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Evaluating Presence Data versus Expert Opinions to Assess Occurrence, Habitat Preferences and Landscape Permeability: A Case Study of Butterflies

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Abstract: We explored how presence data and expert opinions performed with respect to identifying the ecological preferences and the spatial needs of six butterfly species in the Federal State of Saxony, Germany. We used presence records and a land-cover map. In parallel we used expert responses to evaluate the 40 land-cover types occurring in the map, in terms of both suitability and permeability for the six species. Presence data were translated into preferences through Ivlev's electivity indices (IEI). Visual analysis of preference maps based on IEI showed a distinct pattern of suitable versus less suitable areas. Similarly, spatial analyses found that presence-points were closer to suitability areas based on IEI than those that were based on expert data. However, in case of mismatches between expert and presence-based evaluations, independent experts identified the expert evaluation as better and considered IEI outcomes as wrong. We found a medium to high correlation between land-cover class suitability and permeability based on expert opinions for all species. This indicates that expert evaluation of permeability is affiliated with habitat suitability. Integration of species-presence data and expert-knowledge about species could enhance our capabilities to understand and potentially map suitability while gathering information about suitability and permeability separately can improve species conservation planning.

Keywords: biodiversity conservation; habitat suitability; landscape permeability; empirical data; expert opinion; Ivlev's electivity indices (IEI)

1. Introduction

Biodiversity conservation has become a core issue in research and policy due to the recognition of the magnitude of anthropogenic and environmental threats [1]. Failures in achieving the 2010 goals of the Convention on Biological Diversity to slow down the loss of biodiversity, and the setting of new biodiversity targets for 2020, stress an urgent need to expand the current reserve networks and to improve their effectiveness in protecting species and habitats [2]. To facilitate the spatial selection of areas for conservation in a transparent way, a number of methods have been developed [3,4]. Such methods require comprehensive biological databases, especially with respect to species distribution, occurrence, and abundance in different environments. Furthermore, underlying data need to be up to date, sufficiently accurate, detailed, and in a resolution that reflects the environmental requirements of the species or habitats in question [5–7]. Such data, at the required level of resolution and detail, are rarely available [8–10]. Consequently, most strategies for the spatial design of nature conservation efforts depend on incomplete and biased distribution databases [11,12]. This could negatively affect conservation efforts by causing non-optimal performance in identifying priority areas for conservation [13–15].

Wildlife habitat selection models [16], habitat suitability models, and maps that are derived from them, are among the most broadly used tools for identifying the ecological needs of species [17]. They rely on presence only, presence-absence, or abundance data with the former being the most commonly available type of data [18,19]. However, obtaining reliable species occurrence data may be difficult, for instance, because data collection methods are often either non-standardized or even unknown [20–22]. It is increasingly acknowledged that landscape permeability should be another important aspect for conservation planning. Permeability is critical for species' survival in human-altered environments, as it affects the movements of animals across landscapes, and hence their probability to survive in small, otherwise-isolated populations [23,24]. Suitability and permeability are therefore two central aspects in determining the survival of species in patchy landscapes. But these two should not be mixed with each other, as they describe different species-specific attributes. Habitat suitability describes the extent of environmental elements that are required for supporting individual and population persistence. It could be defined along a continuum from low to high, but it should also be perceived as a multidimensional set of variables that depend on the type of resources that are needed, at a given life stage or state, for various functions: survival, reproduction, and population maintenance [25–27]. Permeability, on the other hand, is defined as "the degree to which regional landscapes, encompassing a variety of natural, semi-natural and developed land cover types, are conducive to wildlife movement and sustain ecological processes" [28]. Permeability is a measure of animal-landscape interactions, determined by landscape structure, the tendency to move into (and through) different environments, and the risk of mortality in each of those. Consequently, a range of empirical studies demonstrate that environments that are "unsuitable" for daily functions may be highly permeable for dispersers. A landscape can be highly permeable, but if animals prefer to stay in elements of such a landscape, the average rate of dispersal would be very low, even if they move a lot, and thus show high movement activity. If they prefer to leave, dispersal speed would probably be similar to the level of movement [29–31]. The individual movement can be reduced either due to "mechanical" reasons (e.g., grassland species moving through forest) or the permeability regarding population dispersal can be reduced because of an increasing mortality (lack of connectivity and landscape resistance). To obtain reliable estimates of permeability, one therefore needs information both on the movement capacities of species, their movement decisions in different environments (i.e., both preference and diffusion rates), and indications of habitat-specific mortality rates. This requires intensive research using telemetry or CMR (Capture-Mark-Recapture) that is expensive, and therefore available only for few species [32]. Consequently, knowledge gaps are particularly large with respect to permeability. One means to overcome gaps in knowledge, for both suitability and permeability, could be to rely on expert knowledge in order to gain a better understanding of species-habitat relationships [33,34]. Especially, opinions about species-habitat relationships serve as baseline knowledge for planning of conservation projects, but are rarely tested empirically [35–39].

Here, we explored the question of how presence data and expert opinions perform with respect to identifying the ecological needs of six butterfly species in the Federal State of Saxony, Germany. We particularly focused on differentiating suitability (or proxies for it) from permeability. Butterflies were chosen because they are commonly used as bio-indicators for ecological trends and for advancing conservation theory and practice [40–42], data are readily available through rapidly expanding monitoring efforts [43], and a relatively large number of experts can be consulted.

To complement presence data originating from monitoring efforts which could only offer information on habitat preferences of species, evaluations of both preferences and permeability from six experts have been incorporated. Thereby, we aimed at (a) developing maps that separate habitat preferences from permeability, (b) comparing the outcomes of empirical-based versus expert-opinion based analyses, (c) identifying matches and mismatches between expert-opinion and empirical-data, and (d) proposing insights into what can be learned from each knowledge-source.

2. Materials and Methods

2.1. Study Area

The study was conducted using data from the Federal State of Saxony, in central-east Germany (circa 18,500 km^2). The most dominant land-cover in Saxony is arable fields, while one-fourth of the state area is forested. Grasslands and extensive agricultural practices comprise additional important proportions [44]. The climate is temperate warm and slightly humid, with cool winters and warm summers and colder conditions in the mountain areas, primarily in the south, bordering the Czech Republic (Ore Mountains, up to circa 1200 m) [45]. The average annual precipitation ranges from circa 650 mm in the north-west to 900 mm at the higher altitudes in the south. Average annual temperature follows the same spatial pattern, declining from 8.58 °C in the north-west to 7.58 °C in the south-east [46].

2.2. Species Data

Point presence data were used for six butterfly species: Purple Emperor (*Apatura iris*, Nymphalidae), Grayling (*Hipparchia semele*, Nymphalidae), Large Copper (*Lycaena dispar*, Lycaenidae), Large Tortoiseshell (*Nymphalis polychloros*, Nymphalidae), Dusky Large Blue (*Phengaris nausithous*, Lycaenidae) and Silver-studded Blue (*Plebejus argus*, Lycaenidae). These species differ in their distribution and commonness, as well as in terms of habitat requirements and their movement distances. The conservation status of *Hipparchia semele* is defined as "least concern", while *Lycaena dispar* and *Phengaris nausithous* are categorized under lower risk and "near threatened" categories, respectively. The remaining species are not listed in relevant red lists of threatened species, but all are of conservation concern for the state of Saxony, Germany [47–50].

Data were originated from opportunistic observations collected with an accuracy of 1 km. Data was available from the more distant past, but due to land-use changes in the region following Germany's reunification, as well as for consistency with the land-cover map available (see below), our analyses were based only on presence records from the years 2000–2008. Since observations were not conducted systematically, the data were regarded as "presences" only, and absence data were considered unavailable.

2.3. Land-Cover Data

Land cover data set includes detailed vegetation and land-use patterns for the Federal State of Saxony, Germany. The data set were characterized based on aerial photos taken in 2005 by the Saxon State Agency for Environment, Agriculture and Geology (LfULG) [51]. The 40 land use classes in the BTLNK (Biotoptypen- und Landnutzungskartierung) data set can be displayed, from general (eight classes) to most detailed (See Appendix A). The BTLNK data set was preferred over CORINE (coordination of information on the environment) land cover due to more detailed classification and spatial accuracy. The land cover data set can be used to identify habitat suitability and permeability of six butterfly species.

2.4. Data Preparation and Analysis

To link the butterflies' presence data with the land-cover map, one must consider the coarse spatial resolution of the observation data (1 × 1 km^2). We therefore overlaid the presence data on a 1 km by 1 km grid. The grid was used to generate points based on the coordinates of the grid cells' centers. We then calculated the proportion of each land cover class over all 1 km^2 grid cells, and again for all of the occupied grid cells for each species. We included in the analyses only 1 km^2 cells that fell completely within the borders of Saxony.

To assess the suitability of the various land-cover types, we applied two methods for calculating Ivlev's Electivity Index [52]. This index was originally developed to describe the food preferences of predatory species by calculating the mean amount of the prey organism in the landscape and comparing it to the observed amount of prey taken up by the predator. Later on, the index was adopted for habitat preference calculation, where it can be used to compare how observations of a given species relate to the distribution of available land-cover types, or habitats, in a given landscape [53,54], Ivlev's index is calculated as:

$$E_i = \frac{r_i - p_i}{r_i + p_i} \quad (1)$$

where, r reflects the observed occurrence and p reflects the proportional availability of a given land-cover type for each of the i habitats. The outcome, E_i, varies from −1.0 to +1.0, where positive values indicate preferred (i.e., suitable) habitats, negative values denote avoidance (i.e., unsuitable) and E_i (IEI) = 0 indicates no preference [52,54]. We calculated the index in two ways that reflect different scales of information resolution: In the first approach, we considered information regarding the total number of occupied cells in a given land-cover class, r_i being the relative proportion of number of occupied cells of a given land-cover where butterflies were recorded, and p_i being the relative proportion of number of occupied cells of a given land-cover in the whole of Saxony. Here, the most dominant habitat type is assigned to each cell. In the second approach, which considers the abundance of different land-cover types within each of the 1 km cells, r_i was the relative proportion of all the land cover classes occurring within all 1 km grid cells where a butterfly has been recorded, and p_i was the relative proportion of land cover classes in all 1 km grid cells in Saxony. In the following, we call the former index $\text{IEI}_{\text{occup}}$ and the latter one $\text{IEI}_{\text{abund}}$. To assess, whether the abundance or rarity of a certain land-cover may result in higher IEI value or variance, we correlated both indices with the abundance of land cover classes within 1 km squares. Calculations and statistical analysis were performed using Microsoft Excel 2007 (Microsoft, Redmond, WA, USA).

2.5. Expert Opinions on Suitability and Permeability

To obtain independent information on land cover class suitability and permeability, we contacted about 70 butterfly experts to ask if they were willing to assign values for each of the six butterfly species. Experts could rank land-covers from one to four, where 1 would denote either "very suitable habitat" or, respectively, very high permeability, and 4 denotes highly unsuitable as habitat or, respectively, very low permeability. Out of the experts contacted, six replied and returned a table with estimates for habitat suitability and permeability for all of the 40 land-cover types and all species. We derived the average values and variance from the six expert opinions for each land-cover with species combination. The average values were then adjusted to the same range of Ivlev's electivity index, from −1 (non-preferred) to +1 (preferred) [52] using a linear function ($y = ax + b$). We compared the average land cover class suitability of expert opinions and variance between all expert opinions to detect whether there is a certain systematic bias in the answers provided by experts. We then tested for correlation between expert opinion on permeability and habitat suitability based on both IEI and expert opinion to understand their relationships.

2.6. Preparation of Maps

Maps based on land cover class preferences (from both IEI and experts opinions) were generated by assigning the identified suitability values to the vector map of the biotope and land cover (BTLNK). Presence data for the six butterfly species originated from records during the years 2000–2008 was used to generate points in ArcMap based on their respective co-ordinates. Following number of presence points found for each species: *A. iris* (69), *H. semele* (65), *L. dispar* (51), *N. polychloros* (37), *P. nausithous* (200), and *P. argus* (49). Later, these vector maps and presence points were used in "point to polygon" analysis for distance investigation. Further, maps were then up-scaled to create a second raster map with a resolution of 1 by 1 km, so that suitability maps and the presence-points would have the same spatial resolution. Conversion of the vector maps to raster was performed by using the tool "polygon to raster" (Arc Toolbox, ArcGIS 10.1, Esri, Redlands, CA, USA) [55]. Each 1 km^2 cell was assigned the land cover type value based on "maximum combined area" (i.e., the most dominant land-cover type). We used the "maximum combined area" approach to represent dominant land cover. Presence-points of species were overlaid on the 1 km^2 cell resolution raster maps for visual assessment.

2.7. Comparison of Expert Opinions and Ivlev's Electivity Indices

We compared habitat suitability based on IEI versus expert opinions to assess their respective performance. The following methods were used for comparison: (1) Visual assessment of the habitat suitability maps to identify general patterns of suitability in Saxony; and, (2) In spatial analysis, presence points were overlaid on polygon maps of habitat preference (based on IEI and expert opinions) to calculate distance from the nearest preferred area (IEI values > 0). Here, the assumption was that a small distance should represent a spatial matching between observations and the areas defined as suitable. Higher number of occupied cells in preferred area and shorter average distance of presence-points from preferred area should represent better prediction of preferred suitable area; (3) Finally, we compared the preference values based on IEI versus expert opinions for each of the 40 land-cover types, to identify the correlation levels as well as specific matches and mismatches (also with respect to land-cover rarity). The matches and mismatches provided additional information that was sent back to the experts for re-assessment and remarks about initial outcomes.

2.8. Evaluation of Habitat Preference Results by Experts

Once completing the analyses, we contacted all six experts again to discuss habitat preference outcomes. These experts, as well as additional new experts, were provided the following results and questions: (1) Maps of preference based on the IEI produced next to expert opinions for all six butterfly species, with the presence-points plotted on them to visualize spatial matches and mismatches. Here, we asked whether according to their experience the expert opinion maps or the IEI-based preference maps better reflect true suitability. (2) A table where we listed cases of matches and mismatches between IEI and expert opinions (Appendix B & Appendix C). We listed those land-cover types where both IEI and expert opinion received high preference ranking (i.e., good match), both provided low ranking (still a good match between the expert and IEI), or a mismatch (IEI ranking high but expert opinion low, or vice versa). For the case of mismatches, we asked the experts which evaluation in their opinion is better (IEI or average expert opinion), and if possible, provide a possible reason for mismatch. (3) Finally, experts were provided a table, which was arranged according to the discrepancy (variance) between expert opinion ranking values (from high variance to low) for different habitats. Thus they could see where the opinions of the different experts met or diverged. Here, we asked for their opinion on the potential reason for larger disagreement between experts.

3. Results

3.1. Relationship between Presence-Based Indices: Two Means for Calculating Ivlev's Electivity Index

We found a strong positive relation between the values of IEI_{occup} based on number of occupied cells in land-cover classes, and IEI_{abund} based on abundance of land cover classes within 1 km squares, for three out of six species: *P. argus* (R^2 = 0.7981), *H. semele* (R^2 = 0.7977), and *L. dispar* (R^2 = 0.7123). A slightly weaker relation was found for *P. nausithous* (R^2 = 0.6881) and clearly weaker ones for *N. polychloros* (R^2 = 0.5745) and *A. iris* (R^2 = 0.4372). Results are here presented in the form of a regression instead of Pearson's correlation in order to assess also the slope of the relationship:

Deviation of the regression slope between the two indices from 1, indicating a bias in the IEI values, was observed especially for *A. iris* and *L. dispar* (slope = 1.23 and 1.17, respectively), primarily due to a few outliers occurring for some unfavorable habitats (Figure 1).

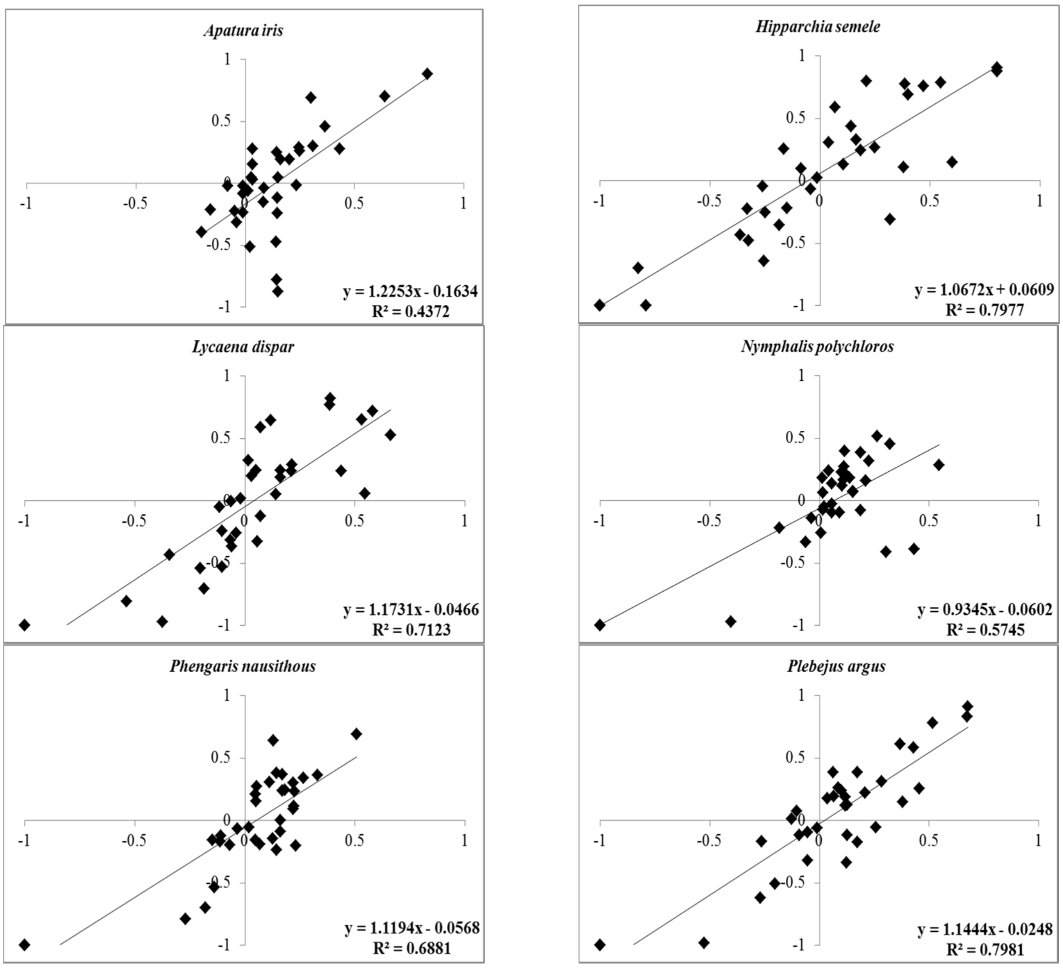

Figure 1. Relationship between IEI_{occup} (X) and IEI_{abund} (Y) in terms of habitat suitability of each land-cover types for the six species, based on presence data.

3.2. Effect of Area on Ivlev's Electivity Indices

In an assessment of the potential effect of land-cover area (abundance of a given land-cover) on IEI values, we found no such effect for three of the species. After removing two outliers, the effect was weak for both indices for *H. semele* (R^2 = 0.2166 for IEI_{occup} and R^2 =0.1863 for IEI_{abund}), and also weak for *P. nausithous* (R^2 = 0.1343) and *P. argus* (R^2 = 0.1128) for IEI_{abund} (Table 1). Results, however, were only marginally significant ($0.05 < p < 0.1$ prior to Bonferroni correction). Main outliers, namely highly abundant land-covers, were grasslands (land-cover code: 41) and arable fields (land-cover code: 81), but also coniferous forests (72) for *H. semele* and *A. iris*, and scree slopes for *A. iris* (52).

Table 1. Effect of land-cover area (X) on Ivlev's electivity indices (IEI) (Y) values for all butterfly species.

Species Name	Indices	R^2-Value *	R^2-Value **	Equation ***
Apatura iris	IEI_{occup}	0.0133	0.025	$y = -1E-08x + 0.1581$
	IEI_{abund}	0.0055	0.0577	$y = 3E-08x - 0.0522$
Hipparchia semele	IEI_{occup}	0.091	0.2166	$y = 1E-07x - 0.2474$
	IEI_{abund}	0.1048	0.1863	$y = 1E-07x - 0.12$
Lycaena dispar	IEI_{occup}	0.0078	0.0287	$y = 3E-08x - 0.0123$
	IEI_{abund}	0.0191	0.0733	$y = 7E-08x - 0.0935$
Nymphalis polychloros	IEI_{occup}	0.0026	0.0277	$y = 5E-08x - 0.0158$
	IEI_{abund}	0.0135	0.0635	$y = 8E-08x - 0.0747$
Phengaris nausithous	IEI_{occup}	0.0055	0.0377	$y = 2E-08x - 0.0234$
	IEI_{abund}	0.0163	0.1343	$y = 4E-08x - 0.1555$
Plebejus argus	IEI_{occup}	0.0083	0.0557	$y = 5E-08x - 0.0104$
	IEI_{abund}	0.029	0.1128	$y = 9E-08x - 0.0488$

*: R^2-value; **: R^2-value after removing outliers; ***: Equation after removing outlier.

3.3. Expert Opinion Habitat Suitability Variance Analysis

We found a strong negative relation for *H. semele* (R^2 = 0.848) between the average expert ranking of habitat suitability and the variance between answers, a medium strength of relation for *N. polychloros* (R^2 = 0.4998), *P. nausithous* (R^2 = 0.476), and *L. dispar* (R^2 = 0.4087), but a substantially lower value for *P. argus* (R^2 = 0.267) and *A. iris* (R^2 = 0.202). This negative relation indicates that experts tended to agree about the less suitable habitats, but provided highly diverse answers with respect to potentially suitable habitats, especially for *H. semele*.

3.4. Visual Analysis of Land Cover Class Suitability Maps

Land cover maps produced using IEI_{occup} values identified distinctive geographical patterns of preference for three of the species (Figure 2). By contrast, maps produced using IEI_{abund} yielded distinctive spatial patterns for all six species (Figure 3). More specifically, the southern and north-eastern regions of the State of Saxony were predominantly the most preferred for species, excluding *P. nausithous,* whereas IEI_{occup} maps did not show a distinctive area of high preference for the species *A. iris, L. dispar* and *N. polychloros.* However, IEI_{abund} maps showed fine patterns of suitable and unsuitable areas in comparison to IEI_{occup} for all 6 species (Figures 2 and 3).

The preference map for *P. nausithous* clearly differed from the maps of the other species (Figures 2 and 3): Most of the preferred areas were located in a more scattered manner from IEI_{abund} maps, mainly in the centre and north-western parts of the study area (corresponding to flatland areas dominated by high coverage of agricultural land-covers). According to the IEI_{occup} maps, the preferred areas were more stretched in the same directions as in IEI_{abund}. Further, for *P. nausithous*, presence points were distributed near preferred areas as identified both by IEI_{occup} and IEI_{abund} values. By contrast, for *A. iris* and *N. polychloros,* preference maps from IEI_{occup} were relatively homogenous and indicated most of the State of Saxony as suitable for the species, whereas for both species IEI_{abund} produced a map with distinct geographic differentiation between suitable and unsuitable regions. Yet note that observation points for the two species were indeed scattered throughout the study area (red stars in Figures 2 and 3).

After conversion of the average expert opinion into suitability maps, the only relatively clear geographic patterns were for *H. semele* and *P. argus*, matching with most of the presence points in north-east Saxony (Figure 4). For the other four species, presence points occurred also in less suitable areas (red stars in Figure 4). All six maps indicated far lower suitability when compared to the maps produced by IEI (compare Figure 4 with Figures 2 and 3). This is due to an overall lower scoring of the suitability given by experts.

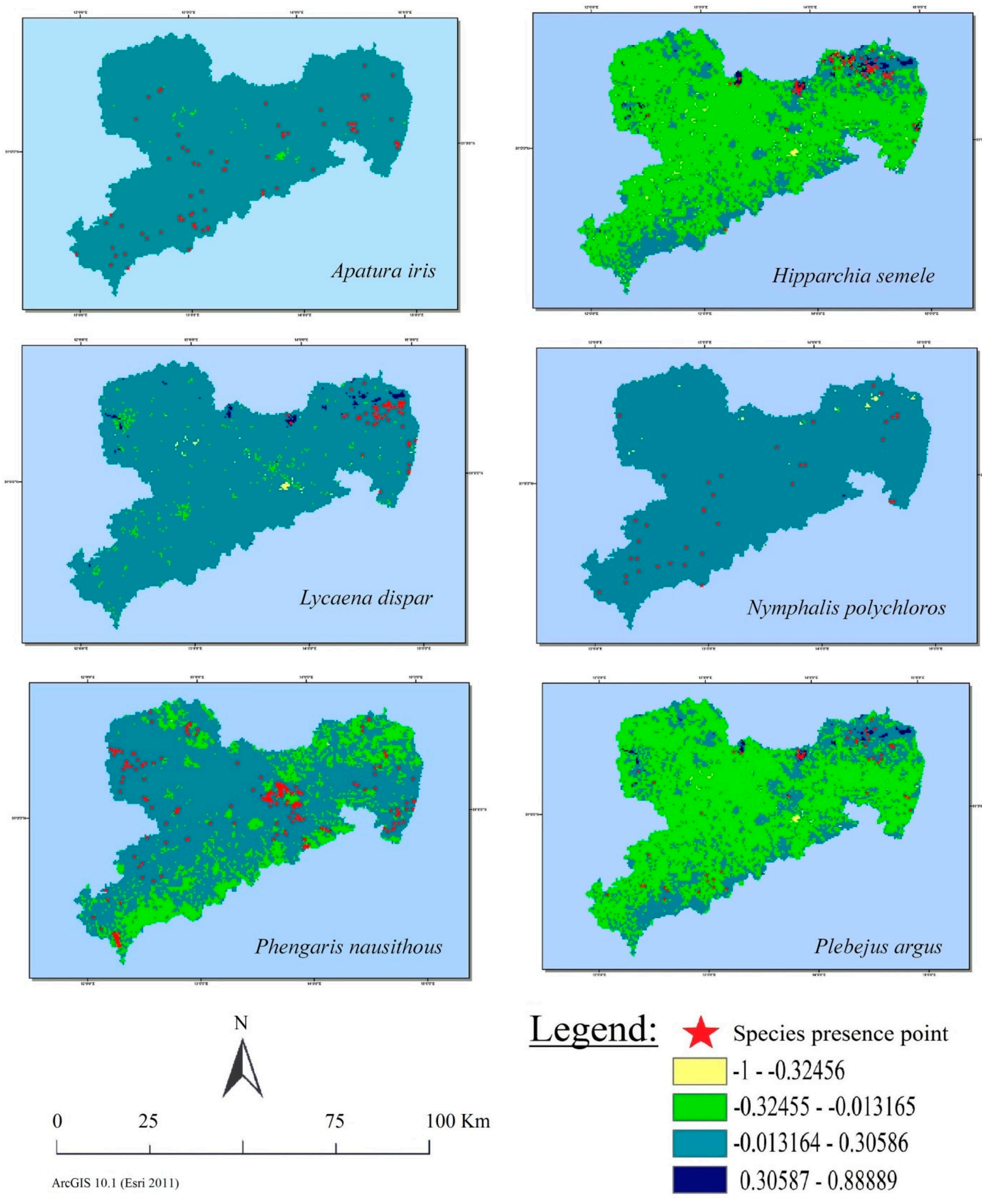

Figure 2. Maps of habitat preference based on IEI_{occup} for all six species (IEI values towards −1.0 indicate avoidance while +1.0 represents suitable).

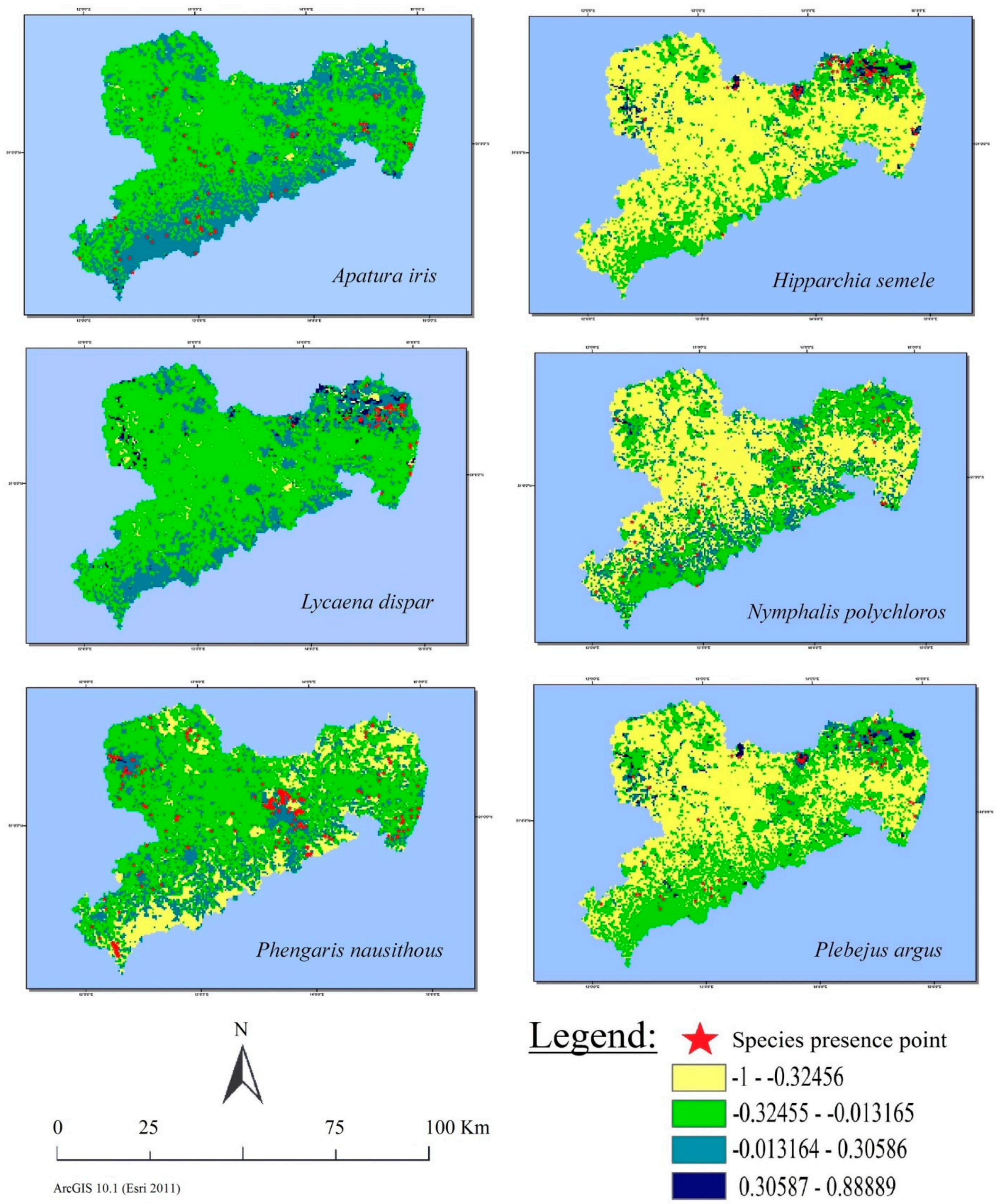

Figure 3. Maps of habitat preference based on IEI_{abund} for all six species (IEI values towards −1.0 indicate avoidance while +1.0 represents suitable).

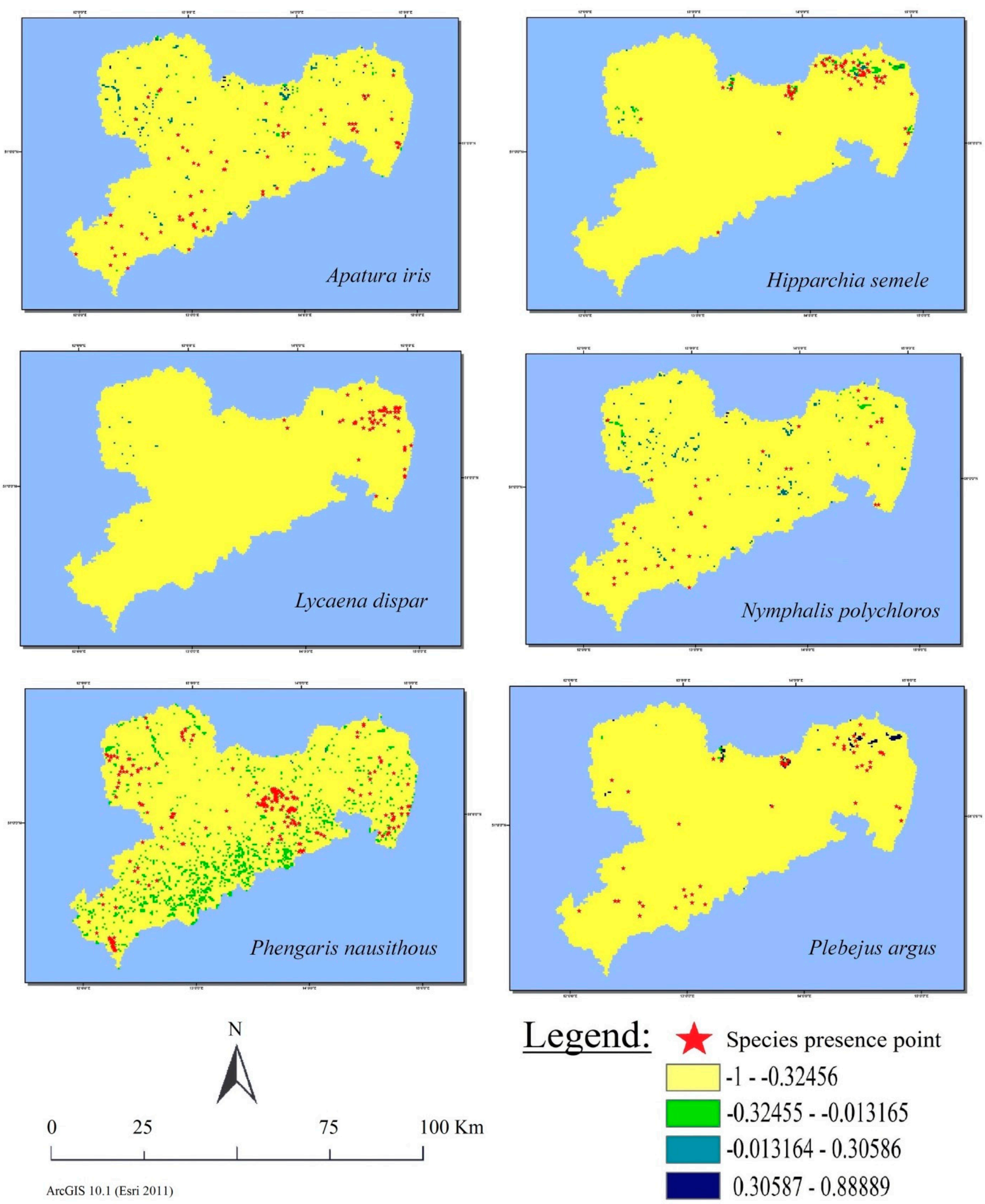

Figure 4. Maps of average habitat suitability based on experts opinions for all six species (HS values towards −1.0 indicate avoidance while +1.0 represents suitable).

3.5. Spatial Relation between Observations and Suitable Habitats

The number of cells with preferred habitat, which also hosted observation points, was much higher for the maps produced from Ivlev's electivity indices than for the maps produced from expert opinions, for all six species. The number of occupancy cells included based on IEI_{occup} was much greater than IEI_{abund} for *P. nausithous*, but otherwise, it was nearly equal for the other five species (Figure 5a).

The average distance between presence points and nearest polygons of preferred suitable habitat was by far larger within the maps produced from expert opinions when compared to those originating from IEI values, for all six species (Figure 5b). While the average values were as low as seven meters for *P. nausithous* based on IEI_{occup} values, they reached 732 meters (*H. semele*), 800 meters (*P. nausithous*) and even 1456 meters on average for expert opinions, with poorest results for *P. argus* (Figure 5b).

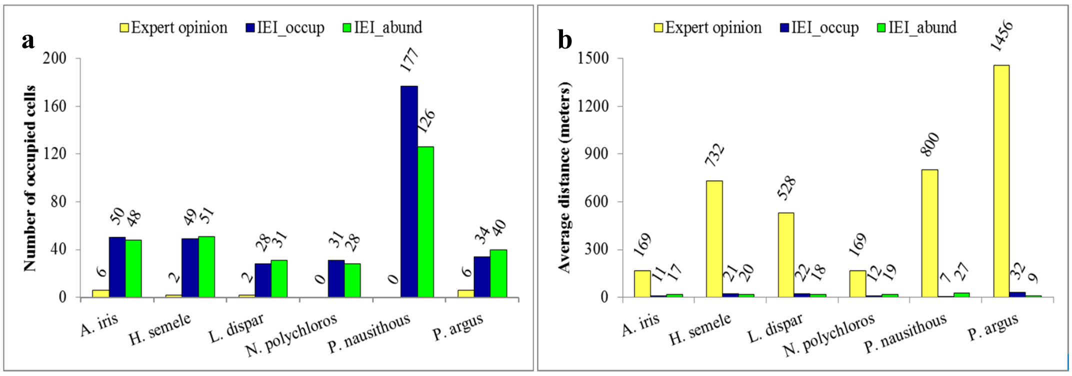

Figure 5. Spatial concurrence between observations and evaluations: (**a**) Number of occupied cells found in preferred suitable area based on IEI and experts opinions, and (**b**) average distance between the occupied cells and nearest suitable habitat.

3.6. Outcomes of Evaluation of the Results by Experts

While performance criteria listed above may seem to indicate the presence-based results (IEI) as better than the expert evaluation, communication with the original experts and additional independent ones indicated otherwise. With regards to mismatches (i.e., IEI indicating very high preference and experts suggesting very low suitability, or vice versa), some evaluators were of the opinion that in most cases the experts performed better. For instance, mismatches for the species *A. iris*, *L. dispar* and *N. polychloros* were explained by the experts as emerging from too high IEI for habitats, such as water bodies, which are clearly unsuitable. Further, scree slopes and bedrocks received low IEI_{occup} values compared to expert opinions for *H. semele*, and the experts identified this habitat as clearly suitable (See Appendix B & Appendix C for a list of all cases of match and mismatch). Experts were further of the opinion that the habitat preferences produced by IEI are incorrect, as all six species have a much broader distribution across Europe and occur across most of the State of Saxony. Thus the experts considered the spatial pattern obtained by the presence-based analysis as incorrect.

3.7. Land Covers Class Permeability versus Suitability

We found no relation between the average expert opinion on permeability and the IEI-based value of habitat preference (Table 2). However, there was a medium to high correlation between the expert ranking of suitability and permeability for some species, with particularly high values for *H. semele*, *L. dispar* and *P. nausithous.* Low correlation was obtained for *N. polychloros*.

Table 2. Relationship between land cover permeability and suitability as rated by experts for all six species.

Species Name	Habitat Suitability	R^2-Value	Equation
Apatura iris	IEI_{occup}	0.0057	$y = -0.0315x + 0.2181$
	IEI_{abund}	0.0076	$y = -0.0676x + 0.1755$
	Expert opinions avg	0.3761	$y = 0.4428x + 0.9587$
Hipparchia semele	IEI_{occup}	0.0005	$y = 0.0183x - 0.0871$
	IEI_{abund}	0.0015	$y = -0.0379x + 0.1334$
	Expert opinions avg	0.6745	$y = 0.8973x - 0.3351$
Lycaena dispar	IEI_{occup}	0.0018	$y = -0.0198x + 0.0759$
	IEI_{abund}	0.0134	$y = -0.0749x + 0.1925$
	Expert opinions avg	0.5745	$y = 1.053x - 0.9407$

Table 2. *Cont.*

Species Name	Habitat Suitability	R^2-Value	Equation
Nymphalis polychloros	IEI_{occup}	0.0082	$y = 0.0646x - 0.1158$
	IEI_{abund}	0.0318	$y = 0.1564x - 0.4051$
	Expert opinions avg	0.1229	$y = 0.2138x + 1.7411$
Phengaris nausithous	IEI_{occup}	0.0038	$y = -0.026x + 0.1072$
	IEI_{abund}	0.0045	$y = 0.0383x - 0.1423$
	Expert opinions avg	0.5757	$y = 0.9888x - 0.5078$
Plebejus argus	IEI_{occup}	0.0007	$y = -0.0129x + 0.0931$
	IEI_{abund}	0.0002	$y = -0.0088x + 0.0638$
	Expert opinions avg	0.449	$y = 0.7903x + 0.1576$

4. Discussion

4.1. Empirical Presence Data versus Expert Opinions for Habitat Suitability

We used different approaches in this study to compare empirical presence data and expert opinions about habitat suitability. At first sight, IEI yield more informative maps and suitability information than expert opinions for all six butterfly species. The habitat suitability preference maps for all six species based on expert opinions did not indicate any spatial differentiation across the topographical gradient (and land-cover differences) in Saxony, with the exception of *Phengaris nausithous* (Figure 4). Secondly, expert-based maps did not spatially match the observed localities (Figure 5). Finally, expert evaluations varied broadly between experts with hardly any clear patterns regarding habitat suitability. These results seem to concur with previous studies, suggesting that empirical data and statistical approaches provide better results than expert-based ones [36,56].

On the other hand, when we communicated with experts, mismatches between expert opinions and IEI-based suitability evaluations were explained by the experts as originating from wrong evaluations by the presence-based analysis (Appendix B & Appendix C). This outcome demonstrates that there is lot of in-field experience of the experts, which clearly extends beyond what presence-data analysis can reach and can serve in adding or removing land-cover types that may be otherwise falsely classified. Furthermore, local experts wished to clarify that the species have a much broader distribution than the state of Saxony, and therefore should not show a strong spatial suitability signature. Thus, our results also support criticism of habitat indices with regard to their mechanistic approach and lack of scientific precision [54,57,58].

At small scales, precision is another issue to consider and could be relatively easily assessed by visiting field sites. However, when working at regional or larger scales it is not possible to verify the given information over the whole region and we thus depend on large datasets on land cover and species distribution [6,59–61]. A visual inspection of the detailed raster when compared to the 1 km^2 maps indicated that the positions of presence-points (red stars), as they were set to a single point within 1 km^2 grid cells, likely do not reflect the exact habitat in which the species was originally observed, and in highly diverse landscape mosaics, they are actually unlikely to do so. In other words, the presences may actually fall into habitats that are of lower suitability because of small nearby patches of high suitability and thus the statistical model is incorrectly assigning high suitability values for more abundant habitat types, while biasing against small-scale habitats. Notably, most of the mismatches occurred for smaller-scale habitat types. Additionally, some presence records seem to be in unusual habitats because of migration events. For example, Reinhardt et al. (2007) explained the single record of *Hipparchia semele* in the upper regions of the Ore Mountains (Erzgebirge) by a single migration event from Bohemia [62]. Further, elevation has not been considered in preparing the IEI-maps. Potential habitats in the mountains, which were considered as suitable, may in fact be unsuitable because of the climatic niche of the assessed species (e.g., *Lycaena dispar*), and therefore, spatial gradients need to be re-inspected to consider more than just land cover. Finally, the suitability of rare habitat types is very difficult to evaluate using presence data, and hence these should be taken with caution. Experts may be better than statistical models to identify such discrepancies.

A crucial point regarding expert evaluations is that all experts expressed their opinions based on broad in-field knowledge of the six species and the biological (habitat) requirements of these—which are not restricted to Saxony, but spans over all of Central Europe and many years of observations. While habitats that are potentially suitable for an individual species may not be inhabited e.g., due to climatic restrictions or other limiting factors that experts may not have considered, e.g., specific management or land-cover patterns in Saxony. For instance, *Lycaena dispar* could have a much broader range of occurrence in Saxony since damp meadows with ample of docks (especially *Rumex crispus* and *R. obtusifolius*; two common larval food plants) are very abundant in Central Europe, but the species only very recently seemed to have expanded in Saxony, which might be linked to climate change [63].

Further sources of error or biases in evaluations are likely to occur due to the definition of land-cover types or because it is not necessary for insects to have a large amount of habitat (scale of study), but rather the right quality (plant species as food for monophagous insect larvae) or management. Also, the mobility of a species can affect suitability evaluations by both experts and statistical models. For instance, *Nymphalis polychloros* is a very mobile species and can often be observed in habitats that do not appear suitable. While observers are likely to record such observations, experts can probably distinguish them as records out of the habitat (namely, dispersal), but such evaluations are usually not recorded in large-scale databases and standardized abundance data that could identify such records are usually lacking.

Land-cover classification is another source of error in analyses based on presence-data: in this study, for instance, land-cover type class 41 (cultivated grasslands) comprise three different types, of which two can serve as excellent habitats for butterflies but the third, defined as intensive grassland, likely is hostile to most species. As these three classes are difficult to distinguish on aerial photos, they are clustered into one habitat code, but this likely affects both expert judgement and the outcomes of presence-data analysis. Finally, expert judgments may be inaccurate because of misunderstandings of the habitat classification. How habitat codes relate to a certain habitat class may be vague although perhaps in German it is all much clearer [36], and may also be sensitive to the scale of perception: open woodland, at a smaller scale, is in fact a mix of two habitats, woods and grasslands. Apart from this, the terms habitat suitability and permeability may themselves be confusing for experts. The quality of expert opinion based analysis could probably be enhanced by adding more experts, especially those who are well acquainted with different parts of the assessed region, but a risk remains that the variability among answers may remain unless these are decided in an interactive or iterative process, e.g., through a set of meetings with all experts.

All in all, we do not regard one approach as superior to the other, but the combination and interaction between the two as an improved route to enhance apprehension of species needs in a way that makes more effective use of data. For instance, the spatial structuring of habitat suitability across Saxony may still reveal more refined segregation that would not have been possible to identify otherwise, while errors in the presence-based evaluation could not have been revealed without the feedback from experts.

4.2. Landscape Permeability

Evaluations of landscape permeability enable us to learn about another potentially important relation between habitat structure and "suitability". More specifically, the permeability values provided by experts seem to be related to habitat structure, e.g., open crops received high permeability for grassland species. However, the relation between seeming structure and suitability has recently been questioned [64]. Exactly for this reason, results are particularly important for cases where low correlation was found between the permeability and suitability evaluations provided by experts. This was the case especially for *N. polychloros* and to a lesser extent *A. iris*. These two species occur in heterogeneous habitats and especially habitat edges (between forest and open habitats). For these species, quite intuitively, both open habitats and forest should be permeable, but presence-based information is very unlikely to reveal any information on this aspect. On the other hand, grassland and open-habitat species, including *H. semele*, which often occurs in open habitats within forests, obtained low permeability values for forests. In this case, it seems that permeability was assigned by the experts as being associated with the structure of the species prime habitat. This, in fact, may not necessarily be true. Information on permeability from independent sources, however, is rare. Hovestadt et al. (2011) observed high dispersal rates of *Phengaris nausithous* in habitat patches that were frequently disturbed by mowing [32], while Nowicki et al. (2014) had recorded nearly no movements in the same species in patches under very slow succession for several years [65]. Sufficient empirical information regarding permeability for all species was not available to compare it with expert opinions.

There are nevertheless potential advantages for an expert evaluation separating suitability from permeability. First, by asking experts to report separately on suitability and permeability, one already enhances awareness to the difference between the two parameters. Secondly, one gains a better mechanistic answer to the question where species may occur, and whether such observations represent occurrence in reproductive habitats or movement through otherwise hostile (dispersal) environment. Such information cannot be obtained from presence data. Furthermore, since observers tend to report on unique observations, there is a plausible chance that presence data based on sporadic observations indeed includes cases of movement through non-reproductive habitats. Such observations, that would bias suitability values, can be rectified by asking experts to make a clear distinction. While it is impossible in this study to evaluate whether the estimations made by experts are correct, or to use them for rectifying erroneous suitability information, they at least provide a template for hypothesis testing, as well as means to separate habitat suitability from permeability for those species where seemingly such association is clearly wrong [66].

5. Conclusions

In this study, empirical presence data yielded very different habitat suitability values and maps than expert opinions. Our results suggest that statistical models based on empirical presence data need to be scrutinized against expert opinions that are well founded on high familiarity with the species and area of concern. Together, knowledge can be maximized regarding habitat suitability. Further, a clear understanding about both suitability and permeability can help in developing sensible conservation policies that could enhance our capacity to achieve species persistence in light of ample environmental risks.

We would suggest rectifying presence-based maps with expert opinions where the latter clearly indicate the suitability evaluation by presence data might be wrong (mismatches between expert opinions and IEI). Further, these results can be tested against independent data, which unfortunately was unavailable in this study but is becoming increasingly available, e.g., through the German Butterfly Monitoring Scheme (TMD) [67]. Additionally, expert opinions on permeability can be used as an additional input for conservation planning tools, such as the software Zonation (University of Helsinki, Helsinki, Finland) [68]. In the future, we intend to compare the maps produced by such tools when considering land cover class preferences only (based on experts or presence-data), as compared to when considering also permeability and hence potential connectivity between natural habitats. Thereby, we can advance the inclusion of functional connectivity in conservation planning.

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Appendix A. Land-Cover Types and Habitat Types (BTLNK) of Saxony Vector Map (Lfulg 2008) [51]

BTLNK	Original German Land Cover Description	English Translation of Land Cover Class
21	Flieβgewässer	streaming water
23	Stillgewässer	standing waterbody
24	Gewässerbegleitende Vegetation	riparian vegetation
25	Bauwerke an Gewässern	construction at waterbody
31	Hochmoor, Zwischenmoor	raised bogs and transitional mires
32	Niedermoor, Sumpf	fens and swamp land
41	Wirtschaftsgrünland	grasslands and (managed) meadows
42	Ruderalflur, Staudenflur	ruderal and herbaceous vegetation
51	Anstehender Fels	bedrock
52	Blockschutthalden	scree slopes
53	größere Lesesteinhaufen und offene Steinrücken	large clearance cairns and open rocks
54	Offene Flächen	open areas
55	Zwergstrauchheiden und Borstgrasrasen	dwarf shrub heath and *Nardus* grassland
56	Magerrasen trockener Standorte	dry abandoned grasslands
61	Feldgehölz, Baumgruppe 100 m^2–1 ha	group of trees 100 m^2–1 ha
66	Gebüsch	scrubland
67	neu ab 2005: Streuobstwiese	meadow with fruit trees
70	Wiederaufforstung	reforestation
71	Laubbaumart (Reinbestand)	broad leaved forest
72	Nadelbaumart (Reinbestand)	coniferous forest
73	Laub-Nadel-Mischwald	mixed forest (broad-leaved-coniferous)
74	Nadel-Laub-Mischwald	mixed forest (coniferous-broad-leaved)
75	Laubmischwald	mixed forest (broad-leaved)
76	Nadelmischwald	mixed forest (coniferous)
77	Feuchtwälder (Moorwald siehe 31300)	mesic forest
78	Waldrandbereiche/Vorwälder	forest edges, pioneer forest
79	Erstaufforstung	afforestation
81	Acker	arable land
82	Sonderkulturen	specialised crop
91	Wohngebiet	residential area
92	Mischgebiet	mixed area
93	Gewerbegebiet	industrial area
94	Grün- und Freiflächen	green spaces
95	Verkehrsflächen	traffic area
96	Anthropogen genutzte Sonderflächen	human used special areas

Appendix B. Habitat Suitability Analysis Based on Expert Opinions versus IEIoccup for Six Butterfly Species

Species Name	BTLNK	BTLNK-Defination	Status	IEI_{occup}	Expert
Apatura iris	75	deciduous mixed forests	Match	high	high
	78	forest edges, pioneer forest	Match	high	high
	67	meadow with fruit trees	Match	low	low
	82	specialized crop	Match	low	low
	25	construction at water body	Mismatch	high	low
	52	scree slopes	Mismatch	high	low
Hipparchia semele	56	dry abandoned grasslands	Match	high	high
	54	open areas	Match	high	high
	67	meadow with fruit trees	Match	low	low
	82	specialized crop	Match	low	low
	31	raised bogs and transitional mires	Mismatch	high	low
	32	fens and swamp land	Mismatch	high	low
	51	bedrock	Mismatch	low	high
	52	scree slopes	Mismatch	low	high
Lycaena dispar	24	riparian vegetation	Match	high	high
	32	fens and swamp land	Match	high	high
	52	scree slopes	Match	low	low
	53	large clearance cairns and open rocks	Match	low	low
	25	construction at water body	Mismatch	high	low
	56	dry abandoned grasslands	Mismatch	high	low
Nymphalis polychloros	78	forest edges, pioneer forest	Match	high	high
	75	deciduous mixed forests	Match	high	high
	52	scree slopes	Match	low	low
	31	raised bogs and transitional mires	Match	low	low
	25	construction at water body	Mismatch	high	low
	51	bedrock	Mismatch	high	low
Phengaris nausithous	24	riparian vegetation	Match	high	high
	32	fens and swamp land	Match	high	high
	31	raised bogs and transitional mires	Match	low	low
	52	scree slopes	Match	low	low
	82	specialized crop	Mismatch	high	low
Plebejus argus	55	dwarf shrub heath and *Nardus* grassland	Match	high	high
	56	dry abandoned grasslands	Match	high	high
	51	bedrock	Match	low	low
	52	scree slopes	Match	low	low
	32	fens and swamp land	Mismatch	high	low
	77	mesic forest	Mismatch	high	low

Appendix C. Habitat Suitability Analysis Based on Expert Opinions versus IEIabund for Six Butterfly Species

Species Name	BTLNK	BTLNK-Defination	Status	IEI_{abund}	Expert
Apatura iris	51	bedrock	Match	low	low
	55	dwarf shrub heath	Match	low	low
	25	construction at water body	Mismatch	high	low
	52	scree slopes	Mismatch	high	low
	77	mesic forest	Mismatch	low	high
	78	forest edges, pioneer forest	Mismatch	low	high
Hipparchia semele	55	dwarf shrub heath	Match	high	high
	56	dry abandoned grasslands	Match	high	high
	67	meadow with fruit trees	Match	low	low
	81	arable land	Match	low	low
	32	fens and swamp land	Mismatch	high	low
	77	mesic forest	Mismatch	high	low
	51	bedrock	Mismatch	low	high
	52	scree slopes	Mismatch	low	high
Lycaena dispar	24	riparian vegetation	Match	high	high
	32	fens and swamp land	Match	high	high
	52	scree slopes	Match	low	low
	53	large clearance and open rocks	Match	low	low
	55	dwarf shrub heath	Mismatch	high	low
	77	mesic forest	Mismatch	high	low
Nymphalis polychloros	75	mixed forest (broad-leaved)	Match	high	high
	78	forest edges, pioneer forest	Match	high	high
	31	raised bogs and transitional mires	Match	low	low
	52	scree slopes	Match	low	low
	24	riparian vegetation	Mismatch	high	low
	76	mixed forest (coniferous)	Mismatch	high	low
	67	meadow with fruit trees	Mismatch	low	high
	82	specialized crop	Mismatch	low	high
Phengaris nausithous	51	bedrock	Match	low	low
	52	scree slopes	Match	low	low
	82	specialized crop	Mismatch	high	low
Plebejus argus	55	dwarf shrub heath	Match	high	high
	56	dry abandoned grasslands	Match	high	high
	51	bedrock	Match	low	low
	52	scree slopes	Match	low	low
	32	fens and swamp land	Mismatch	high	low
	77	mesic forest	Mismatch	high	low

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