

A test of six simple indices to display the phenology of butterflies using a large multi-source database

Valentina Cima^{a,*}, Benoît Fontaine^{a,b}, Isabelle Witté^a, Pascal Dupont^a, Martin Jeanmougin^b, Julien Touroult^a

^a UMS Patrimoine Naturel (PATRINAT), AFB, MNHN, CNRS, CP41, 36 rue Geoffroy Saint-Hilaire, 75005 Paris, France

^b Centre for Ecology and Conservation Sciences (CESCO UMR7204), MNHN-CNRS-Sorbonne University, 55 rue Buffon, 75005 Paris, France

ARTICLE INFO

Keywords:

Opportunistic data
Citizen science
Lepidoptera
Flight period
Seasonality
Bias correction
Sampling effort

ABSTRACT

Biological recording at broad temporal and spatial scales produces large volumes of species occurrence data. Multi-source datasets, which include opportunistic records, are unstructured and contain bias, mainly due to uneven and unknown observation effort, but they also provide meaningful information about species phenology. Butterflies are well known and well represented in citizen-science programs and national inventories, which makes them an interesting case for phenological studies. This work aims to find a simple, flexible, fast-rendering phenology index, which has to prove reliable when compared to standard knowledge. Six indices (two non-corrected and four corrected for observation effort) were built and implemented on butterfly records. They were analysed against blind expert opinion and a set of monitoring data. Surprisingly, all indices produced mostly realistic phenological patterns and non-corrected indices were as good as corrected ones. The number of species records divided by the number of records of all species of the group collected during the same period is the only index that should be avoided, because of an over-correction of recording intensity. Additional work is needed, in particular to refine the analysis by testing the sensitivity of the index to the amount of data, as well as by employing statistical models that are also useful for exploring trends and seasonal shifts.

1. Introduction

The rise of biological recording schemes including broad-scale citizen-science programs has brought new possibilities to conservation and ecological research over the last decades, producing large amounts of species occurrence data (Dickinson et al., 2012; Hochachka et al., 2012; Tulloch et al., 2013; August et al., 2015; Pocock et al., 2015). When gathered into datasets that cover large temporal and spatial extents, these multi-source data (a combination of opportunistic and systematic records) may help unveiling important aspects of biodiversity state and changes (Dickinson et al., 2010; Dickinson et al., 2012; Hochachka et al., 2012; Isaac and Pocock, 2015; Powney and Isaac, 2015), including species phenology. However, multi-source data present different levels of standardisation (depending on the source of collection) and are by nature noisy and unstructured. They suffer from several biases (Dickinson et al., 2010; Robertson et al., 2010; Isaac et al., 2014; Isaac and Pocock, 2015) which primarily relate to variation in recording intensity (Isaac et al., 2014). In fact, sampling effort may vary throughout the year, between the years and among regions and this variability is usually unknown in opportunistic datasets (Giraud

et al., 2016).

Phenology is the study of periodic biological events (such as plant flowering, insect emergence and bird migration) that are regulated by environmental factors. The simplest way to represent animal phenology is by counting the number of species occurrences per period, collating all years' data. This kind of representation is sometimes employed in broad distribution Atlases (some examples: Lumaret, 1990 for dung beetles; the iNaturalist platform of crowdsourcing of data, for instance <https://www.inaturalist.org/taxa/207977-Aglais-io>; the Atlas of butterflies and zygens of Midi-Pyrénées, <http://atlaspapillonsmidipyrenees.myspecies.info/http://atlaspapillonsmidipyrenees.myspecies.info/>) or in more specific studies (such as Bertone et al., 2005; Pozo et al., 2008; Archaux et al., 2011). Other works have reported phenology as weighted or mean counts (van Swaay et al., 2002; Archaux et al., 2015; Manil et al., 2015) as well as modelled counts (Dennis et al., 2013; Schmucki et al., 2016), sometimes accounting for imperfect detection or uneven recording intensity (Strebel et al., 2014).

Butterflies are relatively well known and well represented in citizen-science programs and national inventories. For this reason, they have

* Corresponding author.

E-mail address: valentina.cima@mnhn.fr (V. Cima).

frequently been the subject of studies based on monitoring and citizen-science data (see for example: Maes et al., 2012; Dennis et al., 2013; Schmucki et al., 2016). Here, we focus on the representation of butterfly phenology patterns with multi-source opportunistic records while accounting for sampling effort. More precisely, this study aims to explore the potential of a national biodiversity reference system, the National Inventory of Natural Heritage of France (INPN – <https://inpn.mnhn.fr>), for displaying the phenology of butterflies at a national scale. The goal is to develop a phenology index with the following requirements: 1) the phenology is displayed using multi-source data, including opportunistic observations; 2) the index yields overall patterns that are consistent with standard knowledge on species phenology; 3) the index must be suitable for many species and different type of seasonality and voltinism (refer to Wolda, 1988 for a precise classification of seasonality patterns); 4) the phenology charts will be presented to a general audience on a web portal, so the index must be simple, easily interpretable and fast-rendering. Ideally, the index should inform on species activity over the year or display a lack of knowledge, inducing the community to collect more accurate occurrence data.

Some studies have highlighted the potential of opportunistic data to perform as well as standardised data (see for example, van Strien et al., 2010, 2013). This is generally true when opportunistic data are corrected for bias (van Strien et al., 2013; Isaac et al., 2014). Measures that simply show the number of observations are sensitive to sampling effort and likely to reflect observer activity (Dickinson et al., 2010), while those that account for temporal and spatial variation in effort should better delineate the true phenology of a species. Under this assumption, six relatively simple indices, based on both non-corrected and corrected measures, were designed with butterfly records from the INPN. The indices were analysed against blind expert opinion and a set of monitoring data. We expected corrected indices to yield more realistic patterns than non-corrected ones. The results should lead to recommendations about selecting an accurate but simple index for displaying phenology with multi-source opportunistic data.

2. Materials and methods

2.1. General analysis process

The analysis started by selecting, with the help of a lepidopterologist (PD), a panel of butterfly species that are well known and well represented in the dataset. Their records, which come from different data sources (Appendix 1), were collected in several years and are assumed homogeneous over France. In order to assess the versatility of the indices, the selected panel had to be diverse in terms of phenology type, ecology and latitudinal range. Based on literature review, a series of non-corrected (“raw”) and corrected indices were implemented on multi-source butterfly data and evaluated through two different approaches: a qualitative analysis, based on expert evaluation of the phenological patterns drawn by the indices, and a quantitative analysis to seek for a match between the indices and the patterns based on monitoring data. The different steps of the analysis are developed in the next sections and summed up in Fig. 1. All analyses were carried out in R v.3.5.2 (R Core Development Team, 2018).

2.2. Data description

Data were extracted on July 2017 from the National Inventory of Natural Heritage of France (INPN – <https://inpn.mnhn.fr>). The INPN is a system created by the National Museum of Natural History (MNHN) and managed by MNHN and the National Agency for Biodiversity (AFB) that aims at sharing information and data about biodiversity in France. The INPN gathers multi-source data from scientific surveys, museum collections, citizen science programs, as well as opportunistic observations. These data are collected, standardised and synthesized in order to develop a national reference bank of biodiversity data. One

record in the INPN corresponds to one species occurrence, collected by one observer whatever the number of individuals. A record contains a start and an end date of collection. The interval between the two dates (“temporal resolution”) may vary from 1 day (“precise date of observation”), to several days (the duration of an inventory or sampling campaign) until several years, which is the case of observations derived from literature or museum collections with uncertain temporal information. On the other hand, data from several sources may have different spatial resolution. Nonetheless, when stored in the INPN, records are assigned to 10x10 km cells, according to a national reference grid and a standardised method, which allows for reliable spatial information.

Effort correction required data from a background or target group (Ponder et al., 2001; Phillips et al., 2009; Kéry et al., 2010; Ruete, 2015). Although we focused on butterfly phenology, we extracted all INPN records of diurnal lepidopterans (i.e. butterflies and diurnal moths, hereinafter referred as the “group”, see Table 1) by assuming that survey methods and collector specialties within this group are similar, hence data share similar bias (Ponder et al., 2001; Ruete, 2015). The group includes seven families: Pieridae, Papilionidae, Nymphalidae, Lycaenidae, Hesperidae, Riodinidae, Zygaenidae. The French taxonomic repository TaxRef version 11.0 (Gargominy et al., 2017) was employed for taxonomic references. Assuming that naturalists and collectors have similar knowledge and bias and use analogous survey methods for the group of butterflies and diurnal moths, we defined a “field visit” as a 10x10 km cell surveyed by one observer on a date, regardless of the number of species he or she had observed. In this manuscript, we refer to a species “quadrat” as a 10x10 km cell where the species was recorded at least once in a given period. In the same way, one “group quadrat” is a 10x10 km cell where at least one of the species of the group was recorded. The vocabulary used for this study is summarised in Table 1.

2.3. Data preparation and index design

In the last decades, biological recording has intensified (Isaac and Pocock, 2015). In France, the mission of the MNHN to centralize information and managing a national reference bank of biodiversity started in 1979. Since those years, the collection of records at a national scale have become more frequent and rigorous, in particular with the development of national inventories and atlases (Touroult et al., 2015). On this basis, we presumed data from 1980 onwards to be more uniform and representative of current overall phenological patterns (e.g. number, position, sharpness of peaks). We restricted, therefore, the analysis to those data. Moreover, 1980-today corresponds to the time span of knowledge of the experts who took part in the survey.

In order to minimize errors, outlier data, such as records on January 1st and December 31th (probable by-default dates when the day or the duration of observation, for some reason, is not known) were discarded *a priori*. Ultimately, data for the whole group of butterflies and diurnal moths consisted in 772,307 records (Appendix 1).

Since records had different temporal resolution, we fixed a temporal unit of ten days for displaying phenological patterns. Assuming that non-precise records are still relevant for outlining overall phenological patterns, we kept all data with a temporal resolution (time interval between start date and end date, Table 1) up to 15 days, in order to keep as much data as possible. The uncertainty of dates was compensated with pro rata calculation. First, a record was duplicated or triplicated when its start and end date of collection overlapped two or three successive ten-day periods. Then a pro rata was calculated for each period, according to the number of days covered by the record collection dates. For instance, a record with start date 2015–07–21 and end date 2015–08–03 (temporal resolution: 14-days), is converted to one observation in the last ten-day period of July with a pro rata of $11/14 \approx 0.78$ and one record in the first ten-day period of August with a pro rata of $3/14 \approx 0.22$. Whenever start and end date are within a ten-

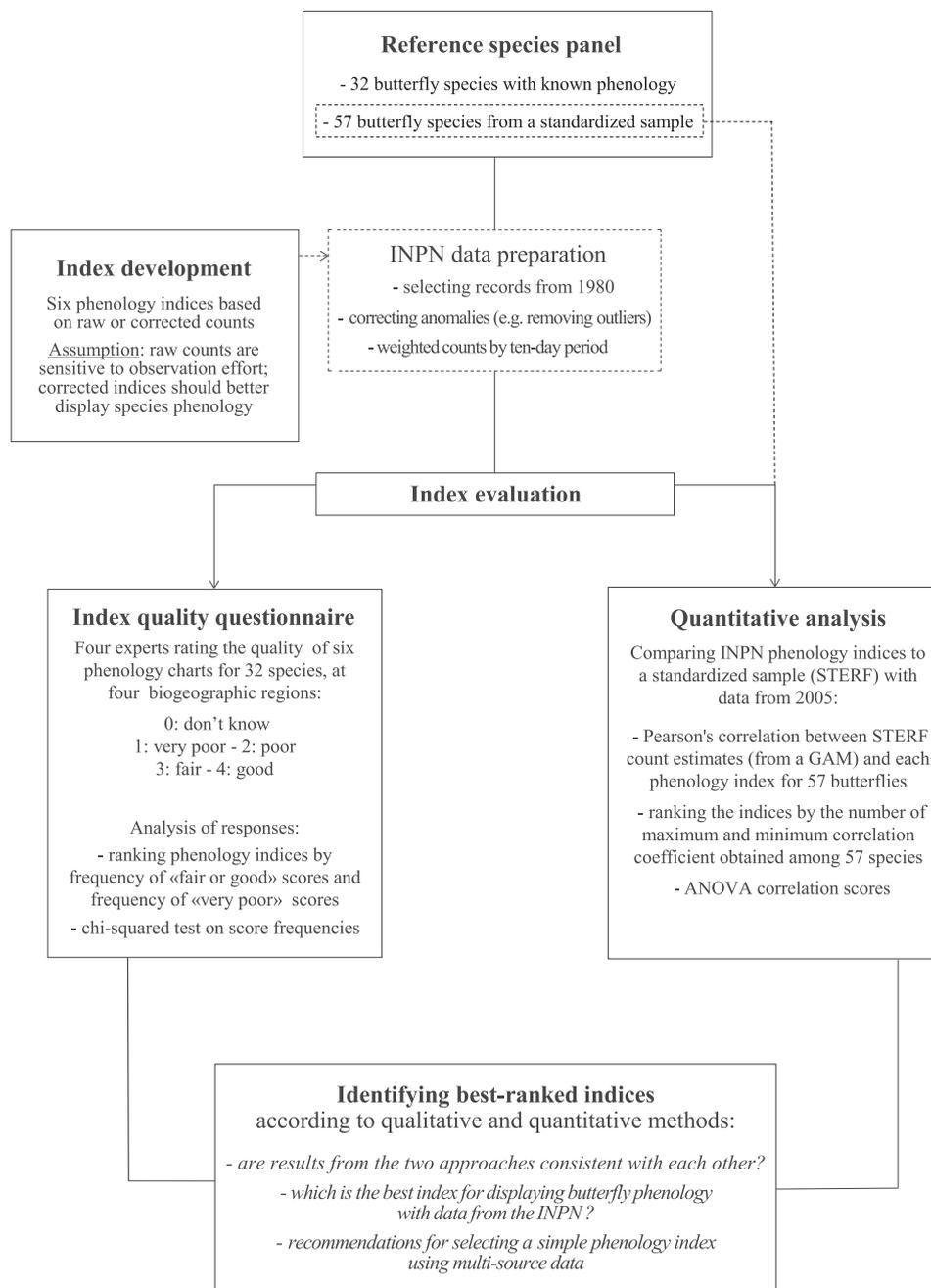


Fig. 1. Scheme of the general analysis process for this study.

Table 1
Vocabulary used in this study.

Temporal resolution	Time interval between start date and end date of an INPN record. It may vary from one day (precise date) to several years
Group	A background or target group. Survey methods and collector specialties within a group are assumed to be similar and share similar bias (Ponder et al., 2001, Ruete 2015). Examples of target groups are orchids, ground beetles, dragonflies, bats. This study focuses on “butterflies and diurnal moths”, a well-known group for which data are abundant and mostly reliable
Record	Observation or collection data of a species provided by one observer on a precise date or time interval, in one locality (a 10x10 km cell), whatever the number of specimens
Quadrat	Spatial unit. A 10x10 km cell where the species was recorded at least once in a period. A group quadrat is a 10x10 km cell where at least one of the species of the group was recorded in a period
Field visit	A unique survey event. One quadrat surveyed by one observer on a date for a group
Species known distribution	Set of 10x10 km cells where the species was recorded at least once since 1980

day period pro rata is 1.

$$\text{Weighted number of records}_k = \sum_{i=1}^n \text{prorata}_i$$

(1)

where $i = 1 \dots n$ records of a species and a ten-day period k , all years combined.

The weighting adjustment was also applied for counting quadrats (weighted number of 10×10 km cells where a species or the group was

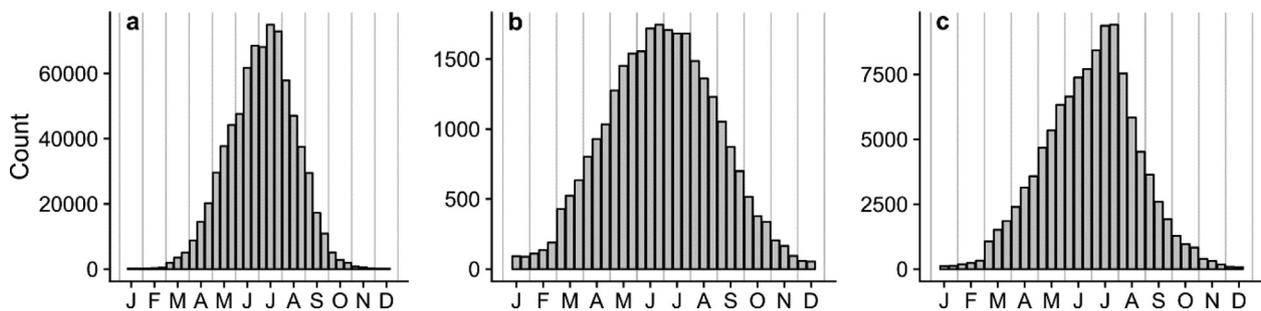


Fig. 2. Seasonal distribution by ten-day period of three proxies for observation effort in diurnal lepidopterans (after data preparation). The x-labels indicate months. (a) group records: number of records of all species of the group; (b) group quadrats: number of quadrats where whatever species of the group was seen; (c) number of field visits: number of quadrats surveyed by one observer on a date for the group. These values were used for normalising counts and building, respectively, index M2, M5 and M3.

detected at least once in a ten-day period k) and field visits. For simplicity, all weighted counts are henceforth mentioned as “number of ...” (records, quadrats, field visits, etc.).

The number of records of all species of the group (“group records”), the number of group quadrats and the number of field visits (Section 2.2; Fig. 2) can be employed as proxy for sampling effort (Lobo, 2008; Phillips et al., 2009; Ruete, 2015) and used for normalising raw counts (see below).

Six indices (Table 2) were built using both species number of records (M1, M2, M3), and number of quadrats (M4, M5, M6). M1 and M4 are raw relative frequencies by ten-day period. The other indices are less intuitive and data preparation requires more computing time to build them. Despite that, they should correct for bias due to uneven recording intensity over time or space (Table 2). They were built by normalising the number of species records or quadrats by: the number of field visits (M3); the number of group records (M2); the number of group quadrats (M5); the number of group quadrats within the species known distribution (M6), where “known distribution” is the set of 10x10 km cells where the species was recorded at least once since 1980.

2.4. Species selection and phenology charts for index quality questionnaire: Expert analysis

The sample selected consisted of a set of 32 univoltine, bivoltine and multivoltine butterflies whose phenology and ecology are relatively well known *a priori* (Lafanchis et al., 2000, 2015). Records of all subspecies were included in the species-rank phenology analysis (see Appendix 1 for the list of species).

For species whose phenology is likely to vary with latitude or altitude, a biogeographic approach was employed. Data were analysed at four separate biogeographic regions, an aggregated version of the environmental zones defined by Metzger et al. (2005): Atlantic, Continental and Pannonian (ATCONP), Lusitanian (LUS), Alpine and Mediterranean Mountains (ALMM), and Mediterranean (MD). For such species, we considered only biogeographic regions where at least 36 total records were available since 1980. The threshold was defined assuming that 36, an average of three records per month, was the minimum sample size for displaying patterns based on pooled counts. This threshold was also a trade-off between avoiding unreliable, insufficient data and maximising information (i.e. keeping regions where some species are rarer). The indices were computed on pre-cleaned data (see previous section), yielding six different phenological patterns that were submitted in the form of bar plots to four experts. The bar plots displayed frequencies by ten-day periods and, in some cases, by biogeographic regions (Fig. 3 and Appendix 2). For every species, the four experts were asked to rate six charts, one per index, on a scale of 1 to 4 (“very poor”, “poor”, “fair”, “good”), according to their quality in representing known seasonal activity (i.e. flight phenology, in the case of diurnal lepidopterans). In order to avoid conditioning and keep their

judgment unbiased, experts were not aware of index design rules. In addition, the disposition of the bar plots was randomized, so that they could not individually identify the indices (Appendix 2). Every index was ranked by counting the number of times it had been rated as “fair” or “good” (i.e. “the phenology chart is representative enough”) on the one hand, and as “very poor” (i.e. “the phenology chart is not representative at all”) on the other hand. In addition, a Chi-squared (χ^2) test was performed on score frequencies to seek any significant difference between the phenology indices according to expert opinion.

2.5. Quantitative analysis: Comparison with the STERF

A comparison with an independent sample was performed in order to quantitatively analyse the pertinence of the indices and complete the analysis based on expert opinion. This sample was provided by the French Butterfly Monitoring scheme (STERF), established from 2005 onwards by Vigie-Nature (<http://vigienature.mnhn.fr/page/suivi-temporel-des-rhopaloceres-de-france>). The STERF provides systematic counts of adult butterflies, which should mirror true species phenology. Each observer performs at least four field visits per year: one visit per month from May to August (other visits during the year are possible). Each survey site is associated with one observer, and is either chosen by the observer or randomly selected. Butterflies are identified and individuals are counted along 5 to 15 transects selected by the observers inside the site, making sure that the habitat within each transect is uniform. Since data collection before May and after August had not been systematic, only STERF records between May and August were kept. The analysis focused on the ATCONP biogeographic region, where phenology is supposed to be uniform and STERF data are more regular and abundant. As in the previous analysis (Section 2.4), we fixed a threshold of 36 records in the ATCONP region.

For each species, annual phenologies were estimated using the *rbms* R package and the regional GAM (generalized additive model) method presented in Schmucki et al. (2016). For each species, weekly basis estimate counts were hence obtained for each week of each year. These weekly and yearly count estimates were used to model the average phenology of each species across the period covered by the STERF. Thus, for each species, weekly count c recorded years i at week t were modeled using a GAM with a Negative-binomial distribution and log link function:

$$E[c_{it}] = \mu_{it} = \exp[y_i + s(t, f)]$$

where weekly count c_{it} is a function of a year effect y and a penalized cubic regression splines smoothing effect over time (week) t with f degree of freedom. GAMs were computed thanks to the *mgcv* package (Wood, 2017) in R 3.5.2. The respective GAM for each species was finally used to predict ten-day period count estimates that could be compared to the phenology indices calculated with INPN data. The resulting flight curve were standardized to one ($\sum \mu_t = 1$). This curve

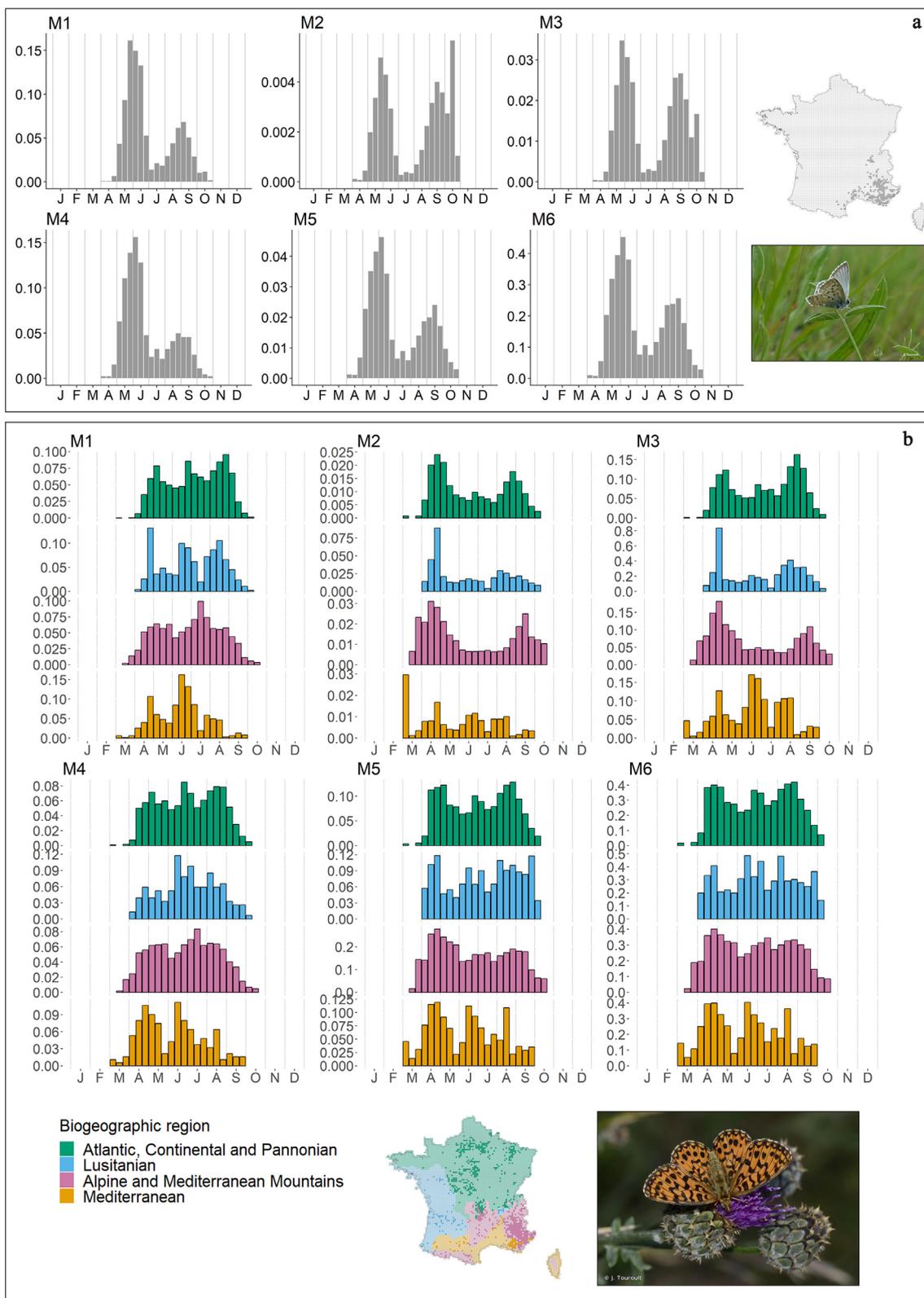


Fig. 3. Phenology and distribution maps (based on INPN records after data preparation) of two butterfly species: (a) Provence chalk-hill blue (*Lysandra hispana*) and (b) Violet Fritillary (*Boloria dia*). Time unit is a ten-day period and the x-labels indicate months. Phenology is represented with six indices (see also Table 2): proportion of records per period (M1); ratio of records to the group (M2); number of records per field visit (M3); proportion of quadrats per period (M4); ratio of quadrats to the group (M5); ratio of quadrats to the group within the species known distribution (M6). When a biogeographic effect was expected, such as for (b), phenology and distribution map were illustrated at four biogeographic regions.

could be calculated for 57 species. The others were excluded for lack of data and because the first GAM failed to yield annual phenologies.

STERF count estimates at ten-day periods were compared to the phenology indices in order to verify: 1) whether the patterns were similar, 2) which index produces a pattern that best matches STERF data and can be used for representing species phenology with INPN data.

Since STERF data are already integrated in the INPN database and start in 2005, the indices were calculated excluding all STERF-derived records and other records before 2005.

For each of the 57 species, STERF count estimates at ten-day periods were compared to each of the six phenology indices computed on INPN data, using the Pearson's correlation coefficient (ρ). In order to highlight which index was most correlated to STERF pattern, all ρ coefficients for the 57 species were analysed together and the indices were ranked by counting the number of times they obtained the maximum and minimum ρ coefficient. Table 3 illustrates with fictitious results how the indices were compared between each other according to the number of maximum and minimum coefficient obtained among several species: for example, M4 is the best correlated index to the STERF for species A and B, while it is the least correlated for species C. In this case, M4 obtains twice the maximum ρ coefficient and once the minimum ρ coefficient (Table 3). In addition, the difference between ρ distributions per index was tested by carrying out a one-way ANOVA (homoscedasticity assumption was met, according to a studentized Breusch-Pagan test: BP = 5.95, df = 5, p-value = 0.31).

3. Results

For each of the 32 species, charts were presented to the experts as in Fig. 3a or b, depending on whether a biogeographic effect was expected or not on species phenology. Unlike Fig. 3, the order and the design rules of the indices were concealed from the experts (see an example in Appendix 3). M6 obtained the highest number of positive scores and the smallest number of negative scores: out of the 4 experts assessments, it was rated as "fair" or "good" 62 times and as "very poor" 11 times, followed by M4 with 61 positive scores and 11 negative scores (Fig. 4). M2 obtained most negative responses (Fig. 4), which affected Chi-squared test results ($\chi^2 = 43.73$, df = 5, p-value < 0.001). In fact,

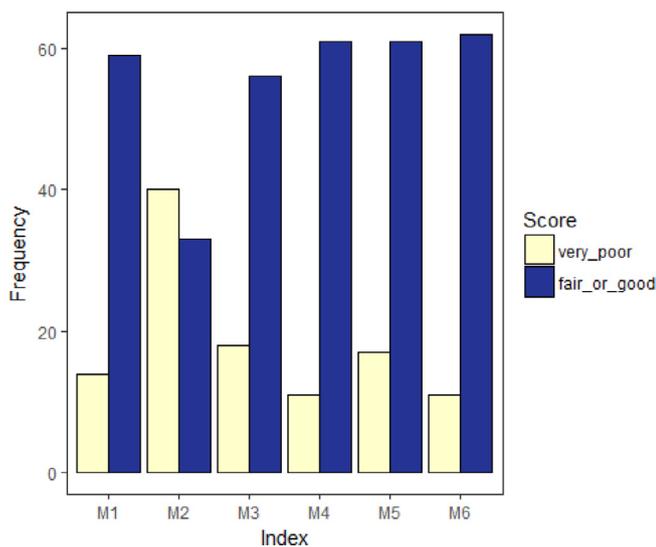


Fig. 4. Frequency of positive ("fair" or "good") and negative ("very poor") scores given by experts to six phenology indices. Index ranking according to the number of "fair or good" scores: M6, M4/M5, M1, M3, M2; index ranking according to the number of "very poor" scores: M2, M3, M5, M1, M4/M6. M2 is the only index that obtained more negative than positive scores. With M2: $\chi^2 = 43.73$, df = 5, p-value < 0.001; excluding M2: $\chi^2 = 3.1$, df = 4, p-value = 0.5.

when the M2-score distribution was excluded from the test, no other significant difference was found among the score distributions of the remaining five indices ($\chi^2 = 3.1$, df = 4, p-value = 0.54).

Fig. 5 shows an example of pairwise comparison between STERF count estimates and the six phenology indices for one of the species, while overall results of this comparison for 57 butterfly species are illustrated in Fig. 6. All indices showed a fair correlation with the STERF, ρ coefficient being 0.77 on average (Fig. 6a). Index M1 and M5 were the best ranked, with the highest frequencies of maximum ρ coefficient and few minimums (Fig. 6b). Most of the times M2 resulted as the least correlated to STERF count estimates (Fig. 6b). M2 ρ distribution varied also considerably, with values below the first quartile that range from -0.34 and 0.56 (Fig. 6a). Nevertheless, the statistical analysis did not highlight any significant difference (ANOVA F = 2.19, df = 5, p-value = 0.05).

4. Discussion

4.1. A priori properties of the indices

Non-corrected indices are easy to understand but they may be subject to several biases when using data that originate from multiple sources and sampling techniques. Corrected indices should approximate the phenology of activity (e.g. flight period for butterflies) with greater precision than raw frequencies, which are more likely to reflect patterns of recording intensity. No robust but simple metrics based on opportunistic, unstructured data that fulfilled the required conditions was found in recent scientific literature. Dennis et al. (2013) and Schmucki et al. (2016) have produced smooth and readable seasonal patterns with GAMs. With a similar approach, we applied GAMs on butterfly monitoring data for outlining phenology patterns to compare with patterns from INPN data. However, GAMs are not suitable for multi-source opportunistic data, because they do not account for uneven recording intensity (Rothery and Roy, 2001). Other approaches, such as correction for sampling effort or imperfect detection in occupancy models, could inspire research for more appropriate measures (references in Table 2). M1 (proportion of records per period; Table 2) is the most simple and intuitive, but may reflect effort variability over time and over space. M4 (proportion of quadrats per period; Table 2), which is also easily interpretable, may correct for some errors (duplicates, oversampled quadrats), but still reflects temporal and spatial bias. Conversely, M2 (ratio of records to the group; Table 2) should correct for uneven recording intensity. However, this index seems to be particularly sensitive to "reporting bias" (van Strien et al., 2013). The number of group records increases sharply from near zero in winter months to near 80,000 in summer months (Fig. 2a), causing over-correction and making peaks shift from the centre to the edges of the distribution. This is particularly true for certain species, whose adults can emerge outside the habitual flight period, for instance on sunny winter days (such as *Aglais io* and *Aglais urticae*, Lafranchis et al., 2000, 2015; phenological patterns of *Aglais io* are shown in Appendix 4). Owing to the unusual event, the species is almost the only one reported at such dates, generating artefact peaks in the phenological pattern (i.e. the ratio "species records/group records" is close to 1). The same may occur to species that are not easy to observe in general during the flight season (i.e. the ratio decreases instead of displaying a peak) and to those that are paradoxically under-reported because considered too common (Dickinson et al., 2010; van Strien et al., 2013). The proxy for observation effort used for building M3 (number of records per field visit; Table 2; Fig. 2c) should also correct for uneven recording intensity. This index, as the following ones, is less intuitive and may not be precise, since observer names are not always well standardized in the INPN. Such as M2 and M3, M5 (ratio of quadrats to the group; Table 2) is based on a proxy for observation effort, the number of group quadrats per ten-day period (Fig. 2b). As shown in Fig. 2b, compared to the other proxy distributions, the number of group quadrats per ten-day period

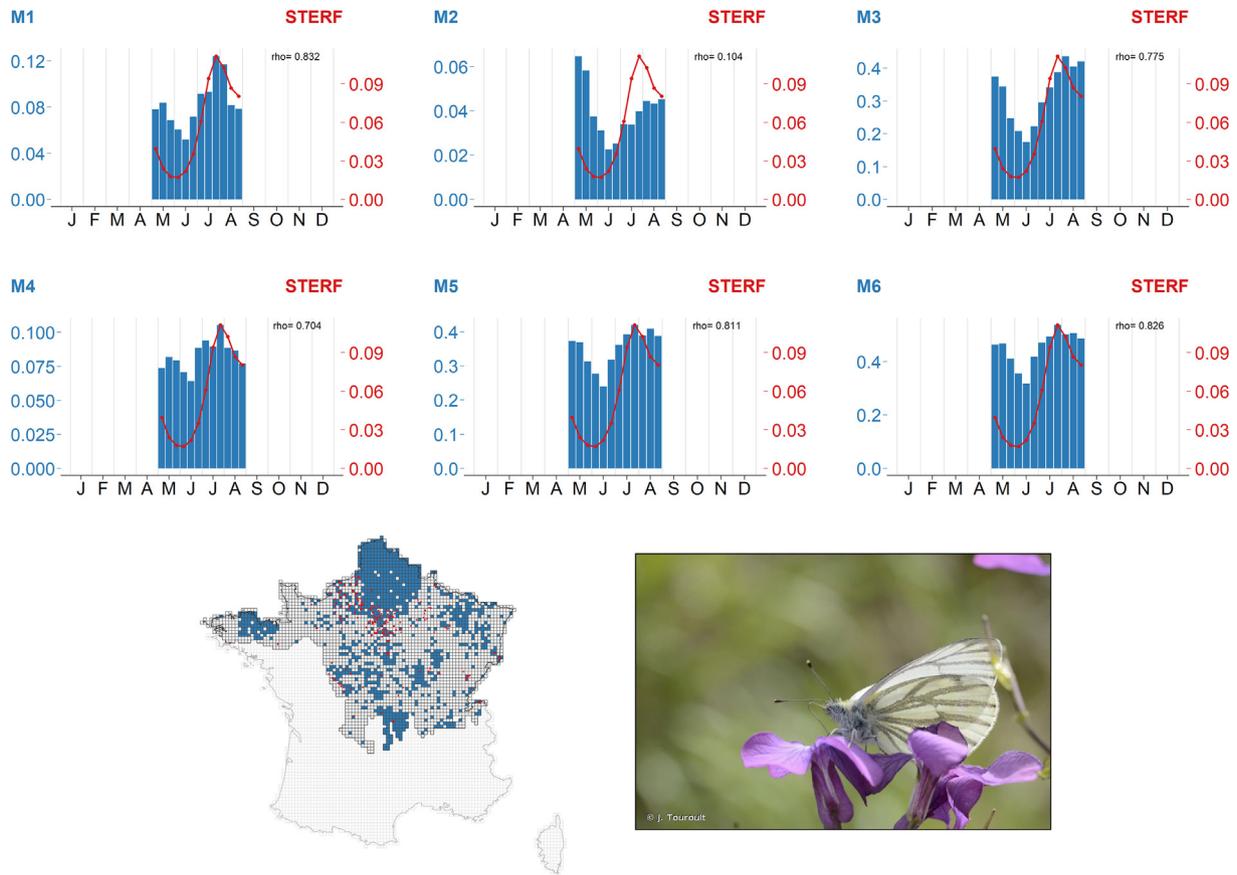


Fig. 5. Comparison between the STERF and six phenology indices computed on INPN data by ten-day period for one of the species, the green-veined white (*Pieris napi*). A Pearson's correlation coefficient (ρ) was calculated between every index (blue bar plots) and STERF count estimates from a GAM (red line). Indices and STERF count estimates were calculated with data collected from 2005, and displayed from May to August in the ATCONP biogeographic region. The map shows the geographic distribution of these data (blue quadrats for the INPN, red points for the STERF).

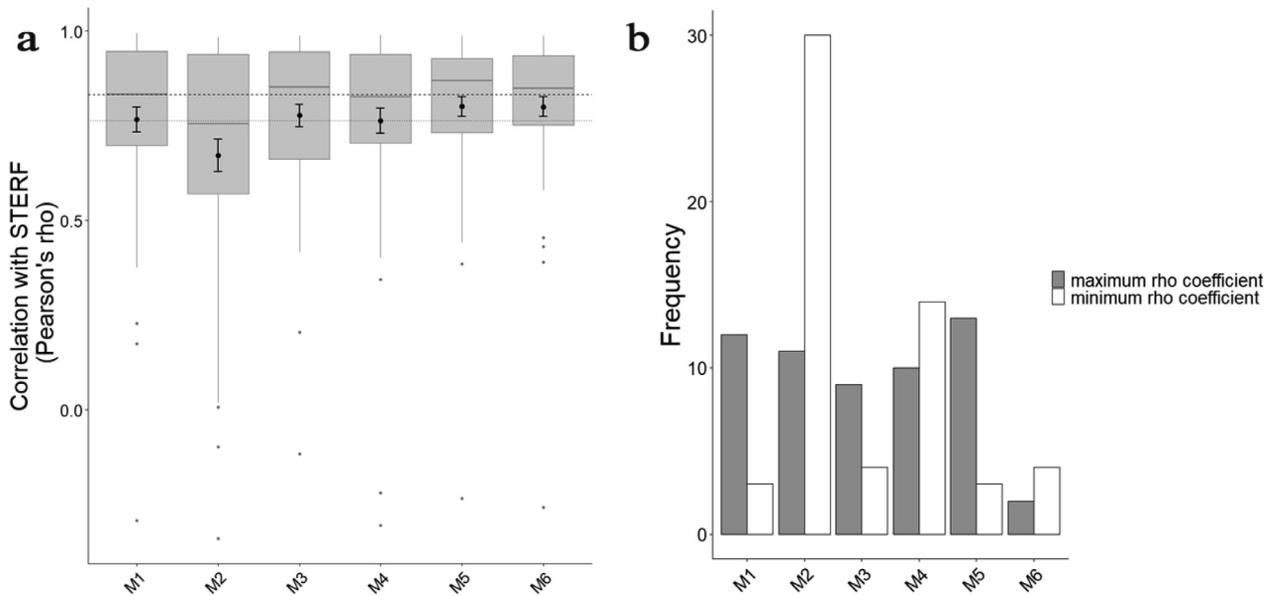


Fig. 6. Comparison between the STERF and six phenology indices computed on INPN data by ten-day periods for 57 butterfly species (a) distributions and mean \pm se of ρ coefficients by index. Dashed and dotted lines are respectively the overall median = 0.83 and the overall mean = 0.77 of all correlations. All phenology indices are equally correlated to STERF count estimates (ANOVA $F = 2.19$, $df = 5$, p -value = 0.05); (b) number of times among 57 species that each index occurred to be the best or the least correlated to the STERF.

Table 2
Phenology indices designed for this study.

Index	Definition	Formula (for a ten-day period k)	Description	Reference work that inspired the design of the index	A priori properties of the index
M1	Proportion of records per period	$\sum_{i=1}^n prorata_i / \sum_{k=1}^{36} \sum_{i=1}^n prorata_i$	Number of records (1... n , see equation (1)) for a species in a ten-day period k divided by the total number of records of the same species in the dataset	Archaux et al. (2011), Lumaret (1990) ("number of observations") van Swaay (1990) ("number of records")	Advantages: very simple and intuitive. Disadvantages: probably biased by uneven recording intensity (spatial and temporal bias).
M2	Ratio of records to the group	$\sum_{i=1}^n prorata_i / \sum_{j=1}^m prorata_j$	Number of records (1... n) for a species in a ten-day period k divided by the number of records of all species of the related group (1... m) in the same ten-day period	van Swaay (1990) ("percentage")	Advantages: simple and intuitive; temporal bias correction. Disadvantages: may be sensitive to reporting bias, emphasizing artefact peaks.
M3	Number of records per field visit	$\sum_{i=1}^n prorata_i / \sum_{j=1}^p prorata_j$	Number of records (1... n) for a species in a ten-day period k divided by the number of field visits (1... p) in the same ten-day period	Archaux et al. (2015) ("mean abundance by field visit") Strebel et al. (2014) ("naïve detectability index")	Advantages: temporal bias correction. Disadvantages: does not correct for spatial bias; less simple and less intuitive.
M4	Proportion of quadrats per period	$\sum_{i=1}^q prorata_i / \sum_{k=1}^{36} \sum_{i=1}^q prorata_i$	Number of quadrats (1... q) where the species was seen at least once in a ten-day period k divided by the total number of quadrats where the species was observed	Archaux et al. (2015) ("number of occurrences")	Advantages: very simple and intuitive; may correct for some bias (e.g. duplicates, quadrat oversampling). Disadvantages: still reflects uneven recording intensity.
M5	Ratio of quadrats to the group	$\sum_{i=1}^q prorata_i / \sum_{j=1}^g prorata_j$	Number of quadrats (1... q) where the species was seen at least once in a ten-day period k divided by the number of visited quadrats (1... g) in same ten-day period (i.e. quadrats where at least one species of the group was seen)	van Swaay (1990) ("percentage of squares") Turin and den Boer (1988)	Advantages: temporal and reporting bias correction; should limit reporting bias. Disadvantages: does not correct for spatial bias; not too simple; less intuitive.
M6	Ratio of quadrats to the group within the species known distribution	$\sum_{i=1}^q prorata_i / \sum_{i=1}^g prorata_i$ where $j = 1...g \in D$	Same as M5, but takes into account only visited quadrats (1... g) where the species was found at least once since 1980 (i.e. included in the species known distribution: D)	Kéry et al. (2010) ("detection history")	Advantages: may correct for temporal and spatial bias. Disadvantages: not too simple and not intuitive.

Table 3
Fictitious Pearson's correlation coefficients (rho) table for three hypothetical species.

	M1	M2	M3	M4	M5	M6	Best correlated index	Least correlated index
species A	0.94	0.8	0.95	0.98	0.92	0.97	M4	M2
species B	0.77	0.5	0.82	0.93	0.75	0.77	M4	M2
species C	0.89	0.85	0.78	0.68	0.82	0.91	M6	M4
mean \pm SE	0.86 \pm 0.05	0.72 \pm 0.11	0.85 \pm 0.05	0.83 \pm 0.09	0.83 \pm 0.05	0.88 \pm 0.06		
Number of max rho	0	0	0	2	0	1		
Number of min rho	0	2	0	1	0	0		

grows and shrinks slower between winter and summer periods and the shape of the distribution is wider. This should limit reporting bias and allow for a better correction of temporal bias, but it does not account for spatial effects (for example, observer activity in coastal and mountain areas is higher during summer than during spring, due to holiday habits of naturalists). Moreover, the proxies for observation effort (Fig. 2) include those records or quadrats where the target species was never seen and might be actually absent. Managing data by biogeographic zone may help reducing spatial bias and over-correction. Additionally, quadrats should be restricted to those included in the known distribution of the species. This approach was applied to M6 (ratio of quadrats to the group within the species known distribution; Table 2), which was expected to perform better, since it deals with both temporal and spatial bias.

4.2. Which is the highest-ranked index according to the two approaches?

According to expert responses, none of the indices, except for M2 (the worst rated) could illustrate the phenology of 32 butterfly species better than the simplest index, M1 (Fig. 4). In order to refine the results and discriminate among the six methods, a quantitative analysis was carried out by comparing the phenology indices based on INPN opportunistic data to the pattern calculated from a monitoring scheme, the STERF. All indices were, on average, positively correlated with STERF patterns (Fig. 6). Surprisingly, in the two tests, the indices that correct for observation effort (M2, M3, M5 and M6) are not statistically better than the non-corrected ones (M1 and M4). However, even if no statistical difference was highlighted, the distribution of rho coefficients for M2 showed large variability (Fig. 6a). This result suggests that this index may perform well for some species, but it is not suitable for a large panel of species with different phenologies. In substance, the expert approach and the comparison with the STERF both lead to reject M2 as a suitable phenology index.

Other studies have compared opportunistic data with monitoring data (Dennis et al., 2017a; van Strien et al., 2013). It is possible that our comparisons lack power. The STERF provides systematic counts of adult butterflies, which should provide phenological patterns that are relatively close to reality. Nevertheless, STERF protocol and measures themselves may not be free from bias, notably because counts are recorded on a monthly basis. However, given the two approaches adopted, the number of species that have been taken into account, as well as the amount of data and the variability of expert opinions, it is not unfounded to believe that, there are no major differences between the tested indices. A possible explanation lies in the large amount of data and sources available for butterflies, which may help attenuate the bias and make raw frequencies of opportunistic observations converge towards overall realistic phenological patterns. Our method may not be suitable for other lepidopterans or other clades for which knowledge and data are much scarcer than for the butterflies analysed here. If data are opportunistic and multi-source, we suggest selecting species with many records, covered by several data sources. We fixed a threshold of 36 total records in the studied area and during the entire period of study (in our case, all data from France or from a biogeographic region, recorded since 1980), and 5 data sources, knowing that for most of the species total records and sources were more numerous (Appendix 1).

Ideally, the minimum number of records and sources should be calculated and standardised. Further work is required to re-define these thresholds on a statistical basis and give more recommendations about the use of our indices for other groups than butterflies.

4.3. Selecting a rigorous but simple index for large opportunistic data and a general audience: Which compromise for butterflies?

Even though they are likely to reflect bias, in our case raw indices (M1 or M4) were not less convincing than corrected ones for butterflies. Following the results and considerations discussed above, and against expectations, it could finally be reasonable to consider the use of raw frequencies. Besides, the choice should head to the most parsimonious method. The best option would probably be to display phenology through raw indices (after data preparation and weighting adjustment), alongside a visual representation of recording intensity (Fig. 2b or c). Spatial bias may be attenuated by splitting data by biogeographic region. In this way, both experts and general public should be able to understand the graphics, while keeping a critical eye on them.

Some authors have appealed to occupancy models for studying phenology and population trends with opportunistic data (see, for example, Kéry et al., 2010; van Strien et al., 2010; Strebel et al., 2014). In fact, by estimating detectability, occupancy models help to correct for observation effort, detection and reporting bias (Kéry et al., 2010; Van Strien et al., 2013). Although we drew inspiration from occupancy models for bias correction approaches, the aim of our study was not to assess occupancy of butterfly species. Nonetheless, we do not exclude the possibility of using a modelling approach in the future, should sufficient data be available, in order to get more unbiased estimates of phenology.

4.4. Other recommendations facing database limitations

Dates in the INPN are compulsory, so when the day of observation is not known a default date (such as January 1st or December 31st) is assigned. We discarded outlier data (see Section 2.3) in order to prevent the appearance of artefacts, although some small winter peaks persisted. In fact, as described in Section 4.1, some butterfly species may be recorded during winter days, even if the actual period of activity is later in the year. Unfortunately, we could not discriminate observations by stage of development or behaviour (activity versus hibernation), since this information is currently lacking in most INPN data sources. However, records of active adult butterflies in the INPN usually far exceed observations of young stage or wintering individuals, so the latter are unlikely to affect the displaying of major activity peaks. There are, however, some exceptions, such as those described in Section 4.1 or the case of *Thecla betulae* (Linnaeus, 1758). This species is hardly detectable during its flight period (Lafranchis et al., 2000, 2015). Conversely, the eggs are easy to recognize and they are regularly used for detecting the geographic presence of the butterfly. These occurrences are often reported as all others in datasets when achieving the INPN. This caused the appearance of improbable peaks in winter (Fig. 7). Correcting for observation effort did not provide any added value, it rather accentuated the aberrations. This underlines the need to support data producers towards a better standardisation of information.

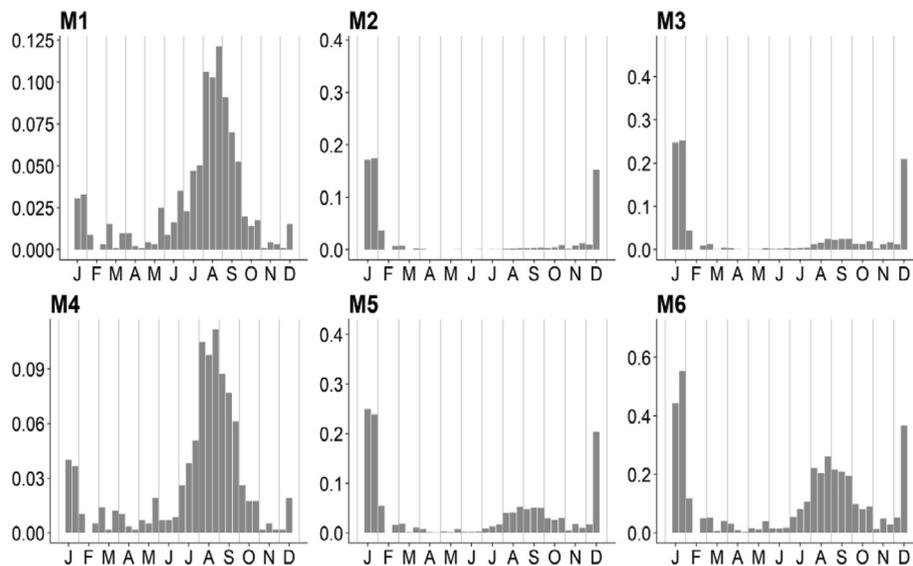


Fig. 7. Phenology of the Brown Hairstreak (*Thecla betulae*). Egg and imago sightings are confused in the INPN, causing artificial peaks in winter, when the adult is not flying but eggs are easily detectable.

Several studies have documented the relationship between climate and phenological shifts (Roy and Sparks, 2000; Walther et al., 2002; Parmesan and Yohe, 2003; Stefanescu et al., 2003; Menzel et al., 2006; Parmesan, 2007; Altermatt, 2009; Prodon et al., 2017; Bell et al., 2019). The impact of climate change on phenology may have major consequences on ecological systems and their conservation (Schwartz, 2013), hence the importance of long-term collection of observational and monitoring data. Phenological shifts of the order of some days may have occurred in the last decades (Roy and Sparks, 2000). Admittedly, we could not point out phenological shifts due to coarse temporal resolution. A finer temporal resolution would entail the loss of useful data. Furthermore, we chose to collate all years' data in order to compensate for uneven recording intensity and species detectability across the years. This also precluded the study of phenological shifts. However, we believe that our methods are adequate to provide a simple measure for a general audience that bears overall phenological patterns for many species. Nevertheless, we will consider investigating with more accuracy the phenology of those butterflies for which precise dates of observation are abundant and consistent through the years by adapting methods that use statistical models, which account for phenological changes over time, observation effort, detection and reporting bias, such as those proposed by Dennis et al. (2017b) and Strebel et al. (2014).

5. Conclusion

Multi-source national databases such as the INPN may contain bias or redundant information but they compile large volumes of data, centralize and spread knowledge on biodiversity distribution and activity. The study showed, against all odds, that raw frequencies can perform as well as corrected measures, probably due to the characteristics and the large amount of butterfly multi-source data. This is so far the first attempt at correcting large amounts of opportunistic records in order to illustrate species seasonality in France through a simple phenology index.

For groups with large amount of data and replicated visits, such as butterflies, non-corrected multi-source records (i.e. that combine standardised and non-standardised observations) probably provide sufficient information about overall phenological patterns. The next question is whether raw frequencies would fit as well on species with less available data, or on those that are a seasonal (e.g. occur constantly around the year or variations are irregular and not season-related, see

Wolda, 1988). Further work will help investigate whether the properties of non-corrected and corrected indices are affected by the amount of data, as well as the variability of data sources and the type of phenology. Further analysis may also include the use of statistical models for estimating phenological shifts in connection with climate change.

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.

Acknowledgments

We thank the respondents of the index quality questionnaire: Frédéric Archaux, Olivier Delzons, Eric Drouet and Antoine Leveque. We also thank all the respondents of a previous version of the questionnaire, which included more species and groups that are not treated in this manuscript. Thanks to Marie-Lyne Einspinner, Chiara Elettra Ferrario and Paula R. M. B. for constructive help on previous drafts of the manuscript. We also thank all the volunteers who took part in the long-term STERF scheme and provided the data.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2019.105885>.

References

- Altermatt, F., 2009. Climatic warming increases voltinism in European butterflies and moths. *Proc. R. Soc. B: Biol. Sci.* 277, 1281–1287. <https://doi.org/10.1098/rspb.2009.1910>.
- Archaux, F., Chatard, P., Fauchaux, F., Lévêque, A., 2015. Papillons du Loiret: atlas des rhopalocères et zygènes du Loiret (2000–2013). So. MOS & Alexanor.
- Archaux, F., Jacquemin, G., Leconte, R., Luquet, G.C., Mora, F., Noël, F., Pinston, H., Robert, J.-C., Ruffoni, A., 2011. Synthèse des observations récentes et anciennes de Libelloides coccajus (Denis & Schiffermüller) et L. longicornis (Linné) dans la moitié nord de la France (Neuroptera, Ascalaphidae). *Bulletin de la Société entomologique de France* 116, 365–388.
- August, T., Harvey, M., Lightfoot, P., Kilbey, D., Papadopoulos, T., Jepson, P., 2015. Emerging technologies for biological recording: emerging Technologies for Biological Recording. *Biol. J. Linn. Soc. Lond.* 115 (3), 731–749. <https://doi.org/10.1111/bij.12534>.
- Bell, J.R., Botham, M.S., Henrys, P.A., Leech, D.I., Pearce-Higgins, J.W., Shortall, C.R., Brereton, T.M., Pickup, J., Thackeray, S.J., 2019. Spatial and habitat variation in

- aphid, butterfly, moth and bird phenologies over the last half century. *Glob. Change Biol.* 25 (6), 1982–1994.
- Bertone, M., Green, J., Washburn, S., Poore, M., Soprenson, C., Watson, D.W., 2005. Seasonal activity and species composition of dung beetles inhabiting cattle pastures in North Carolina. *Entomol. Soc. Am.* 98, 309–321.
- Dennis, E.B., Freeman, S.N., Brereton, T., Roy, D.B., 2013. Indexing butterfly abundance whilst accounting for missing counts and variability in seasonal pattern. *Meth. Ecol. Evol.* 4, 637–645. <https://doi.org/10.1111/2041-210X.12053>.
- Dennis, E.B., Morgan, B.J.T., Brereton, T.M., Roy, D.B., Fox, R., 2017a. Using citizen science butterfly counts to predict species population trends. *Conserv. Biol.* 31, 1350–1361.
- Dennis, E.B., Morgan, B.J., Freeman, S.N., Ridout, M.S., Brereton, T.M., Fox, R., Powney, G.D., Roy, D.B., 2017b. Efficient occupancy model-fitting for extensive citizen-science data. *PLoS One* 12 (3), e0174433.
- Dickinson, J.L., Shirk, J., Bonter, D., Bonney, R., Crain, R.L., Martin, J., Phillips, T., Purcell, K., 2012. The current state of citizen science as a tool for ecological research and public engagement. *Front. Ecol. Environ.* 10, 291–297. <https://doi.org/10.1890/110236>.
- Dickinson, J.L., Zuckerman, B., Bonter, D.N., 2010. Citizen science as an ecological research tool: challenges and benefits. *Annu. Rev. Ecol. Syst.* 41, 149–172. <https://doi.org/10.1146/annurev-ecolsys-102209-144636>.
- Gargominy, O., Tercerie, S., Régnier, C., Ramage, T., Dupont, P., Daszkiewicz, P., Poncet, L., 2017. TAXREF v11.0, référentiel taxonomique pour la France : méthodologie, mise en œuvre et diffusion. *Muséum National d'Histoire Naturelle, Paris Rapport Patrimoine* 2017–116.
- Giraud, C., Calenge, C., Coron, C., Julliard, R., 2016. Capitalizing on opportunistic data for monitoring relative abundances of species. *Biometrics* 72, 649–658. <https://doi.org/10.1111/biom.12431>.
- Hochachka, W.M., Fink, D., Hutchinson, R.A., Sheldon, D., Wong, W.K., Kelling, S., 2012. Data-intensive science applied to broad-scale citizen science. *Trends Ecol. Evol.* 27, 130–137.
- Isaac, N.J.B., Pocock, M.J.O., 2015. Bias and information in biological records. *Biol. J. Linn. Soc.* 115, 522–531. <https://doi.org/10.1111/bij.12532>.
- Isaac, N.J.B., van Strien, A.J., August, T.A., de Zeeuw, M.P., Roy, D.B., 2014. Statistics for citizen science: extracting signals of change from noisy ecological data. *Meth. Ecol. Evol.* <https://doi.org/10.1111/2041-210X.12254>.
- Kéry, M., Royle, J.A., Schmid, H., Schaub, M., Volet, B., Häfliger, G., Zbinden, N., 2010. Site-occupancy distribution modeling to correct population-trend estimates derived from opportunistic observations. *Conserv. Biol.* 24, 1388–1397. <https://doi.org/10.1111/j.1523-1739.2010.01479.x>.
- Lafranchis, T., Geniez, P., Goffart, P., Guillosion, J.-Y., 2000. Les papillons de jour de France, Belgique et Luxembourg et leurs chenilles. *Biotope, Mèze*.
- Lafranchis, T., Jutzeler, D., Guillosion, J.-Y., Kan, P., Kan, B., 2015. *La Vie des Papillons*. Diatheo.
- Lobo, J.M., 2008. Database records as a surrogate for sampling effort provide higher species richness estimations. *Biodivers. Conserv.* 17, 873–881. <https://doi.org/10.1007/s10531-008-9333-4>.
- Lumaret, J.P., 1990. *Atlas des Coléoptères Scarabéides Laparosticti de France*. Muséum National d'Histoire Naturelle. Secrétariat de la Faune et la Flore Paris Paris.
- Maes, D., Vanreusel, W., Jacobs, I., Berwaerts, K., Van Dyck, H., 2012. Applying IUCN Red List criteria at a small regional level: a test case with butterflies in Flanders (north Belgium). *Biol. Conserv.* 145, 258–266. <https://doi.org/10.1016/j.biocon.2011.11.021>.
- Manil, L., Lerch, A., Fontaine, B., Julliard, R., 2015. *Suivi Temporel des Rhopalocères de France (STERF) Bilan 2005–2014*. *Gestion* 2010, 1–82.
- Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aaasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P., Braslavská, O., Briede, A., Chmielewski, F.M., Crepinsek, Z., Curnel, Y., Dahl, Å., Defila, C., Donnelly, A., Filella, Y., Jatzcak, K., Måge, F., Mestre, A., Nordli, Ø., Peñuelas, J., Pirinen, P., Remišová, V., Scheffinger, H., Striz, M., Susnik, A., Van Vliet, A.J.H., Wielgolaski, F.E., Zach, S., Züst, A., 2006. European phenological response to climate change matches the warming pattern. *Glob. Change Biol.* 12, 1969–1976. <https://doi.org/10.1111/j.1365-2486.2006.01193.x>.
- Metzger, M.J., Bunce, R.G.H., Jongman, R.H.G., Múcher, C.A., Watkins, J.W., 2005. A climatic stratification of the environment of Europe. *Glob. Ecol. Biogeogr.* 14, 549–563. <https://doi.org/10.1111/j.1466-822X.2005.00190.x>.
- Parmesan, C., 2007. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Glob. Change Biol.* 13, 1860–1872. <https://doi.org/10.1111/j.1365-2486.2007.01404.x>.
- Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421, 37–42. <https://doi.org/10.1038/nature01286>.
- Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J., Ferrier, S., 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecol. Appl.* 19, 181–197. <https://doi.org/10.1890/07-2153.1>.
- Pocock, M.J.O., Roy, H.E., Preston, C.D., Roy, D.B., 2015. The biological records centre: a pioneer of citizen science. *Biol. J. Linn. Soc.* 115, 475–493.
- Ponder, W.F., Carter, G.A., Flemons, P., Chapman, R.R., 2001. Evaluation of museum collection data for use in biodiversity assessment. *Conserv. Biol.* 15, 648–657. <https://doi.org/10.1046/j.1523-1739.2001.015003648.x>.
- Powney, G.D., Isaac, N.J.B., 2015. Beyond maps: a review of the applications of biological records. *Biol. J. Linn. Soc.* 115, 532–542. <https://doi.org/10.1111/bij.12517>.
- Pozo, C., Luis-Martínez, A., Llorente-Bousquets, J., Salas-Suárez, N., Maya-Martínez, A., Vargas-Fernández, I., Warren, A.D., 2008. Seasonality and Phenology of the Butterflies (Lepidoptera: Papilionoidea and Hesperioidea) of Mexico's Calakmul Region. *Florida Entomol.* 91, 407–422. [https://doi.org/10.1653/0015-4040\(2008\)91\[407:SAPOTB\]2.0.CO;2](https://doi.org/10.1653/0015-4040(2008)91[407:SAPOTB]2.0.CO;2).
- Prodon, R., Geniez, P., Cheylan, M., Devers, F., Chuine, I., Besnard, A., 2017. A reversal of the shift towards earlier spring phenology in several Mediterranean reptiles and amphibians during the 1998–2013 warming slowdown. *Glob. Change Biol.* 23, 5481–5491. <https://doi.org/10.1111/gcb.13812>.
- R Core Development Team, 2018. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing Vienna, Austria.
- Robertson, M.P., Cumming, G.S., Erasmus, B.F.N., 2010. Getting the most out of atlas data. *Divers. Distrib.* 16, 363–375. <https://doi.org/10.1111/j.1472-4642.2010.00639.x>.
- Rothery, P., Roy, D.B., 2001. Application of generalized additive models to butterfly transect count data. *J. Appl. Stat.* 28, 897–909.
- Roy, D.B., Sparks, T.H., 2000. Phenology of British butterflies and climate change. *Glob. Change Biol.* 6, 407–416. <https://doi.org/10.1046/j.1365-2486.2000.00322.x>.
- Ruete, A., 2015. Displaying bias in sampling effort of data accessed from biodiversity databases using ignorance maps. *Biodivers. Data J.* 3, e5361. <https://doi.org/10.3897/BDJ.3.e5361>.
- Schmucki, R., Peer, G., Roy, D.B., Stefanescu, C., Van Swaay, C.A.M., Oliver, T.H., Kuussaari, M., Van Strien, A.J., Ries, L., Settele, J., Musche, M., Carnicer, J., Schweiger, O., Brereton, T.M., Harpke, A., Heliölä, J., Kühn, E., Julliard, R., 2016. A regionally informed abundance index for supporting integrative analyses across butterfly monitoring schemes. *J. Appl. Ecol.* 53, 501–510. <https://doi.org/10.1111/1365-2664.12561>.
- Schwartz, M.D., 2013. Phenology: An integrative environmental science. *Phenology: An Integrative Environmental Science*: pp. 53–65. doi: 10.1007/978-94-007-6925-0.
- Stefanescu, C., Peñuelas, J., Filella, I., 2003. Effects of climatic change on the phenology of butterflies in the northwest Mediterranean Basin. *Glob. Change Biol.* 9, 1494–1506. <https://doi.org/10.1046/j.1365-2486.2003.00682.x>.
- Strebel, N., Kéry, M., Schaub, M., Schmid, H., 2014. Studying phenology by flexible modelling of seasonal detectability peaks. *Meth. Ecol. Evol.* 5, 483–490. <https://doi.org/10.1111/2041-210X.12175>.
- van Strien, A.J., van Swaay, C.A.M., Termaat, T., 2013. Opportunistic citizen science data of animal species produce reliable estimates of distribution trends if analysed with occupancy models. *J. Appl. Ecol.* 50, 1450–1458. <https://doi.org/10.1111/1365-2664.12158>.
- van Strien, A.J., Termaat, T., Groenendijk, D., Mensing, V., Kéry, M., 2010. Site-occupancy models may offer new opportunities for dragonfly monitoring based on daily species lists. *Basic Appl. Ecol.* 11, 495–503. <https://doi.org/10.1016/j.baae.2010.05.003>.
- van Swaay, C.A.M., Plate, C.L., van Strien, A.J., 2002. Monitoring butterflies in the Netherlands: how to get unbiased indices. *Proc. Sect. Exp. Appl. Entomol. Netherlands Entomol. Soc.* 13, 21–27.
- van Swaay, C.A.M., 1990. An assessment of the changes in butterfly abundance in The Netherlands during the 20th Century. *Biol. Conserv.* 52, 287–302.
- Touroult, J., Poncet, L., Keith, P., Boulet, V., Arnal, G., Brustel, H., Siblet, J.P., 2015. *Inventaires et atlas nationaux de distribution: pour une approche plus itérative et un rééquilibrage taxinomique*. *Revue d'écologie*.
- Tulloch, A.I.T., Possingham, H.P., Joseph, L.N., Szabo, J., Martin, T.G., 2013. Realising the full potential of citizen science monitoring programs. *Biol. Conserv.* 165, 128–138. <https://doi.org/10.1016/j.biocon.2013.05.025>.
- Turin, H., Den Boer, P.J., 1988. Changes in the distribution of carabid beetles in The Netherlands since 1880. II. Isolation of habitats and long-term time trends in the occurrence of carabid species with different powers of dispersal (Coleoptera, Carabidae). *Biol. Conserv.* 44, 179–200. [https://doi.org/10.1016/0006-3207\(88\)90101-2](https://doi.org/10.1016/0006-3207(88)90101-2).
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. *Nature* 416, 389–395. <https://doi.org/10.1038/416389a>.
- Wolda, H., 1988. Insect seasonality: Why. *Annu. Rev. Ecol. Syst.* 19, 1–18. <https://doi.org/10.1146/annurev.ecolsys.19.1.1>.
- Wood, S.N., 2017. *Generalized Additive Models: An Introduction with R*. Chapman and Hall/CRC.