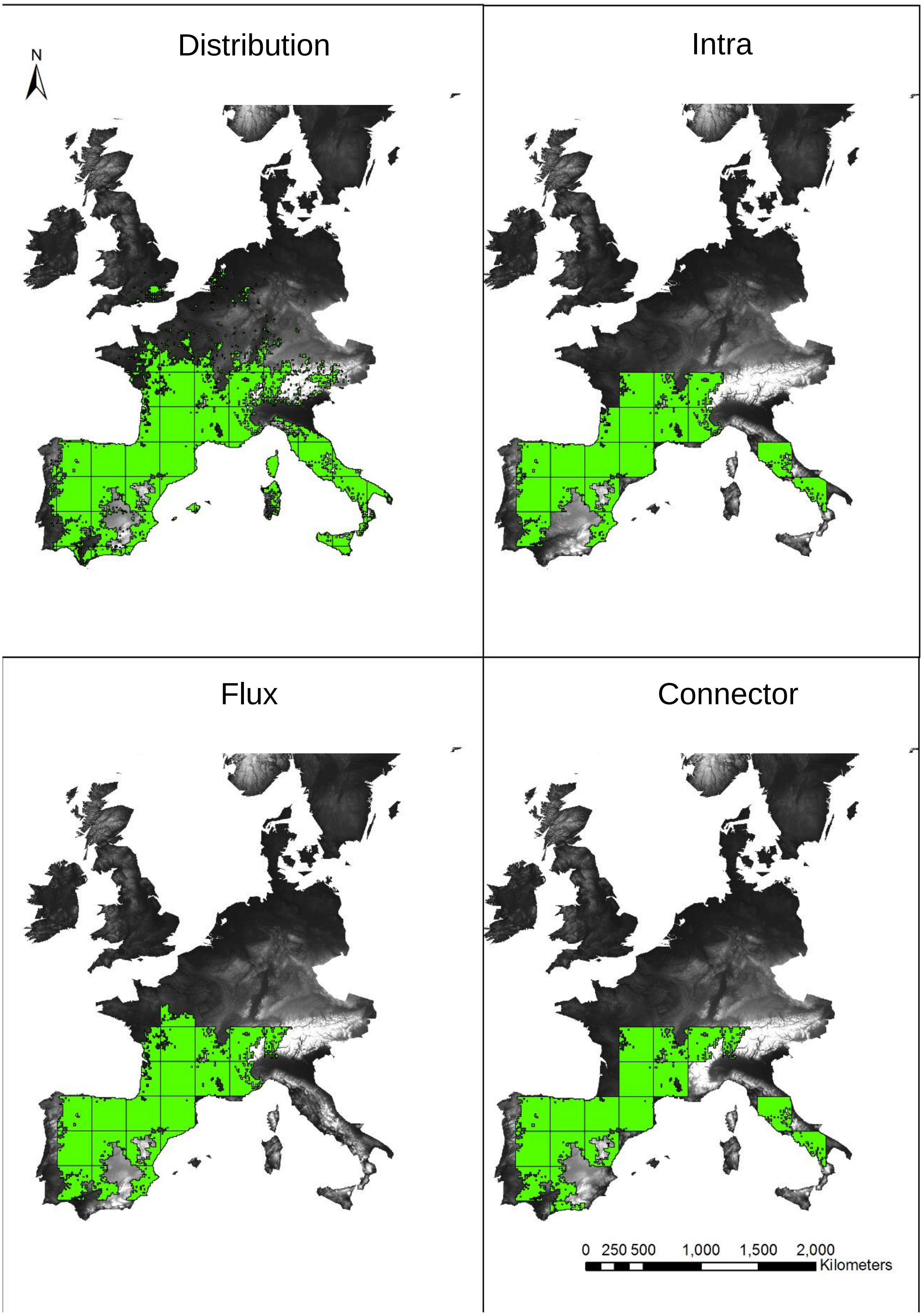


Figure 33- Pipistrellus kuhlii results regarding species distribution and patches with connectivity importance higher or equal to 1%

Pipistrellus nathusii

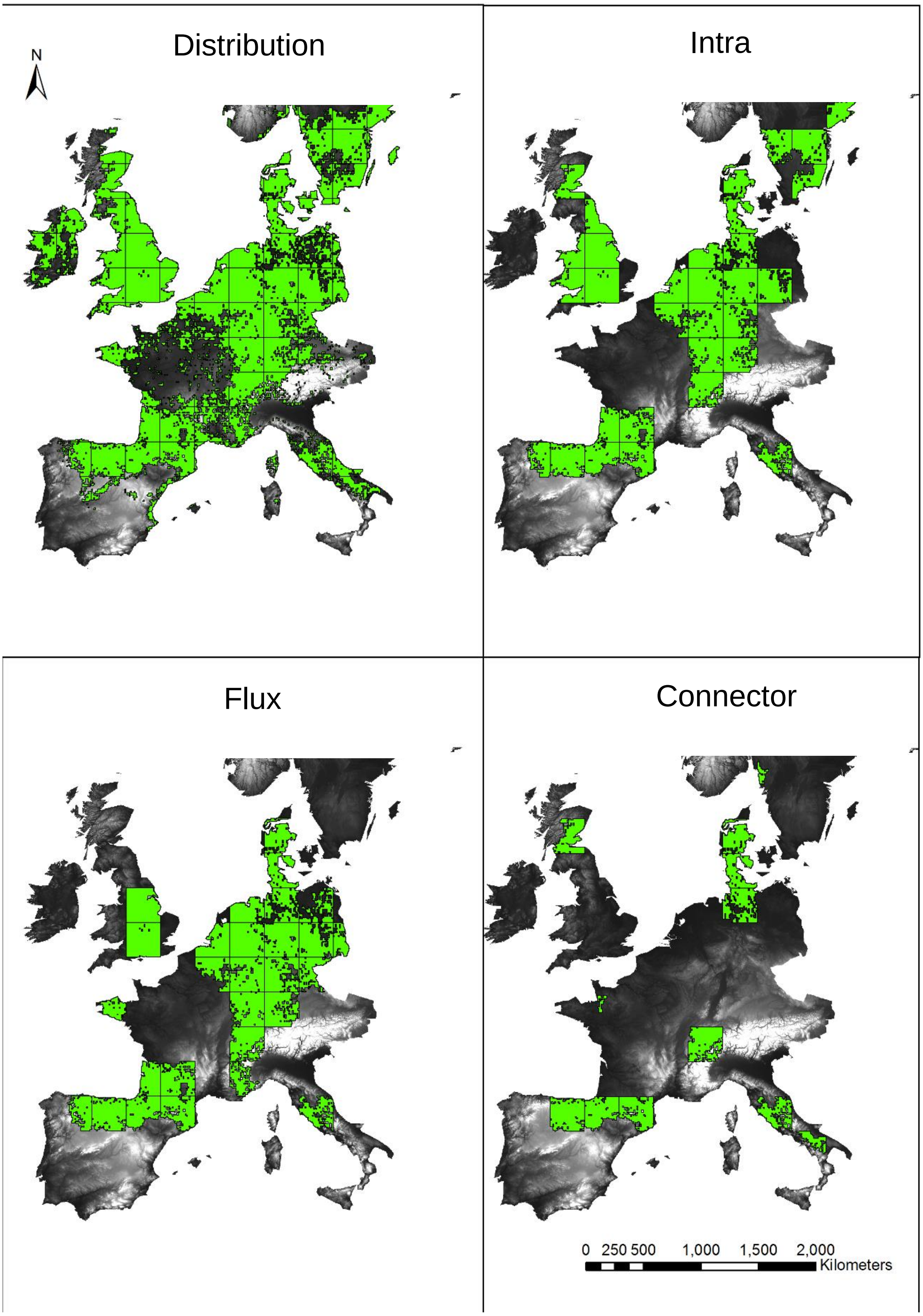


Figure 34- Pipistrellus nathusii results regarding species distribution and patches with connectivity importance higher or equal to 1%

Pipistrellus pipistrellus

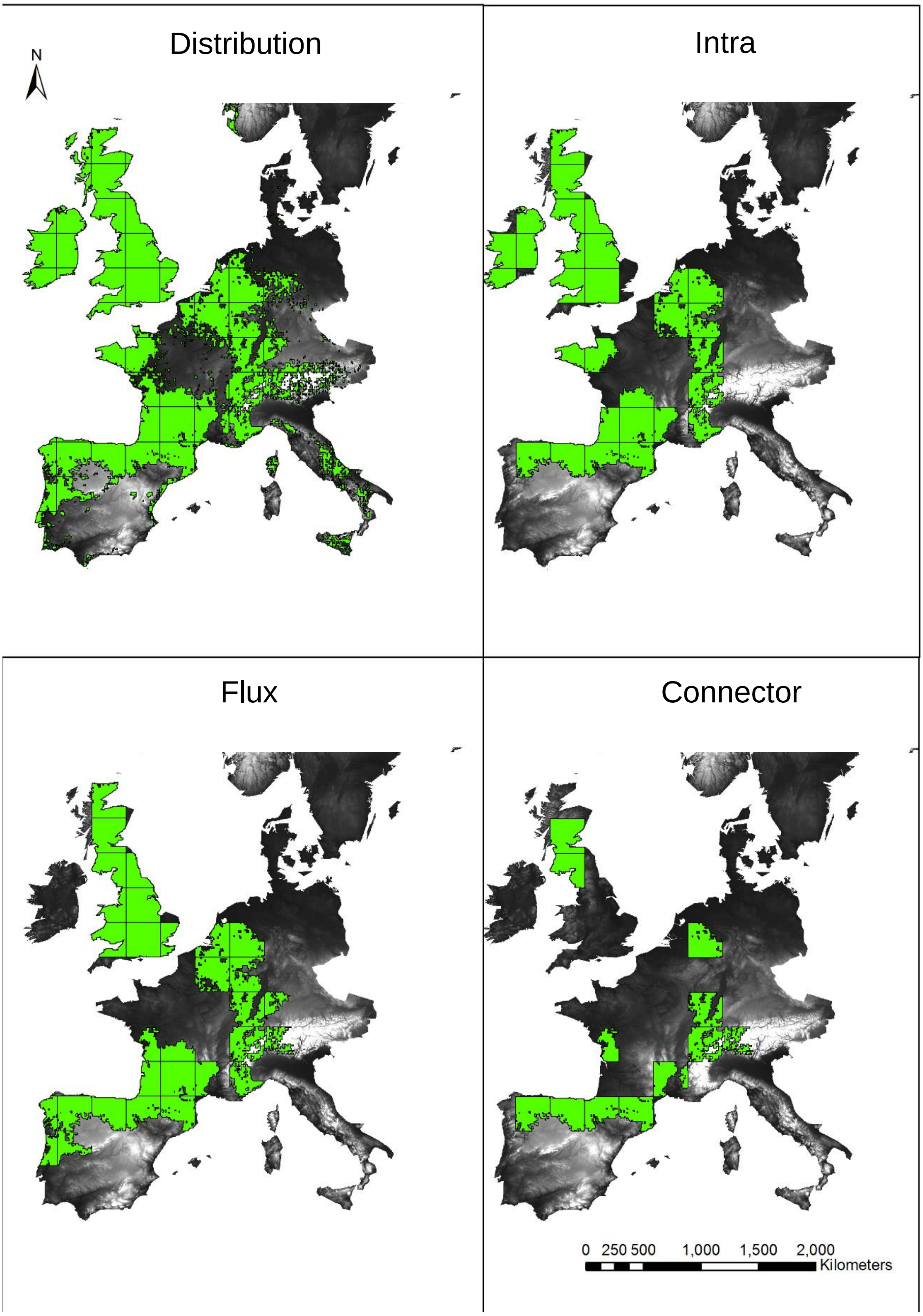
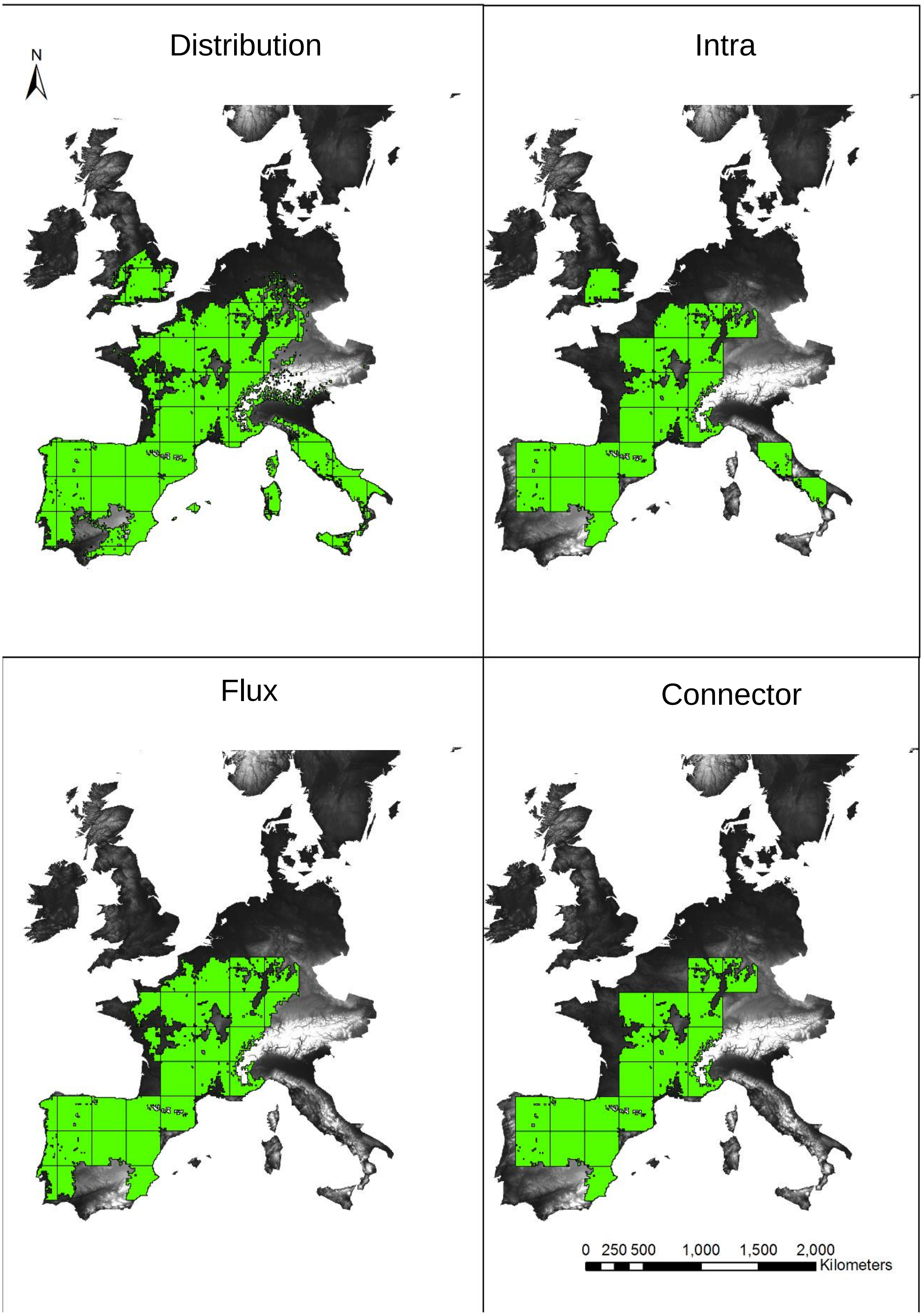


Figure 35- Pipistrellus pipistrellus results regarding species distribution and patches with connectivity importance higher or equal to 1%

Plecotus austriacus


Distribution

Intra

Flux

Connector

Figure 36- Plecotus austriacus results regarding species distribution and patches with connectivity importance higher or equal to 1%

Rhinolophus euryale

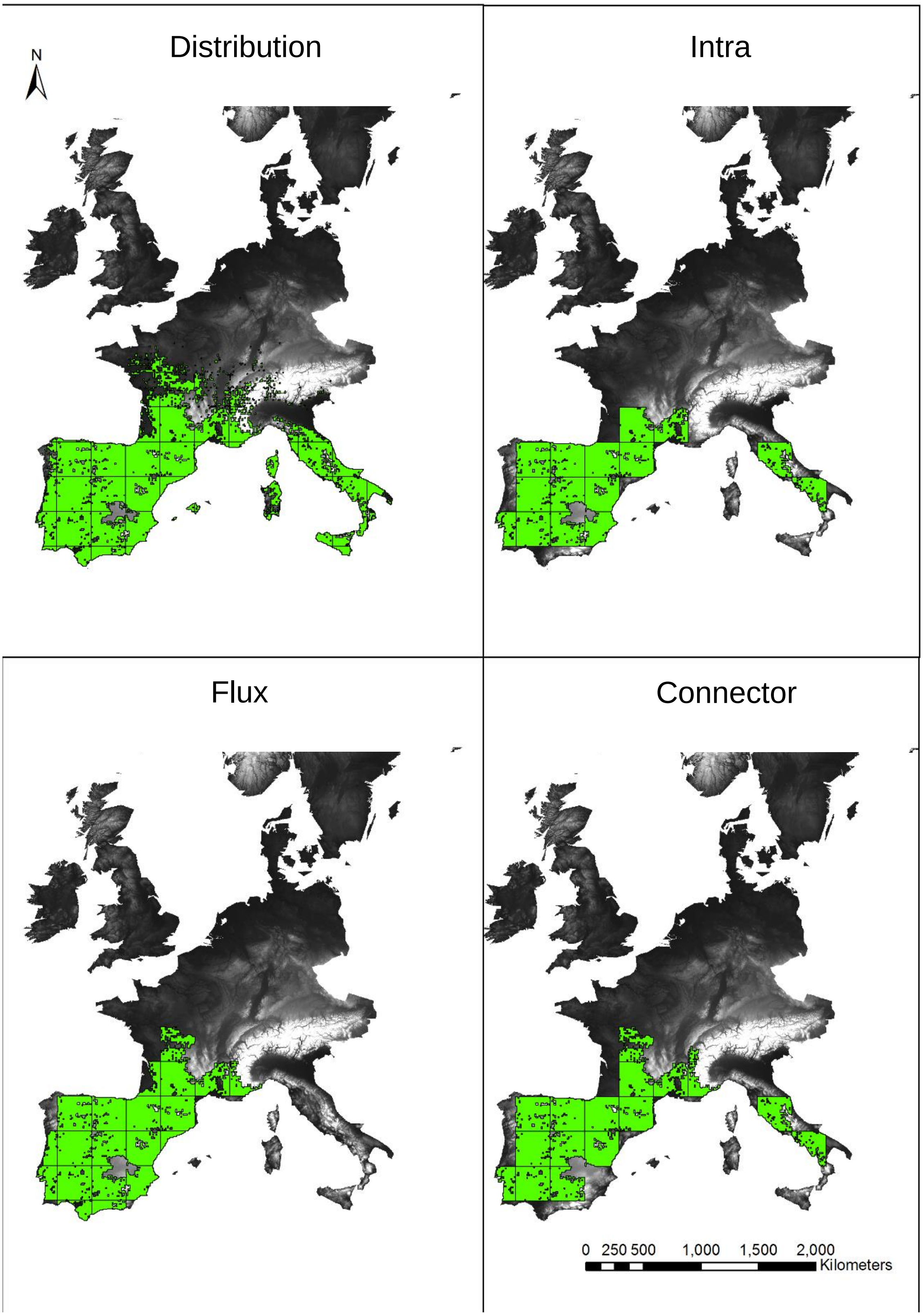


Figure 37- Rhinolophus euryale results regarding species distribution and patches with connectivity importance higher or equal to 1%

Rhinolophus ferrumequinum

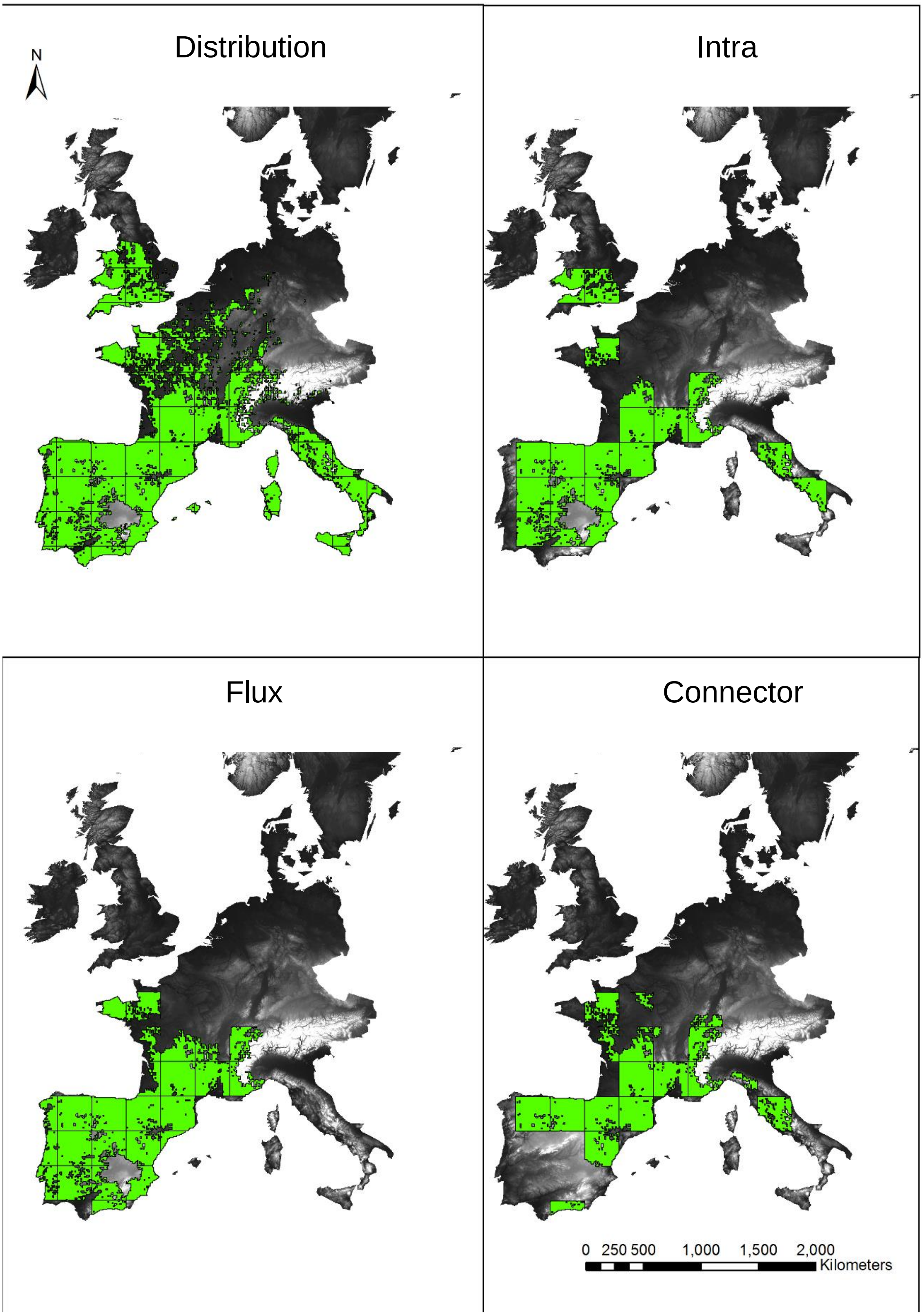


Figure 38- Rhinolophus ferrumequinum results regarding species distribution and patches with connectivity importance higher or equal to 1%

Rhinolophus hipposideros

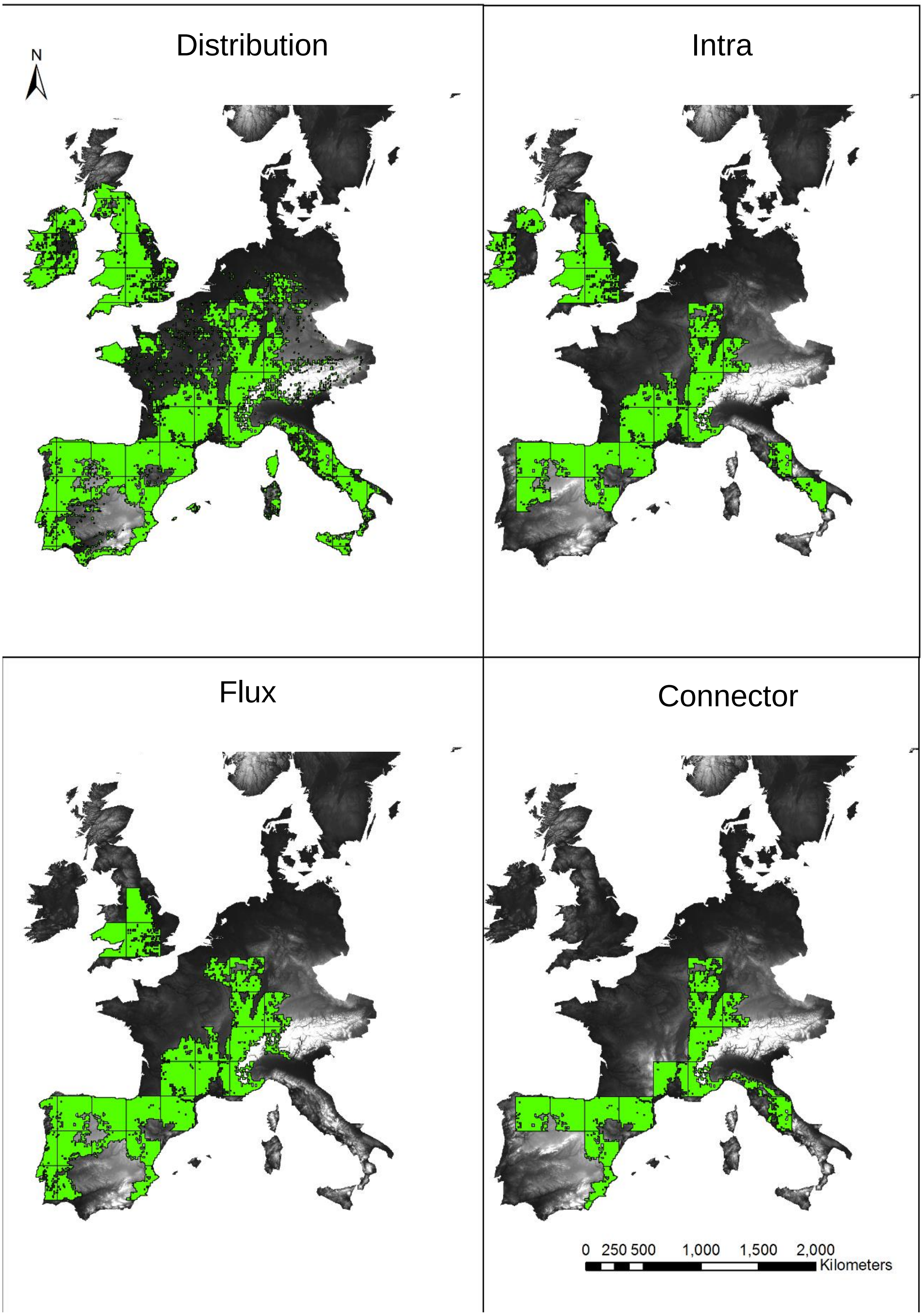


Figure 39- Rhinolophus hipposideros results regarding species distribution and patches with connectivity importance higher or equal to 1%

Rhinolophus mehelyi

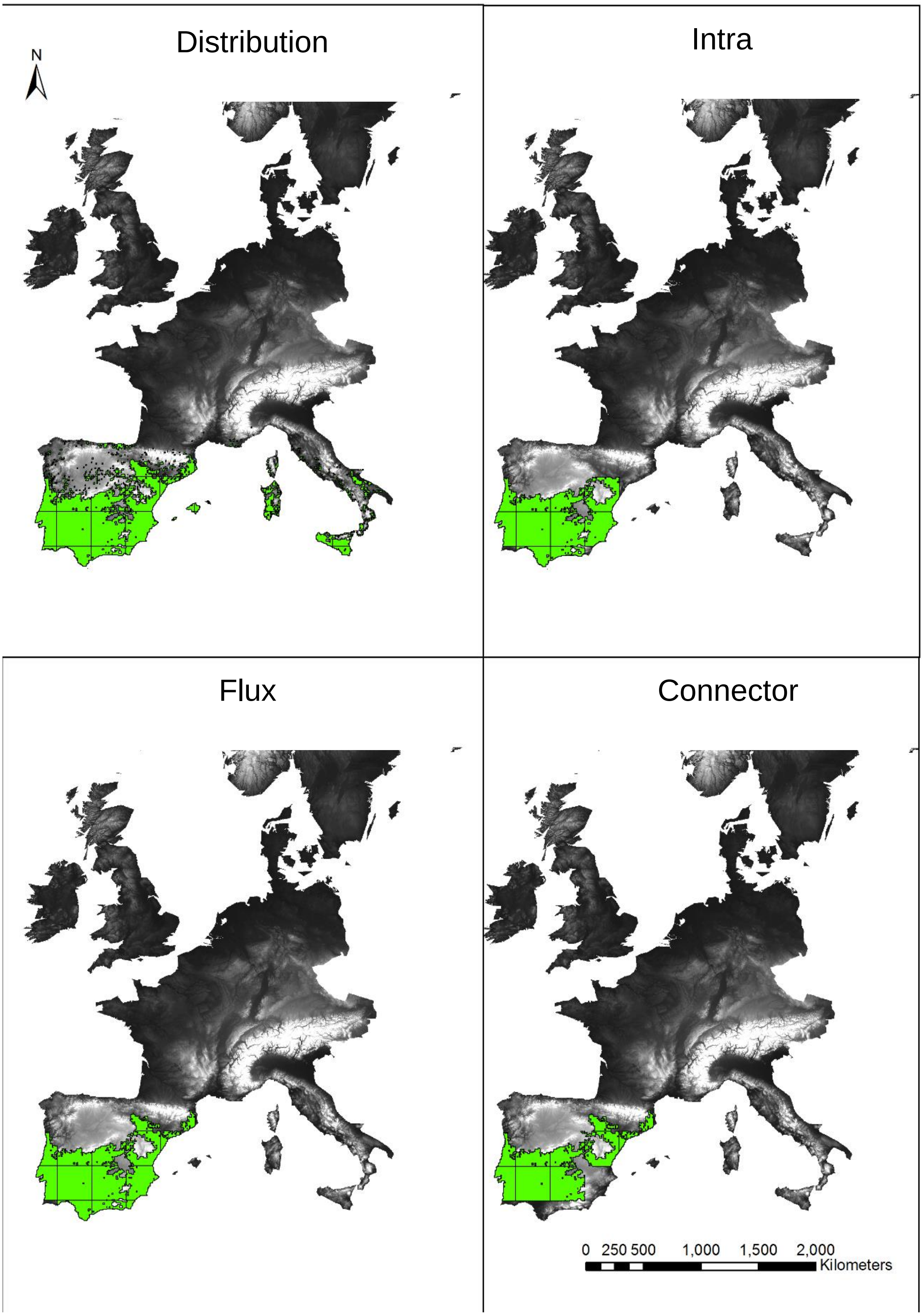


Figure 40- Rhinolophus mehelyi results regarding species distribution and patches with connectivity importance higher or equal to 1%

Tadarida teniotis

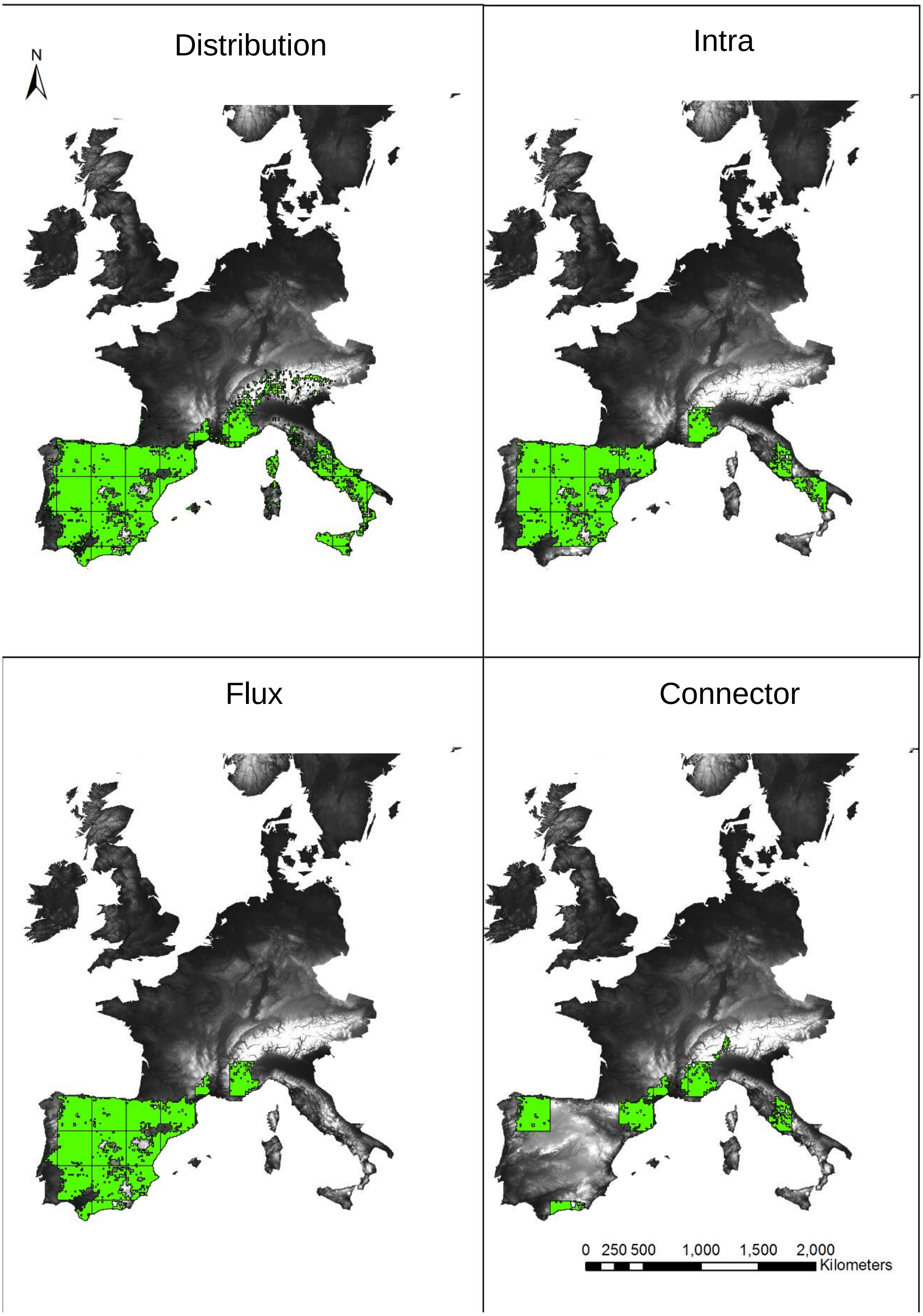


Figure 41- Tadarida teniotis results regarding species distribution and patches with connectivity importance higher or equal to 1%

Vespertilio murinus

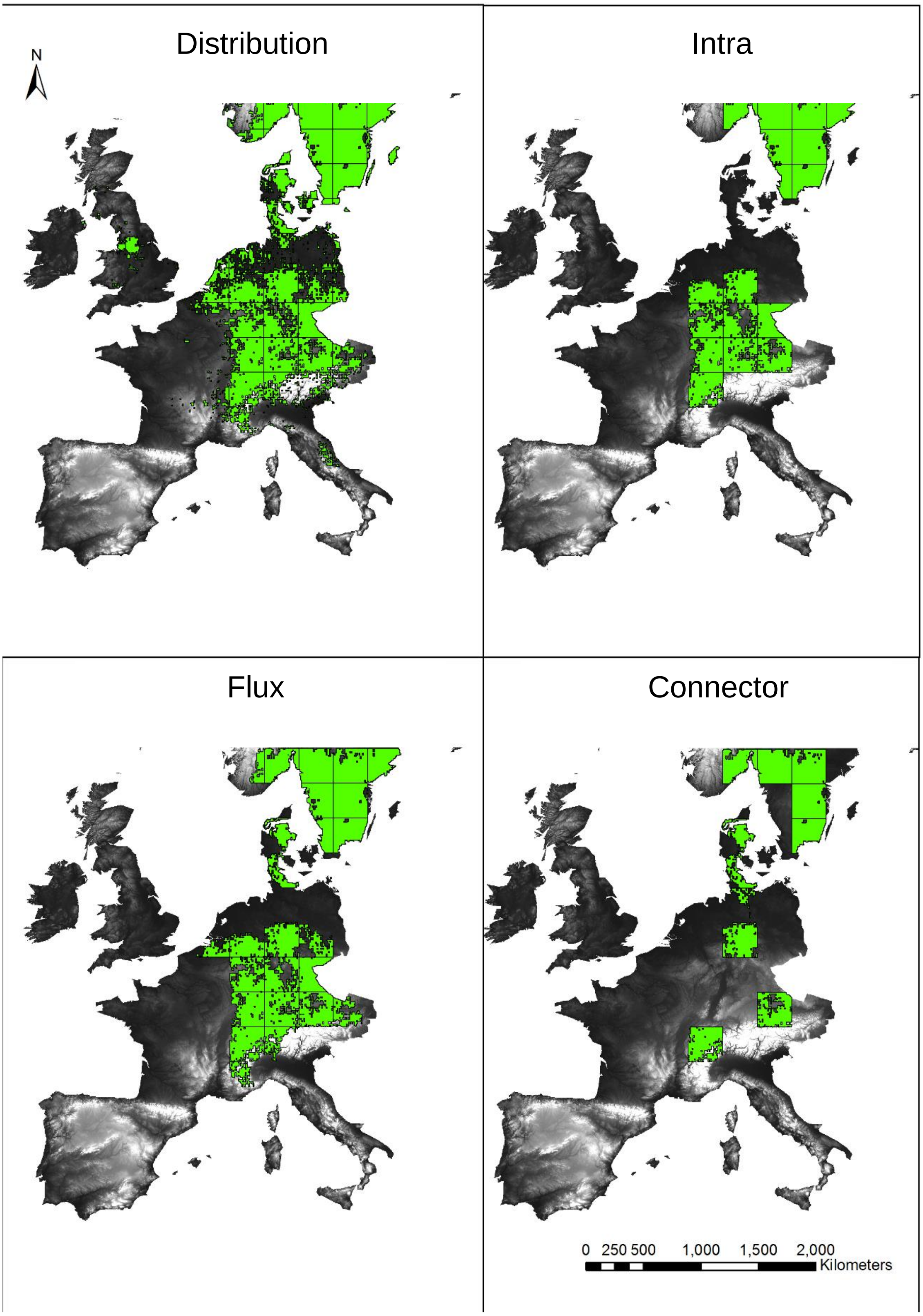


Figure 42- Vespertilio murinus results regarding species distribution and patches with connectivity importance higher or equal to 1%