Relationships between ergodic indicators of dispersal intensity, IUCN Red List values, and selected environmental variables in connection with European birds whose foraging and flying behavior is associated to roads and highways

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ABSTRACT

Displaying an appropriate dispersal intensity (DI) in response to environmental fluctuations may determine if a given species goes extinct or not. Thus, developing indicators of the DI necessary to harness a given ecological niche breadth is urgent due to the changing latitudinal boundaries between the Earth's great climate belts because of global warming. So, a better assessment of extinction risk should require DI as a complementary indicator. However, the IUCN Red List, indirectly linked to niche assessments, does not take into account DI, and its values are expressed on an ordinal scale. In contrast, there is a theoretical consensus about the link between DI and extinction risk, as well as about the continuous nature of species extinction, which therefore should be measured on a ratio scale. This paper proposes solutions to the above-mentioned issues. Assuming the trait of ergodicity, successfully applied in several publications in ecology so far, measurements of the average values of recent indicators of DI of birds at the species level as well as at the plot level were performed starting from 52 samplings of roadkill events, in eight European countries. DI values were correlated with the respective values of extinction risk reported by the IUCN Red List. Collaterally, a comparative study between DI and two key environmental variables (traffic intensity, and average temperature over land areas) was performed. Inverse and significant correlations between DI and the ordinal scale of IUCN Red List values were obtained, indicating that higher DI values seem to reduce extinction probability. Our results also show that birds seem able to display rapid adaptive behaviors to the increase of traffic intensity. It was found that DI peaks of European birds are associated with deviations of only half a degree Celsius above the general background of temperature over land areas. This set of results, based on a new theoretical framework (Organic Biophysics of Ecosystems –OBEC–; see references and explanatory notes in the main text), is in favor of the appropriateness to rescue the classical foundations of ecosystem ecology based on interdisciplinary links between ecology and physics to promote a better management of the Anthropocene challenges, all of them typified by interdisciplinary traits that require holistic approaches.

1. Introduction

1.1. Problems to quantify ecological niche kinematics, and their importance to assess the extinction risk in birds

A sixth mass extinction of species is underway (Evans et al., 2018; Ceballos et al., 2020), mainly because the current extinction rates are significantly higher than would be expected from the fossil record (Barnosky et al., 2011). Birds species have been deteriorating in status at a rate that may be ten to one hundred times higher than in pre-human times (Brooke et al., 2008). Species extinction is frequently associated with a low dispersal capability compared to the speed of environmental changes that hinders the search for alternative resources (i.e., niche breadth: the variety of resources, habitats, or environments used by a given species; Sexton et al., 2017). So, assessing the dispersal capability of birds is crucial to apply suitable conservation measures because birds are found everywhere; they perform a broad spectrum of trophic niches, and the dispersal of many other species like mollusks, annelids, insects as well as a wide range of parasites depends, in turn, on the dispersal of birds. These traits, in addition to their behavioral and morphological attractiveness, explain why people care about birds far more than they do about most forms of biodiversity (Robinson, 2019).

In order to understand the association between species extinction and niche breadth it is necessary to measure the quickness of niche harnessing, because if environmental conditions change, but species do not move at the same rate in space, then the risk of extinction rises. The main drawback in this field is that the niche definition stated by Hutchinson (1957) as an *'n-dimensional hypervolume'* (with *n* qualitatively changing from one species to another and with a quantitative tendency to infinity), notwithstanding its theoretical elegance, is complex and almost impossible to measure as a whole in practice with the required accuracy (Milesi & López de Casenave, 2005; Holt, 2009; Rodríguez et al., 2015a). From the point of view of georeferenced data of species abundance, there is a close relationship between extinction risk and niche shrinking (Breiner et al., 2017; Diamond & Chick, 2018; Pacifici et al., 2020), or reduction of the hypothetical *'n-dimensional hypervolume'*, albeit the relationship between extinction and niche shrinking deserves further investigation (Scheele et al., 2017).

As a logical result, the IUCN Red List of Threatened Species (IUCN, 2012a, b) indirectly deals with the niche concept, even if that has not been the explicit goal since its foundation date (1964). However, the current set of extinction risk values used by the IUCN Red List has two drawbacks: (i) it is expressed on an ordinal scale, in spite of the general consensus about the gradual nature (i.e., ratio scale) of extinction processes in the absence of sudden environmental changes; and (ii) none of the five criteria (IUCN, 2012a) used to classify species in the IUCN risk categories includes the intensity of dispersal activity at the species level as an explicit indicator. Contrastingly, dispersal activity is a strong determinant of species range areas (Arribas et al., 2012; McCauley et al., 2014) and, therefore, of niche breadth (Slatyer et al., 2013; Sexton et al., 2017). Besides, the connection between patterns of speciation, extinction and diversification, and dispersal activity, is a well-known fact (Qiao et al., 2016; Stier et al., 2019). Thus, the two above-mentioned drawbacks should be overcome.

1.2. General theoretical framework

In regard to the issue described in the previous section, Rodríguez et al. (2015c) have shown that performing an ecological niche means to keep open a sort of bubble of biological order supported by functional trade-offs (Willig, 2011; Rodríguez et al., 2013). According to these authors, trade-offs are typical of stationary or quasi-stationary conditions (i.e., large-scale inputs and outputs in equilibrium with each other, in such a way that ecological indicators either remain constant over time or change very slowly). The trade-off between trophic energy and species diversity is the foundation of the ecological state equation

(Rodríguez et al., 2012; Eq. (1), below) as one of the main models developed so far by the Organic Biophysics of Ecosystems (OBEC, a new research line in ecology; for a summary, see Rodríguez et al., 2019). OBEC is based on equations whose mathematical structure is fully equivalent to those used in conventional physics. This is easily verifiable by comparing Eq. (1) with the ideal gas state equation (Eq. (2)).

$$2N_p\left(\frac{1}{2}m_{ep}\bullet I_e^2\right) = \frac{N_p \bullet k_e}{H_p} \tag{1}$$

$$2N\left(\frac{1}{2}m\bullet v^2\right) = N\bullet k_B \bullet T \tag{2}$$

where, N_p: number of individuals per plot, N: number of molecules in a given mass of gas; m_{ep}: mean body weight per individual per plot, m: molecular weight; I_e: mean value of the indicator of dispersal intensity per individual per plot (Eq. (7), below) expressed in dispersal units (đ, a unit introduced *ad hoc* to allow derivative calculations), v: molecular velocity; k_e: ecological equivalent of Boltmann's constant (k_B); H_p: species diversity at the plot level (Eq. (3), below), and T: temperature. Each variable has been described in paired order with its interdisciplinary equivalent to highlight the structural equivalence between both equations. These equations are mirror images of each other: the main state variable (H_p) in Eq. (1) is in the denominator on the right side of the equality because of its anti-kinetic (reduction of I_e) and therefore anti-thermic influence compared to the opposite relationship that occurs between T and v in Eq. (2) (i.e., T increases with v).

The replacement of v in Eq. (2) by I_e in Eq. (1) has been so suitable that, while the value of Boltzmann's constant in physics is $k_B = 2N$ $(\frac{1}{2}m\bullet v^2)/(N\bullet T) = (m\bullet v^2)/T = 1.38065\text{E} - 23$ Joule/Kelvin $(\text{kg}\bullet\text{m}^2\bullet\text{s}^{-2}\bullet\text{K}^{-1})$ per molecule, the significand or mantissa of its ecological equivalent has the same value of $k_e = (2N_p(\frac{1}{2}m_{ep}\bullet I_e^2)\bullet H_p)/N_p$ $= m_{ep}\bullet I_e^2 \bullet H_p = 1.38065\text{E}$ ecoJoule$\bullet$nat$\bullet$individual^{-1} $(\text{kg}\bullet\text{đ}^2\bullet\text{nat}\bullet\text{ind.}^{-1})$; where φ (arbitrarily selected symbol *ad hoc*) can reach the values of $-x_i$, $\ldots, -3, -2, -1, 0, +1, +2, +3, \ldots, +x_i$ depending on the type of taxocene (Rodríguez et al., 2013). Since k_e is the product of three variables, its constant value over a gradient of species diversity (ΔH_p) is based on trade-offs in the following way: $[m_{ep}^{\downarrow}, I_e^{2\uparrow}, H_p^{\downarrow}]$; $[(m_{ep}\bullet I_e^2)^{\uparrow}, \overline{H}_p]$; $[m_{ep}^{\uparrow}, I_e^{2\downarrow}, H_p^{\uparrow}]$; where $^{\downarrow}$, $\overline{x}$, and $^{\uparrow}$ mean increasing, average and decreasing values, respectively. This trade-off between the indicator of mean trophic energy per individual per plot used in OBEC ($E_{ep} = \frac{1}{2}m_{ep}\bullet I_e^2$, in a similar way in which kinetic energy in physics is $E = \frac{1}{2}m\bullet v^2$) and species diversity (H_p) explains stationarity: given that energy supply is the "fuel" to increase H_p, species diversity cannot either decrease or increase if the two elements of trophic energy (m_{ep} and I_e^2) change in opposite senses on the edges of ΔH_p.

It has been indispensable to explain the relationship between Eq. (1) and Eq. (2) because the key foundation to write this article depends on the successful replacement of v by I_e (its structure and application are explained below) from Eq. (2) to Eq. (1). In other words, without prior empirical verification that I_e can function as the analogue of an ecological speed, it would be unjustified to apply this indicator to study the dispersal intensity of European birds.

1.3. Goal and hypothesis

Resource availability fluctuates in space and time. Therefore, species display a behavior of "firefighters" on several fronts that is facilitated when dispersal intensity values are high. This means that the concept of niche breadth cannot be separated from the quickness at which the resources involved can be used.

With the goal of resolving the situation described in Section 1.1, two analytical simplifications have been assumed: (i) if a given species is recorded in a given place, then this place is part of the performance of its ecological niche; and (ii) those species with a greater homogeneity of the abundance of individuals in the spectrum of places have a broader niche

that they harness in a faster way. In brief, the goal of this article is to test if I_e (mean dispersal intensity per individual per plot) and its subsidiary variable I_{ei} (mean dispersal intensity of species i, see below), can be so useful to study the relationship between dispersal intensity and extinction risk of birds, as they have been to develop Eq. (1). Consistently with this goal, the central hypothesis of this article is that there must be negative and significant correlations between the dispersal indicators used in this article and the values of extinction risk of the IUCN Red List assigned either at the species level or at the average level per plot.

2. Materials and methods

2.1. Data sources

An exploration of academic and grey literature (35 sources, see spreadsheet 'lsrb') that gathers data on geographical coordinates, species richness and abundance per species of death birds per transects due to vehicle impacts on/and at the edge of roads and highways across Central-Western Europe was performed. Sampling via roadkill events is not the most common procedure. However, any kind of methodological concern about the quality and adequacy of roadkill data to perform this work must be resolved considering that:

1) A continental and highly anastomosed system of roads is capable of a certain random sampling of birds, something like a large trawling net, that does not distinguish among species (Morelli et al., 2020). This trait raises its importance even more if we take into account the statistical influence of the Law of Large Numbers and the influence on it of the Central Limit Theorem. That is, when the samples are large enough (regardless of the underlying distribution of the random variables) the distribution of standardized differences between the sum of random variables and the expected value of this sum converges to a standard normal random variable. Under this circumstance, the application of parametric statistical tests is fully justified. This is the case of this article, in which a total of 317 species of birds and 56,418 individuals have been included, sampled throughout a total of, at least (because in some of the references consulted the length of the transect was not declared), 296,738.46 km. This indicates that, regardless of the nature of the sampling method applied, the sample is plausibly reliable for reaching consistent conclusions.

2) This sampling method has been applied many times with noticeable success before. For example, according to González-Gallina et al. (2016), the richness and abundance values derived from roadkill samplings can be used to predict trends for wild populations. In this case, the species richness of rodents sampled in parallel by trapping (9 species) was even lower than the species richness for roadkill samplings (14 species); although the dominant species was the same in both methods. These authors state that roadkill event were a very representative source of information for the purposes of biological inventory and even for identifying the dominance pattern in species composition. They conclude that the interpretation of roadkill data can be a useful tool whose value for biologists has not yet been fully appreciated. Besides, the results from da Silva et al. (2018), indicate that the curve of species accumulation of medium and large-sized roadkill mammals in a sampling performed in an area of high species diversity in Brazil showed no tendency for stabilization. This means that, the larger the sample of roadkill, the closer it will be to reflecting the natural metric of the species composition of the communities bordering the highways and roads. It is a simple matter of scale, which we consider has been largely surmounted in our case due to the large total size of the sampling explained above (item 1). In an additional example, Medrano-Vizcaíno & Espinosa (2020) have found that even elusive species whose recording is difficult by applying other methods, can be found by sampling dead animals on the roadside even in biodiversity hotspots. In a similar way,

according to Allio et al. (2021), the thousands of yearly mammalian roadkill provide a useful source material for genomic surveys that means an underexploited resource in a context of ongoing biodiversity erosion, reaching the precision enough to obtained a genome-scale Carnivora phylogeny included the discovery of a new aardwolf species.

3) According to one of the most important classical founding publications in ecosystem ecology (Margalef, 1963), the structure of biotic communities is never known exactly, but it is always grasped as modified or 'sieved' by a given sampling method (roadkill events in this case), provided that the same method is applied uniformly to a given research framework, as it has been the circumstance in this work. That is to say, nobody works in ecology at the level of a community as a whole kept in a "pure" state; but at the level of *taxocene* or *taxocenosis* (a group of species that belong to a particular supra-specific taxon and occur together in the same association or ecological community because they have been caught in a combined way by a given sampling method; Barrows, 2011; Quirós, 2016) or, using a more modern term in ecological jargon, at the level of *ecological assemblage*. It is also possible that this all-encompassing rule of ecological methodology has been neglected due to a sort of "intellectual snobbery" that pervades modern ecology because of a lack of appreciation of past literature which causes that issues come in and out of fashion in ecology without scientific resolution (Belovsky et al., 2004). In this regard, the specific taxocene on which the authors have worked is explicitly stated in the article title itself.

4) Finally, there is a surprising recent advance in ecosystem ecology (which will likely be neglected for several years due to its interdisciplinary nature) which dispels any concern about the relevance of using data sampled by roadkill events (or whatever other method); due to the alleged alteration that this type of sampling produces on the natural metric of ecological communities: Rodríguez et al. (2015a,b,c, 2016) have discovered the theoretical framework empirically testing its feasibility, regarding the action of key quantum traits that influence, in an underlying but decisive way, on the dynamics of ecosystems. What is the essential feature of an observation, always interpreted as a process of measurement of some parameter, in the field of quantum mechanics? The essential feature is that it is in principle impossible (that is, in a way totally independent of the well-known observer's paradox in social science; see Cukor-Avila, 2000) to carry out any measurement regardless the method applied on the system without altering its properties (Penrose, 2007), in this case the metric of the observed bird communities. Therefore, taking into account both this last item, as well as the previous three, the concern about whether an ecological sampling based on roadkill events is reliable or not in this case, is ungrounded.

2.2. Requirements and structure of indicators, and statistical processing

The assessment of dispersal intensity values of many species of a taxocene with such a high level of vagility as birds seems to be a daunting task, mainly when tracking devices have not been used. A fruitful shortcut is to assume the ergodic nature of ecosystems under stationary or quasi-stationary conditions. Ergodicity means statistical equivalence between mean values measured over time and mean values measured across space (Gould et al., 1996; Greiner et al., 1997). This concept has its origin in physics and, although its analytical importance has been somewhat undervalued in biology, it has been used by several authors in ecology (e.g., MacArthur, 1955; Kerner, 1957; Kikuzawa et al., 2009). Ergodicity can be studied by applying complex mathematical methods (e.g., Hopf, 1932) but, qualitatively speaking, is a general background curtain in biology. For instance: (i) the space that separates two species in a cladogram is proportional to the remoteness of the common ancestor of both species in time; (ii) if it is possible reconstructing the lineage of a taxocene is because the sequence of geological strata in space is equivalent to a sequence of evolutionary

variations of species over time; and (iii) the coexistence of more modern species with the so-called 'living fossils' is a sign of ergodicity. It is also possible to find relict ecosystems coexisting with more modern ecosystems.

According to the definition of ergodicity and its relationships with stationarity and Eq. (1), analyzing many samples taken in different places over a long period of time requires to explore whether the Central-Western Europe bird taxocene as a whole has remained, approximately, under stationary conditions at the large scale (1959–2019). With such a goal, Pearson linear correlations were calculated between time (sampling date) and the following variables:

species richness per transect or plot (*S*),

total abundance per transect or plot (*N_p*), and

species diversity per transect or plot (*H_p*, see Eq. (3); according to Shannon, 1948).

If in these correlations $-1 \ll r \ll 1$ and $P > 0.05$ it is possible to assume that the basic requirements for stationarity and ergodicity are fulfilled, because the values of correlation slopes are neither strong nor significant over time. Thereby, the statistical processing of non-simultaneous samples is possible, just as if they would be located in a commonly shared framework in space and time (ergodicity).

$$H_p = -\sum_{i=1}^{S}\left(\frac{n_i}{N_p}\cdot\ln\frac{n_i}{N_p}\right) \qquad (3)$$

where *S* is species number per transect, n_i is number of individuals of species *i*, and $N_p = \sum_{i=1}^{S} n_i$.

The geographic coordinates (*x, y*) of the center point of each transect were obtained by means of Google Earth Pro 7.3.2.5776 and expressed in meters on the UTM coordinate system. The following indicators of dispersal intensity were calculated, in order to compare its mean values with the ordinal scale of the IUCN Red List:

$$d_{i,j} = \frac{\sum_{k=1}^{m}\left(\left(\sqrt{(x_j-x_k)^2+(y_j-y_k)^2}\right)\times\left(\frac{2i_{j,k}}{i_j+i_k}\right)\right)}{m} \qquad (4)$$

$$I_{e_{i,j}} = \left(\frac{d_{i,j}}{\sigma_{i,j}}\right)\times 100 \qquad (5)$$

$$I_{ei} = \frac{\sum_{j=1}^{m}\left(I_{ei,j}\right)}{m} \qquad (6)$$

$$I_e = \frac{\sum_{i=1}^{S}\left(I_{e_{i,j}}\right)}{S} \qquad (7)$$

where $d_{i,j}$ is the mean dispersal activity of species *i* in transect *j* with central geographic coordinates (*x, y*) within a total space divided into an *m* number of *k* transects; $\sqrt[2]{(x_j-x_k)^2+(y_j-y_k)^2}$ is the Pythagorean theorem that allows the estimation of Euclidean distances (ED) between transect *j* and all the remaining *k* elements within the set of *m* transects; i_j and i_k are the respective abundances of species *i* in transect *j* and *k*; $i_{j,k}$ is the shared number of individuals of species *i* in transects *j* and *k* (e.g., if $i_j = 7$ and $i_k = 12$, then $i_{j,k} = 7$); $(2i_{j,k})/(i_j + i_k)$ is the Bray-Curtis similarity index which ranges from 0 to 1 (Washington, 1984); $\sigma_{i,j}$ is the standard deviation of $d_{i,j}$ (given that $d_{i,j}$ is an arithmetic mean); $I_{ei,j}$ is the ergodic indicator of the intensity of dispersal activity of species *i* in transect *j* according to the analytical simplifications introduced in the second paragraph of Section 1.3; I_{ei} is the ergodic indicator of the intensity of dispersal activity of species *i* in regard to the set of *m* transects as a whole; I_e is the ergodic indicator of the intensity of dispersal activity of the species group included in transect *j*; and *S* is the species number in transect *j*. In regard to Eq. (4) to Eq. (7), it is important to highlight their mathematical simplicity in comparison to other models in this field (e.g., Génard & Lescourret, 2013; Heer et al., 2019; Kleyheeg et al., 2019). A detailed explanation about Eq. (6) and Eq. (7), as well as their main

traits can be seen in Rodríguez et al. (2013). A hypothetical example improves the understanding of these equations. Let us assume that there are 3 transects (*τ*) with coordinate values (*x, y*) of: $τ_1$: 45, 32; $τ_2$: 123, 13; $τ_3$: 115, 261. In addition, there are 3 species (*s*) with abundance values per transect of: $s_{1,τ1} = 21$, $s_{1,τ2} = 0$, $s_{1,τ3} = 144$; $s_{2,τ1} = 125$, $s_{2,τ2} = 10$, $s_{2,τ3} = 82$; $s_{3,τ1} = 100$, $s_{3,τ2} = 210$, $s_{3,τ3} = 36$. Table 1 shows the results of applying Eq. (4) to Eq. (7) to the above hypothetical data.

Accordingly, by establishing a statistical equivalence between space and time, the ergodic approach mitigates the well-known difficulties associated with adding the temporal dimension to quantify ecological niches in the particular case of birds (e.g., Eyres et al., 2017).

A matrix of dispersal intensity values (spreadsheet 'dim'), fully equivalent to Table 1, was obtained starting from the data set described in Section 2.1. Alternatively, every value in 'dim' was replaced by its respective ordinal value according to the IUCN Red List (IUCN, 2019) to obtain an extinction risk matrix (spreadsheet 'erm'). The species set comprised five IUCN Red List categories ('least concern', 'near threatened', 'lower risk', 'vulnerable', and 'endangered'). In turn, there are four population trends ('unknown', 'increasing', 'stable', and 'decreasing') within each IUCN category. Thus, the sampling yielded an observed spectrum of 20 combined categories of increasing extinction risk, from nine to 28, interspersed in between the expected IUCN category of minimum risk ('not applicable & unknown population trend' = 1) and the category of maximum risk ('extinct in the wild as well as under artificial breeding conditions' = 41). The structure of the total set of 20 combined risk categories are included in cells from BE8 to BG28 of spreadsheet 'dim', and the actual spectrum of observed extinction risk categories per species (13, from category nine to category 28 excluding categories 19, 20, 21, 23, 25, 26, and 27 because of the absence of species) can be seen in cells from BC9 to BC325 of spreadsheet 'dim'.

The number of observations (*S*, total number of observed species) according to the IUCN Red List for categories from nine to 12 was high and with a relatively low fluctuation ($S_{mean} = 71.75$; coefficient of variation, CV = 33.65). Therefore, the values used for these categories were the raw values of categories themselves (non-clustered). On the contrary, the value of *S* from the IUCN Red List categories 13 to 28 was lower and more disperse than the former one ($S_{mean} = 3.33$; CV = 128.16). As a result, categories from 13 to 28 were grouped into three clusters (C1: IUCN's categories 13–16; C2: IUCN's categories 17–24; and C3: IUCN's category 28, with *S* = 1). C3 was kept apart due to its singularity because of the lack of species belonging to IUCN's categories 25, 26 and 27. This latter procedure increased the average value of richness and decreased its fluctuation ($S_{mean} = 10.00$; CV = 79.37) in comparison with the raw values. These clustered values were also used as mean values of the IUCN Red List categories. The Spearman correlation (because in this case N = 7) between the mean values per set of rows, both clustered and non-clustered, according to the IUCN Red List categories between 'dim' (mean I_{ei}, according to Eq. (6)) and 'erm' (extinction risk matrix) was calculated. Orthogonally (see row I_e in comparison with column I_{ei} in Table 1) in regard to the analysis described before, a Pearson correlation analysis between the average value of categories of the IUCN Red List per transect *vs.* the respective average value of I_e (Eq. (7)) was performed to explore if a higher risk of extinction was associated to a lower average value of dispersal intensity per transect.

Table 1
In italics, the results of the calculation of Eq. (5) based, in turn, on Eq. (4). Values in the last column (I_{ei}: row averages) are the results of Eq. (6). Values in the last row (I_e: column averages) are the results of Eq. (7).

	$τ_1$	$τ_2$	$τ_3$	I_{ei}
s_1	*57.735*	—	*57.735*	57.735
s_2	*63.241*	*77.433*	*83.084*	74.586
s_3	*93.385*	*110.902*	*104.488*	102.925
I_e	71.453	94.167	81.769	

It is foreseeable that the variables involved in this study are influenced by some key environmental variables. Therefore, traffic intensity and temperature values at the continental scale over time were considered the two most important variables; the former one due to obvious reasons, and the latter one because it has been reported as an essential factor to predict species' responses to the combined effects of habitat and climate in European birds (Barnagaud et al., 2012). Based on this, the fluctuations of traffic intensity expressed in million passenger-kilometers (*IPM/K*) per year and the values of European average temperatures (*T* in °C) over land areas were analyzed over time (*IPM/K*), as well as their relationship with the respective I_e values. All the statistical analyses described in this section were performed by using the statistical software package Statistica 12 (StatSoft, Inc., 2014).

3. Results

The set of samplings includes five of the nine European biogeographic regions, as well as a representative exploration (33 transects, i. e., 63.5% of the total number of transects) of the largest terrestrial vertebrate hotspots in Europe (Mediterranean basin) (Fig. 1).

Since birds deploy a high dispersal activity in comparison with other terrestrial vertebrates, and given the structure of Eq. (6) and Eq. (7), it is plausible to assume that the ecological influence of all European biogeographic regions is implicitly included in this study (Fig. 1). The data set included 56,418 individuals (abundance per species per transect in spreadsheet 'Np'; abundance data collected, in turn, by reviewing the literature referenced in spreadsheet 'lsrb') belonging to 317 bird species sampled in 52 transects embracing over 40 ecoregions from eight different countries (Bulgaria, Denmark, Italy, Norway, Poland, Portugal, Spain and United Kingdom). The average of killed birds was 0.353 ± 1.617 (SD) birds/km. There were no significant correlations of time *vs.* species richness (*S*), abundance (*N_p*) and species diversity (*H_p*) per transect (Fig. 2). Hence, it is possible to assume that the requirements of stationarity and, therefore, ergodicity are fulfilled to apply the calculations from Eq. (4) to Eq. (7).

Fig. 3a and Fig. 3b provide additional evidence about the stationary state of this taxocene. Fig. 3c and Fig. 3d show high and significant negative correlations between the indicators of dispersal intensity (Eq. (6) and Eq. (7), respectively) and the mean value of Ordinal Extinction
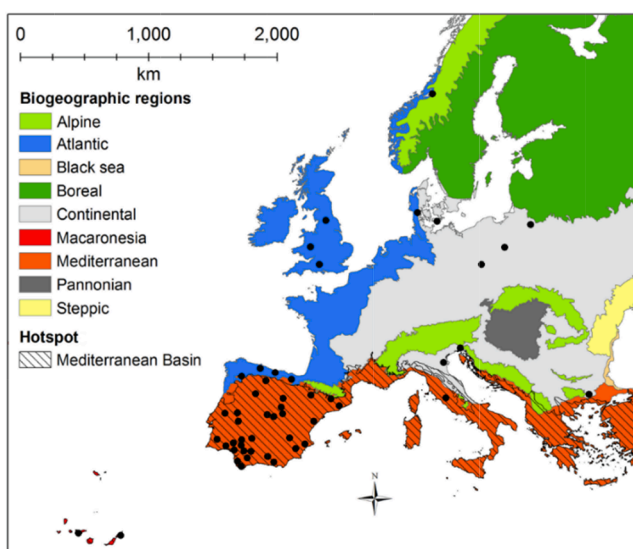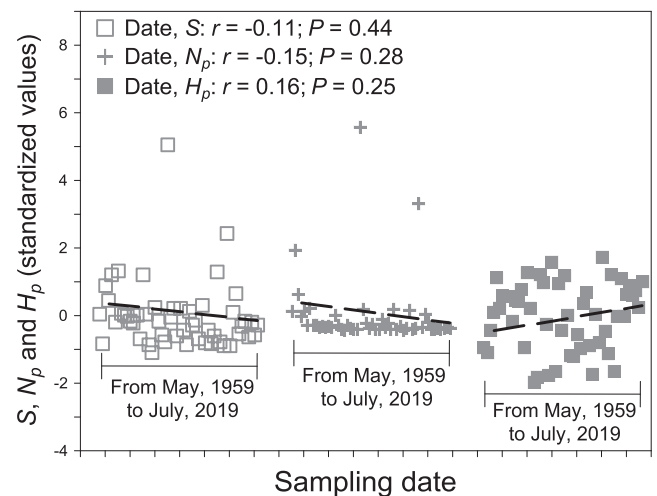

Fig. 2. Pearson correlations between sampling date and total species richness (*S*), abundance (*N_p*) and species diversity (*H_p*) per transect. Original and standardized data in spreadsheet 'pc'.

Risk (OER) according to the IUCN Red List.

4. Discussion

A first intriguing issue is the seeming contradiction between the stationary state of this taxocene (Fig. 2, Fig. 3a, and Fig. 3b) despite an almost constant increment of the inland transport (Fig. 4a) from 1970 to 2018.

At the first instance, there are three plausible explanations: (i) increasing conservation measures either *in situ* (e.g., fences, and wildlife underpasses) or in breeding sites (e.g., avoiding unusual noises during the incubation period, scaring away the collectors of pigeons and eggs as well as those predators that are invasive species, and building artificial refuges for pairs of hatching birds when possible); (ii) adaptive changes in the behavior of birds caused by transport itself, or due to changes in migration patterns because of the influence of climate change on Europe (Maiorano et al., 2013); and (iii) declines in bird abundance over time that would lead to reduced likelihood of car-bird encounters. Option (i), that is to say, fences and wildlife underpasses, being more effective *in situ* for other vertebrates that are unable to fly, is more difficult for birds due to obvious reasons. However, other types of conservation interventions may have reduced the number of global extinctions of birds from 19 to three, and slowed the extinction trajectory of 33 endangered species (Brooke et al., 2008). Bird species have become extinct at a rate that is two (Australia) to 10 (globally) times lower than predicted by the IUCN Red List (Brooke et al., 2008). This mismatch between reality and predictions highlights the importance of proposing complementary indicators of the capability of birds to take advantage of the niche breadth, as expressed by Eq. (6) and Eq. (7).

About option (ii), nature can show rapid evolutionary responses, mainly if these responses depend on behavioral habits. As a result, the potential probability of roadkill events could decline over time for some species, thereby compensating for the increasing influence of traffic until it produces the trend to stationarity shown in Fig. 2, Fig. 3a, and Fig. 3b. Birds are able to display rapid adaptation responses to road traffic through selection of favored individuals that avoid being hit (Brown & Brown, 2013), just as it was early remarked by Bumpus (1899) in regard to the selective influence of a single severe storm on a sparrow population. This option is even more underpinned by the results shown in Fig. 4b, that are in agreement with the influence of climate change on Europe reported by Maiorano et al. (2013): despite the remarkable differences between the correlations temperature (*T*) *vs.* time ($r = 0.837$, $P < 0.001$) and mean dispersal intensity per species per plot (I_e) *vs.* time

Fig. 1. Geographical positions of 52 transects (black dots) related to the European biogeographic regions within the sampling area. Map of biogeographic regions from Maiorano et al. (2013). Data of sampling date, sampling site, country, ecoregion, and UTM coordinates per transect are included in spreadsheet 'dim'.
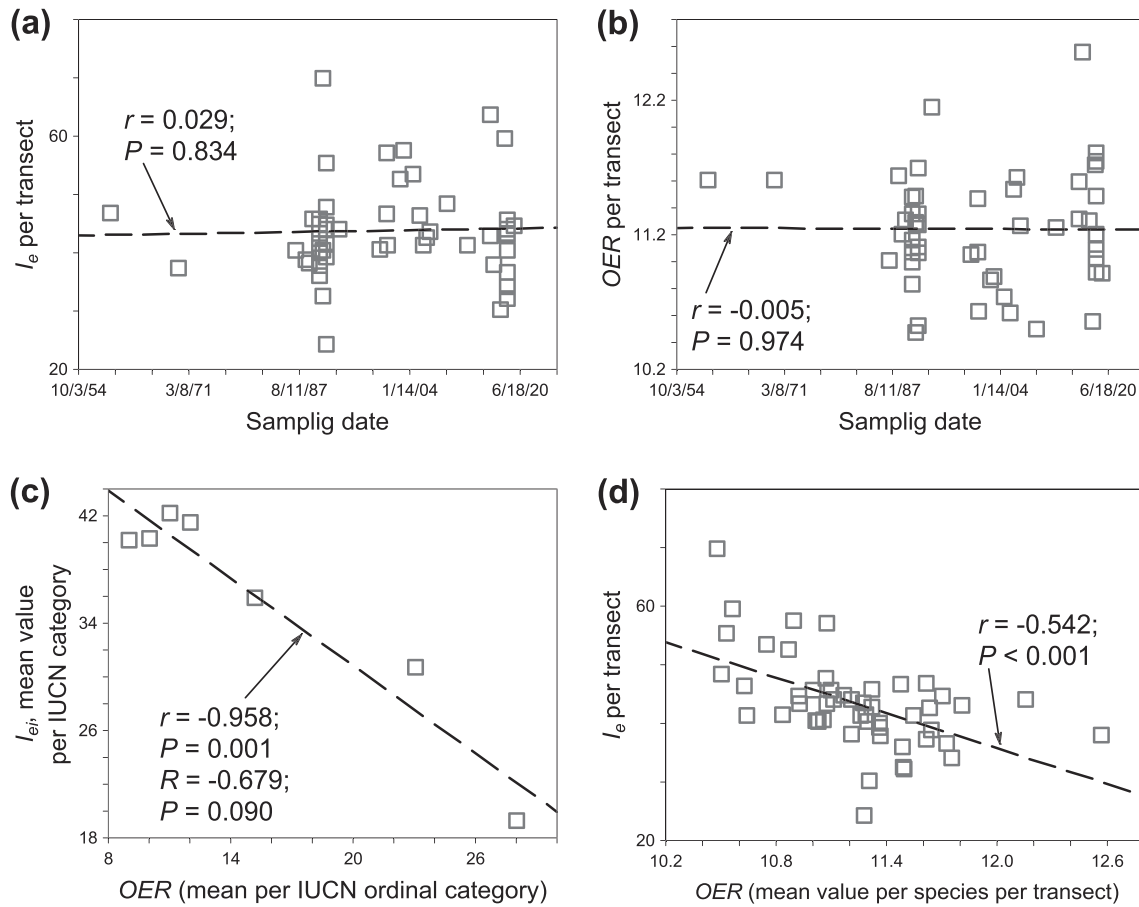
Fig. 3. Associations between matrices 'dim' and 'erm' with transect sampling date, as well as with each other. (a) Pearson correlation (r) between sampling date and I_e (Eq. (7)). (b) Pearson correlation between sampling date and mean Ordinal Extinction Risk (OER; data from IUCN, 2019) per species per transect (data in spreadsheet 'dim *vs.* erm-1'). (c) Spearman (R) and Pearson correlations between average I_{ei} (Eq. (6)) for all the species included in a same cluster of IUCN categories and the respective mean value of OER (data in spreadsheet 'dim *vs.* erm-2'). (d) Pearson correlation between I_e (Eq. (7)) per transect and the respective mean value of OER; two outliers were excluded from the analysis (data in spreadsheet 'dim *vs.* erm-1').
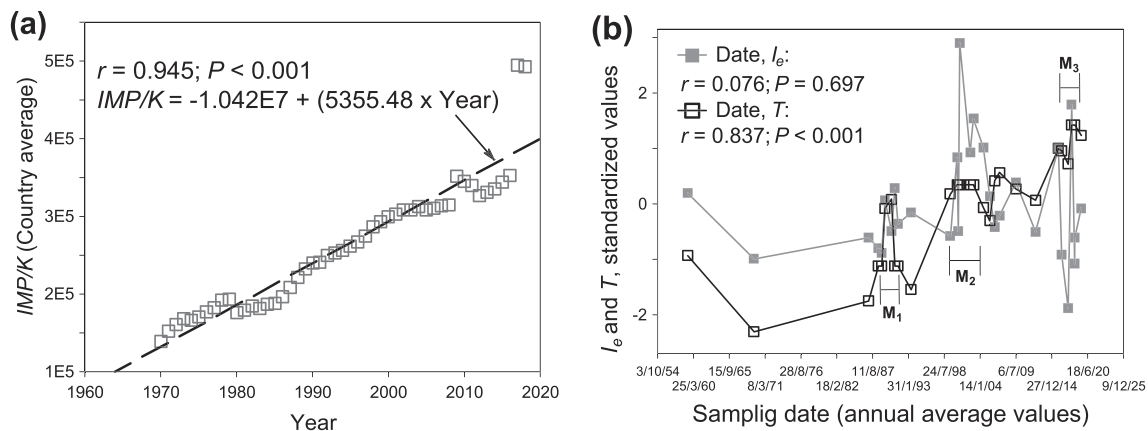

Fig. 4. Environmental factors with a strong potential influence on the dispersal activity of birds. (a) Traffic intensity (1970 – 2018) as mean inland transport expressed in million passenger-kilometers (*IPM/K*) per year for the eight European countries encompassed by the sampling area. Data from OECD (2020). (b) Fluctuations of dispersal intensity per species per plot (I_e, Eq. (7)) and European average temperatures (T in °C) over land areas from 1959 to 2019 relative to the pre-industrial period. I_e and T have been standardized to allow their inclusion on a single axis. M$_1$, M$_2$, and M$_3$: periods in which peaks of dispersal intensity of birds coincide with temperature peaks in accordance with the three stages commented in the main text. Temperature values from Clark (2020). Original data and calculations in spreadsheet "temp-disp."

($r = 0.076$, $P = 0.697$), there are three time lapses (M$_1$, M$_2$, and M$_3$; Fig. 4b) in which noticeable escalations in dispersal activity coincide with noticeable increases in the European average temperatures over land areas. That is to say, dispersal intensity does not follow, gradually, the same quasilinear increase of continental temperature over time. On the contrary, it is very probable that a particularly intense dispersal

activity looking for better environmental conditions is triggered when the temperature over land areas surpasses a threshold value in comparison with previous environmental conditions already 'known' by birds from an evolutionary point of view. For example, the lapse from 1959 to 2019 can be partitioned in three sections (1, 2, and 3) separated by the respective peaks of bird dispersal intensity (i.e., 1959 – 1990; 1991 – 2000; 2001 – 2018). The respective background of mean temperatures for these periods are: $\overline{T}_1 = 0.797\ °C$; $\overline{T}_2 = 1.156\ °C$; and $\overline{T}_3 = 1.612\ °C$ (data and calculations in spreadsheet "temp-disp"). Starting from these average values, the respective peaks of dispersal activity were triggered in those years in which $T_1 = 1.400\ °C$ ($\Delta T_1 = 1.400 - \overline{T}_1 = 0.603$); $T_2 = 1.540\ °C$ ($\Delta T_2 = 1.540 - \overline{T}_2 = 0.384$); and $T_3 = 2.120\ °C$ ($\Delta T_3 = 2.120 - \overline{T}_3 = 0.508$). Since $(0.603 + 0.384 + 0.508)/3 = 0.498 \approx 0.5\ °C$, it seems that a temperature increase of half a degree Celsius at a continental scale can produce enough stress in birds to trigger a conspicuous response of dispersal activity looking for better environmental conditions.

As for option (iii), since the sensitivity of species to the influence of selection pressures is not uniform, the decline in the abundance of birds over time should lead to a concurrent reduction of diversity (H_p) in the long run. However, Fig. 2 does not show evidence in favor of this possibility. After all, the killing of birds by road vehicles do not represent a higher risk for highly evolutionarily unique birds than for other common avian species in Europe (Morelli et al., 2020). Hence, a combination of options (i) and (ii) is the most plausible explanation to the seeming independence between Fig. 4a and dispersal intensity.

In Fig. 3c, the Pearson correlation (r) is negative, high, and significant. However, Spearman correlation (R), despite its high negative value, is on the threshold of significance. This may be explained by the relatively narrow spectrum of the IUCN Red List categories observed ($[13/41] \times 100 = 31.7\%$ of the total spectrum of possible categories). This result could leave some doubt concerning the inverse statistical association between the indicator of the speed of harnessing of niche breadth expressed in a ratio scale starting from Eq. (6) and the ordinal-scale extinction risk reported by the IUCN. However, at the transect level (Fig. 3d), there is a significant inverse correlation between I_e (Eq. (7)) and the average value of Ordinal Extinction Risk (OER) according to the IUCN Red List. The results of this research reinforce the opinion (e.g., Breiner et al., 2017; Trull et al., 2018; Brooks et al., 2019) about the suitability of promoting the application of additional indicators in order to enhance the warning role of the IUCN Red List in managing species to avoid their extinction.

At a more general level of analysis, that is, epistemological, it is evident that we cannot protect isolated species, but rather the ecosystem where they live as a whole. But the mainstream of thought in contemporary ecology is based, rather than on a general paradigm useful for describing the functioning of any ecosystem under any circumstance, on isolated proposals to describe the functioning of small fractions of nature (e.g., see Lawton, 1999; Linquist, 2015; Lean, 2019). In reality, the only sprout of a feasible ecological paradigm remains the classic proposal for an ecology based on links between natural history, as defined by Schmidly (2005), and conventional physics (e.g., Lindeman, 1942; Margalef, 1963; Odum, 1968, 1969). Nonetheless, this proto-paradigm seems to have been prematurely marginalized due to a misunderstanding of the physical concept of equilibrium in ecology (Riera et al., 2018). The broadest and deepest meaning of this work is to provide added evidence that highlights the importance of rescuing the interdisciplinary approach mentioned above; for example, by completing the development of OBEC, in order to achieve a more reliable and empirically manageable conservation of nature.

5. Conclusions

The findings of this work indicate that a minimal environmental variation (for example, of only 0.5 °C in this case) on a large scale can

trigger sudden dispersal processes and alterations in the niche breadth of many species. This result emphasizes the importance of applying the precautionary principle with the utmost rigor in regard to nature conservation.

Furthermore, the results of this study support the inverse relationship between the proposed indicators of dispersal intensity and the extinction risk category of the respective species in the IUCN Red List. As these results do not justify the rejection of the initial hypothesis, it is therefore theoretically and empirically feasible to use interdisciplinary indicators (Eq. (6) and Eq. (7)) to assess extinction probability on a ratio scale complementary to the IUCN Red List values.

Nevertheless, this work should only be seen as a first step in this direction, due to two elements that need experimental reinforcement: additional explorations including a wider spectrum of IUCN Red List categories are desirable, as well as the need to apply the ecological state equation (Eq. (1)) and its associated models to birds. These models could explain the status of the Central-Western Europe bird taxocene in a more complete way. Although this topic remains pending, it can be developed in a near future by taking the set of data used in this work as an initial empirical foundation.

Declaration of Competing Interest

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

Data availability statement

Data and supporting calculations are available in PANGAEA (cod. PDI-29411) (https://issues.pangaea.de/browse/PDI-29411).

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