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Distribution of butterflies (Lepidoptera : Papilionoidea) in Estonia: Results of a systematic mapping project reveal long-term trends

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The distribution of butterflies was mapped throughout entire Estonia in 2016 and 2017. Butterflies were surveyed during three phenologically targeted visits at more than 1200 pre-selected sites. In total, over 180 000 individuals belonging to 97 species were recorded. We compare the resulting distribution maps with historical records, and discuss changes in the species' distribution. We conclude that, within the time frame of century, the changes in the Estonian butterfly fauna were moderate. For about 75% of species, there was no conclusive evidence of a change in distribution or abundance. In case of the remaining 25%, there were more butterfly species with an increasing rather than a decreasing trend in abundance and/or distribution. Some but not all of those changes could be associated with ongoing climate change. The decline of several dry-meadow specialists can be regarded as the most urgent conservation concern.

Introduction

Recording distributions of organisms on Earth has been one of the fundamental tasks of biological science since its dawn. In recent times, the (applied) value of faunistic research has been amplified by concerns about the consequences of anthropogenic environmental changes. For butterflies in particular, there is ample evidence of recent distribution shifts attributable to both climate warming (Parmesan 1999, Hickling *et al.* 2006, Pöyry *et al.* 2009, Maes *et al.* 2010, Breed *et al.* 2013) and changes in habitats and landscapes (Maes & van Dyck 2001, Kuussaari *et al.* 2007, Krauss *et al.* 2010, Melero *et al.* 2016). Nevertheless, the frequently non-systematic character of faunistic data hampers quantitative analysis of such processes. The development of volunteer-based monitoring schemes has dramatically increased the amount of high-quality data

available (e.g. Brereton *et al.* 2018, van Swaay *et al.* 2018). However, those areas with a high coverage of monitoring transects still cover just a small fraction of Europe. For the rest, obtaining snapshots of distribution patterns suitable for quantitative analysis must rely on carefully designed short-term projects with a repeatable methodology.

In this paper, we report the results of a systematic butterfly mapping project (BMP) that covered the entire territory of Estonia (45 227 km^2). The country lies between the northern latitudes of 57.5° and 59.5°, and hemiboreal forests cover about 50% of its area. Human population density is rather low (28 people/km^2). In Estonia, natural open landscape is largely limited to raised (*Sphagnum*) bogs and flooded meadows, with various semi-natural open elements in agricultural and forest landscapes providing significant habitat for most butterfly species.

For the BMP, over 1200 study sites were systematically pre-selected on the basis of topographic maps and orthophotos while care was taken to ensure repeatability of the selection procedure. Each site was surveyed three times during one of the two seasons to cover different phenological phases. Encountered butterflies were recorded using timed surveys (Kadlec *et al.* 2012). Comparing the resulting distribution maps with historical records allowed us to discuss changes in the abundance and distribution of particular species that occurred both within the time frame of a century, and also during more recent decades. Our retrospective approach also gives the present paper features of a general overview of Estonian butterfly faunistics.

Material and methods

The background: Past and present of butterfly faunistics in Estonia

Lepidopterological studies in Estonia can be traced back to the mid-19th century. The work by Nolcken (1868) constitutes the earliest overview of the Estonian butterfly fauna. Though his publication covered a wider territory, a total of 78 species of butterflies can with certainty be identified as having been recorded within the contemporary borders of Estonia by the 1860s. These are the species for which Nolcken (1868) either specifically mentioned Estonian localities or characterized the species as being common throughout the study area.

The next major work summarizing the results of the early period of lepidopterological research in Estonia was *Lepidopteren-Fauna von Estland* by Wilhelm Petersen (1902). A revised version of this monograph was published two decades later (Petersen 1924). Some additional data were presented in the first ever butterfly book in the Estonian language (Petersen 1927). In total, there were 97 butterfly species known from Estonia in Petersen's time. The 100-species count was soon surpassed when the first post-war country-level summary (Viidalepp & Möls 1963) comprised 106 species. Subsequent publications by Thomson (1967), Möls and Viidalepp (1969), Šulcs and Viidalepp (1974), Remm and Viidalepp (1977, 1986), Kesküla (1992), Viidalepp (1995), and Viidalepp and Remm (1996) expand the list of Estonian butterflies to 110 species. The three most recent works summarizing the fauna of Estonia (Jürivete & Õunap 2008, Õunap & Tartes 2014, Aarvik *et al.* 2017) consensually report 113 butterfly species recorded in Estonia, with *Lasiommata megera* having been added as the 114th species in 2018 (*see* below). The numbers reported above do not include the species reported for the Estonian fauna erroneously; these species are *Parnassius apollo*, *Pyrgus carthami*, *Thymelicus acteon*, *Polyommatus dorylas*, *Neptis sappho*, *Argynnis pandora*, *Pyronia tithonus*, *Erebia euryale*, *E. medusa*). The reasons for excluding these species from the list of Estonian butterflies are discussed by Petersen (1924, 1927), Šulcs and Viidalepp (1974), Jürivete *et al.* (2000) and Kesküla (2000).

Currently, there are about 10 butterfly collectors in Estonia actively involved in faunistic research, as well as an increasing number of nature photographers making their observations publicly available. Several ecological research projects (e.g. Sang *et al.* 2010, Tiitsaar *et al.* 2013, Viljur & Teder 2016, 2018) have recently increased faunistic knowledge. Yearly surveys of noteworthy faunistic records are published in the local lepidopterological journal *Lepinfo*, as well as in public databases such as the Estonian Nature Observations Database and eElurikkus, which are

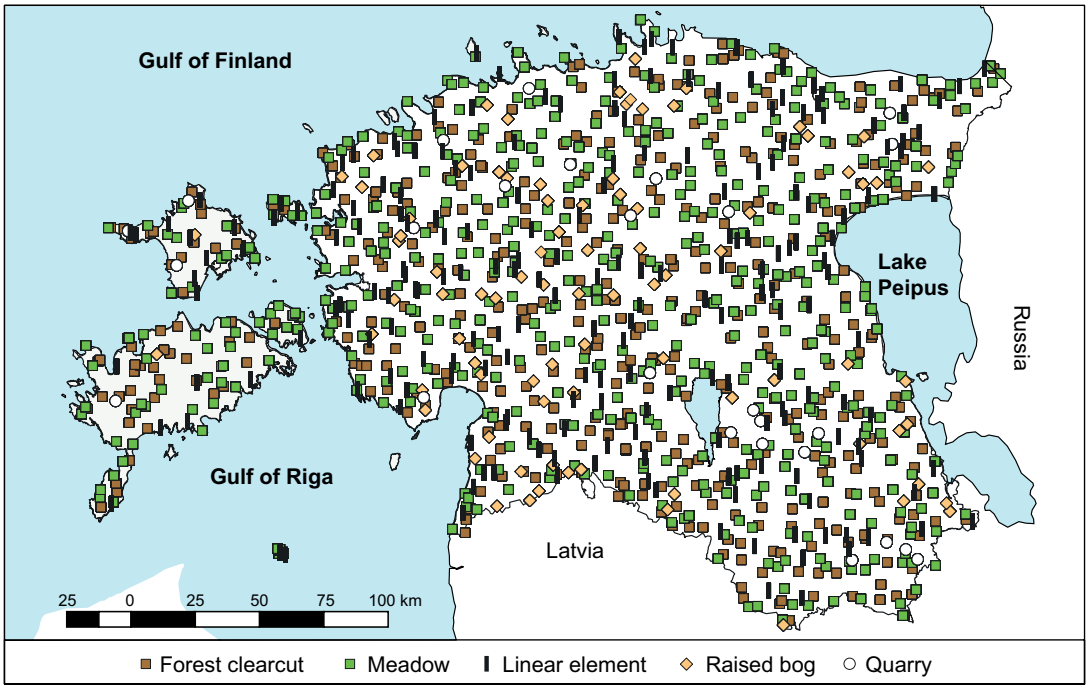

Fig. 1. The location of study sites in Estonia by habitat type.

gaining popularity. A butterfly monitoring programme has been running in Estonia since 2004 with 14 transects being surveyed 6 times a year. Despite a relatively solid knowledge obtained in the course of these activities, the territory of the country has remained quite unevenly studied, as indicated by the most recently published distribution maps (Kesküla 1992), and the situation has not changed much since then. In fact, most of the records are concentrated in 'interesting' regions (such as the island of Saaremaa and the extreme SE of the country), frequently visited by amateur lepidopterists, as well as in the surroundings of major urban centers.

The mapping project: selection of study sites

For the mapping project of 2016–2017, the study sites (Fig. 1) were selected on the basis of orthophotos and base maps (Estonian Land Board, 2016) following predefined criteria. In particular, the aim was to select as a minimum three study sites in each 10 × 10 km Universal Transverse Mercator (UTM) square. Whenever possible, one grassland (a total of 490 sites in the final data set) and one forest clear-cut of the size of 1–5 ha (431 sites) were selected in each UTM square. Clearcuts are a dominant open landscape element in northern European managed forests and have been shown to provide habitats for the majority of butterfly species in Estonia (Viljur & Teder 2016, 2018) and elsewhere (Blixt *et al.* 2015, Korpela *et al.* 2015). Linear elements of open landscape (e.g. power line corridors, forest road verges; n = 210), raised bogs (n = 85) or abandoned open (mostly gravel) mines (n = 27) were included depending on the presence of these landscape elements. The selection of study sites was representative of (open) butterfly habitats in Estonia. The absence of closed forest habitats should not constitute a problem as butterflies tend not to fly below tree cover of most types of boreal forest, and, moreover, nearly all forest species can readily be recorded in clearcuts and forest road verges (M.-L. Viljur *et al.* unpubl. data). The use of predefined criteria in site selection facilitates the repeatability of the study. All the study sites were selected by a single person to ensure uniformity. The chosen person was largely unaware of traditions within the Estonian lepidopterist com-

munity, which helped to avoid any bias towards frequently visited 'good' butterfly sites.

Recorders

People involved in the fieldwork were primarily professional and amateur entomologists and students of zoology or related fields. Nearly all field recorders had previous experience with butterfly identification. Novice recorders were trained prior to the field season. In addition, identification help was provided throughout the field season by e-mail and through a Facebook group (*see* also 'Data validation' below). A total of 48 persons were employed as recorders, in addition to at least 14 volunteers (*see* Acknowledgments). Each of the recorders was responsible for a subset of study sites (up to 50 per year, upon agreement). The sites were assigned to the recorders prior to the field seasons and formed one or (usually) more geographical clusters.

Fieldwork

Fieldwork was conducted during two field seasons, 2016 and 2017. All sites were visited three times (the three observation rounds, hereafter) during one of the two years (either 2016 or 2017) to cover different phenological aspects of the butterfly flight season (Table 1). The dates of fieldwork differed between the years due to among-year phenological differences (spring was late in 2017, *see* Table 1 for accumulated degree-days), and the observation rounds were postponed with the aim to cover similar phenological phases in both years. The latter aspect was essential to minimize the effect of year in future quantitative analyses of the data. A more precise phenological tuning was not possible as recorders had to be notified about the fieldwork periods well in advance. The areas covered in either of the fieldwork years are shown in Appendix 1.

The locations of the study sites were communicated to the recorders in the form of geographic coordinates of the approximate center of the habitat patch in focus. The recorders were asked to evaluate the site during the first visit, especially ease of access and/or its current state. If the site was deemed totally unsuitable for butterflies due to e.g. a recent change in land use, the recorder was redirected to a suitable back-up site nearby, or allowed to choose another site representing the same habitat type as the original one. As a result, less than 4% of the originally selected sites were replaced.

The recorders were instructed to move around the study sites to detect as many butterfly species as possible. To standardize the research effort, the observation time was set to 30 minutes of active search per site visit, excluding the time spent identifying the butterflies. If two or more people were simultaneously involved in recording, the search time was reduced accordingly. It was, however, impractical to strictly define the area where the observations were carried out: the recorders were thus instructed to remain in the

Table 1. Timing of recording rounds in the two years of study. The total degree-days (base = 5 °C) accumulated by the starting date of each observation round are presented for three locations in Estonia to characterize the phenological stage (Estonian Weather Service).

Round	Start date	End date	Accumulated degree days		
			Roomassaare	Tallinn	Võru
2016					
1st	29 May	8 June	242.7	242.9	273.2
2nd	1 July	10 July	624.2	600.3	676.4
3rd	25 July	5 August	931.4	893.0	998.0
2017					
1st	1 June	10 June	176.2	157.65	201.7
2nd	5 July	15 July	497.6	444.8	515.8
3rd	1 August	10 August	808.2	731.6	820.7

same habitat type, and to avoid inspecting the same areas repeatedly. In practice, applying the time restriction also limited the area which could be covered.

All encountered butterfly individuals were counted, or — for the most abundant species — the number of individuals seen was estimated. If the recorder reported the number of individuals as a range, the average was used in the analysis. In addition, weather parameters (temperature, wind, cloud cover) were recorded. Fieldwork was conducted only under weather conditions conducive to butterfly activity (following Pollard & Yates 1993) and during active butterfly flight time (between 10:00 and 18:00). Butterfly species observed outside the 30-min period, or outside a study site (as defined by the criterion of homogeneous habitat) were also noted. Respective data were included when constructing distribution maps presented here but will not be used in future quantitative analyses.

Data validation

As recorders inevitably varied in their butterfly-identifying skills, data validation was an important issue. A multi-layer approach was used to confirm identifications. First, we designated a list of species for which proof was required (Appendix 2). This proof could be a photo or a sample specimen depending on the species and its conservation status. The recorders were instructed to collect species that could not be unambiguously identified in the field. In particular, species pairs *Leptidea sinapis*/*juvernica* (all caught individuals were preserved) and *Plebejus idas*/*argus* (a maximum sample of 15–20 specimens per site) were later identified in the laboratory by inspecting genitalia (*Leptidea* spp.), or using several other morphological traits (*Plebejus* spp.). Furthermore, the recorders were instructed to photograph or collect any butterflies that they thought they were not able to reliably identify. All photos and sample specimens were checked by the authors of this paper and, when necessary, the data were corrected accordingly. In addition, some sites first visited by novice butterfly recorders were revisited by professionals, mainly in 2017.

Results

In total, 1247 sites in 513 10×10 km UTM squares were surveyed; 981 sites were visited in 2016 and 406 in 2017, with little overlap. As a result, 186 012 butterfly individuals belonging to 97 species were registered (Appendix 3). The median numbers of specimens and species per UTM square were 306 and 28, respectively, with respective figures for study site being 126 and 17. The median number of recorded specimens per butterfly species was 348, and a species was recorded at 123 sites and in 102 UTM squares, both being median values. The most common species, *Aphantopus hyperantus*, was detected at 90.4% of the studied sites and in 98.2% of the UTM squares.

Distribution maps

In the following, we present the results of the butterfly mapping project (BMP) in the form of distribution maps with 10×10 km UTM squares. To allow for comparisons with historical distribution data, we also included the distributions as presented on maps by Kesküla (1992). Additionally, we incorporated more recent (1992–2019) data from the following sources: (1) annual lists of noteworthy records of Macrolepidoptera, published in the Estonian entomofaunistic journal *Lepinfo*, (2) entries available in an online database (GBIF 2019) which merges the data of the Estonian Nature Observations Database, eElurikkus and PlutoF, and (3) ecological study on western Estonian calcareous meadows (Sang *et al.* 2010, Tiitsaar *et al.* 2013).

It should be noted that assembling a complete database of available historical records was beyond the scope of our study. We present older records based on few selected sources only (which still include the majority of published data, and virtually all the available data for rare species, i.e. those with no more than a few dozen records), and only for the purpose of discussing recent changes in the distribution of the species. *Lepinfo* publishes records of only a limited number of species (rare species and those not considered to be widespread in Estonia), and the list of species included has somewhat changed over the years

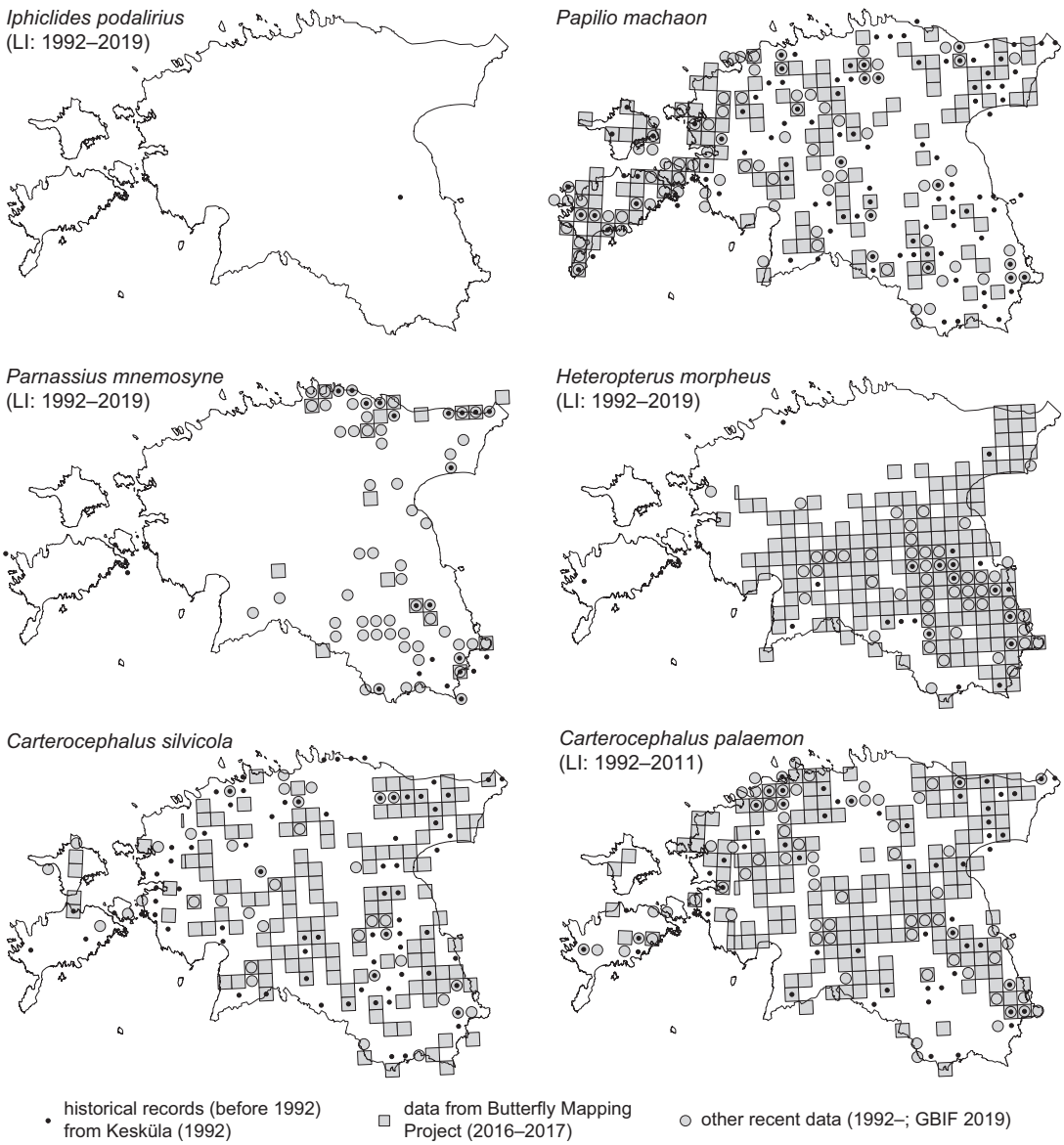

Fig. 2. Distribution of Estonian butterflies in 10 × 10 km UTM squares. 'LI:' followed by the years indicates that distribution data were systematically collected and published in *Lepinfo* in the period indicated. *Lepinfo* does not publish data on species considered common and widespread.

due to changes in distribution and abundance (Tammaru 2003, 2015). As a consequence, there are relatively more recent records available for less common species, which must be kept in mind when interpreting the maps. For this reason, the status of each species in the '*Lepinfo* lists' is indicated on the distribution maps (Fig. 2). Moreover, a relative overrepresentation of earlier records from western Estonia has to be taken into account, this bias arising from the studies of calcareous meadows (Sang *et al.* 2010, Tiitsaar *et al.* 2013) carried out in that region (*see* above).

Here, we largely refrain from re-evaluating the reliability of historical records, primarily because we see no reason to question the conclusions of previous critical analyses (Jürivete *et al.* 2000, Kesküla 2000, and other references above). Nevertheless, to unify the cri-

teria, we excluded two records of *Iphiclides podalirius*, which were based on sightings only (Thomson 1967). Moreover, we here express our doubts regarding the authenticity of several records (*Lysandra coridon*, *Lycaena tityrus*, *Melitaea didyma, Melanargia galathea*) made by J. Mõttus between 1942 and 1944 (Viidalepp 1961). This is because a suspiciously high number of species that were not known to occur in Estonia at that time were reported from a limited area (around the town of Viljandi) during a short period of time. Nevertheless, following the general practice, we still did not omit them from the data set of Estonian butterfly records, so that they are shown on distribution maps.

Species accounts

Below, species-specific results of the butterfly mapping project (BMP) are presented and discussed in the light of earlier knowledge about species' distributions and abundance in Estonia. The historical data are primarily from Petersen (1924) and Šulcs and Viidalepp (1974); these sources are not always cited in species accounts. Systematics and nomenclature follow Wiemers *et al.* (2018). At the end of each species account, we give the conservation status based on the latest evaluation (2017; data in Maes *et al.* 2019). The Red List categories for Estonia are given in accordance with the IUCN recommendations (IUCN 2012a, 2012b): LC = least concern, NT = near threatened, VU = vulnerable, EN = endangered, CR = critically endangered, RE = regionally extinct, NA = not applicable, NE = not evaluated) following the regional evaluation criteria (IUCN 2012b). For each endangered species, the exact criteria met, and brief comments on those, are given in Appendix 4.

Iphiclides podalirius (Linnaeus, 1758): Not recorded during the BMP. The only documented Estonian record of this species is from 1936 (Mihkelson 1971, *see* Fig. 2 for distribution map). Two more records (Thomson 1967, Kesküla 1992) are based on sightings only and we treat them as unreliable. The species is not considered resident in northern Europe. NA.

Papilio machaon Linnaeus, 1758: During the BMP found at 164 sites in 137 UTM squares (henceforth 'squares'); 315 indiv. recorded (Fig. 2). Distributed across the entire country but rarely numerous. Results of the BMP suggest that the species is more common in the western parts of the country. No indication of change. LC.

Parnassius mnemosyne (Linnaeus, 1758): Found at 17 sites in 17 squares; 92 indiv. recorded (Fig. 2). At the beginning of the 20th century, the species was known to occur on the NE coast of the country, and on the island of Saaremaa. The Saaremaa population is now considered extinct (Viidalepp 2000, Ruben & Viidalepp 2016). The species was first recorded in SE Estonia in 1984 (Õunap & Sarv 2002), and the SE population has been spreading north- and westwards since then (Meier *et al.* 2005, Liivamägi *et al.* 2013). At present, the SE and NE Estonian populations appear to be connected but the species is still absent in the western part of the country. LC.

Heteropterus morpheus (Pallas, 1771): Found at 259 sites in 177 squares; 853 indiv. recorded (Fig. 2). Petersen (1924) reported just two records of the species in Estonia, while Šulcs and Viidalepp (1974) described the species as uncommon and restricted to the SE part of the country. More recent checklists (Remm & Viidalepp 1977, 1986, Viidalepp 1995, Jürivete & Õunap 2008) still consider the species uncommon or even rare (Jürivete *et al.* 2000). The BMP results indicate that the species is now ubiquitous in the S and E parts of the country, but is still absent from the islands in the west, and a large area in the north and northwest. This species is one of the few with a distinct distribution boundary within the country. During the recent decades, the species clearly increased in abundance within its distribution range, which has shifted NW and W by about 50–100 km since the study by Šulcs and Viidalepp (1974). LC.

Carterocephalus silvicola (Meigen, 1829): Found at 153 sites in 135 squares; 290 indiv. recorded (Fig. 2). Widespread. As this is primarily a forest butterfly, its abundance may have been underestimated in the BMP which focused on open habitats. No indication of change. LC.

Carterocephalus palaemon (Pallas, 1771): Found at 233 sites in 187 squares; 642 indiv. recorded (Fig. 2). Widespread according to the BMP and earlier sources, though not considered common. Possibly increasing. Nevertheless, scarcity of the BMP records from SE Estonia may deserve attention. LC.

Ochlodes sylvanus (Esper, 1777): Found at 670 sites in 404 squares; 3188 indiv. recorded (Fig. 3). Widespread and numerous throughout the country. No indication of change. LC.

Hesperia comma (Linnaeus, 1758): Found at 36 sites in 36 squares; 123 indiv. recorded (Fig. 3). Widespread in the N and W parts of the country. The BMP results re-confirmed the presence of the species in other regions as well. No indication of change. LC.

Thymelicus sylvestris (Poda, 1761): Found at 204 sites in 160 squares; 932 indiv. recorded (Fig. 3). Widespread in the continental part of the country. According to Petersen (1924), just one record. Later considered uncommon (e.g. Viidalepp & Möls 1963, Remm & Viidalepp 1986, Viidalepp 1995, Jürivete & Õunap 2008). There may, therefore, be an increasing trend through the last century. This should, nevertheless, be treated with caution, as the species is easy to overlook due to its high similarity to its abundant congener *T. lineola* (Vantieghem *et al.* 2017). LC.

Thymelicus lineola (Ochsenheimer, 1808): Found at 973 sites in 472 squares; 10 439 indiv. recorded (Fig. 3). One of the most abundant butterflies in the country (5th, according to the BMP). As Petersen (1924) characterized the species just as 'not rare', there appears to be an indication of an increasing trend during the last century. LC.

Carcharodus floccifera (Zeller, 1847): Found at 1 site in 1 square; 1 indiv. recorded (Fig. 3). This species was first recorded in Estonia in 1995 (Köstner *et al.* 1996). The specimen found while conducting the BMP was the second for the country. As the two localities are separated by only 20 km, there may well be a resident population of this species in S Estonia. NA.

Erynnis tages (Linnaeus, 1758): Found at 29 sites in 26 squares; 74 indiv. recorded (Fig. 3). The species is primarily distributed in the W and NW parts of the country, and is primarily associated with calcareous meadows. Not recorded during the BMP in the SE but there are other recent records (e.g. Jürivete *et al.* 2016b) of the species from that area. No indication of change. NT.

Pyrgus malvae (Linnaeus, 1758): Found at 199 sites in 161 squares; 472 indiv. recorded (Fig. 3). Distributed across the entire country. No indication of change. LC.

Pyrgus serratulae (Rambur, 1839). Not recorded during the BMP but has been regularly observed in the extreme SE of the country at least since the early 1990s (Pedmanson *et al.* 1993, Pedmanson & Viidalepp 1994) (Fig. 3). The first record for Estonia is from 1950 when the species was observed in the vicinity of Tartu (Veldre 1959). There are, however, no recent records from that area. VU.

Pyrgus alveus (Hübner, 1803): Found at 30 sites in 30 squares; 44 indiv. recorded (Fig. 4). Earlier sources considered this species widespread but not numerous. Overall, this is corroborated by the results of the BMP. However, the absence of the BMP records from the N (excluding NE) part of the country was unexpected, hence the status of the species in that part of the country requires further studies. LC.

Leptidea juvernica Williams, 1946: Found at 323 sites in 245 squares; 1005 indiv. recorded (Fig. 4). First reported by Kesküla and Pöyry (2003, under the name *L. reali*) but a subsequent study (Bichele 2005) showed that *L. juvernica* had been collected in Estonia as early as in 1938. The abundance of *L. juvernica* has substantially increased since the first record (Bichele 2005). According to the BMP, *L. juvernica* is currently the more numerous one of the two sibling species in Estonia. LC.

Leptidea sinapis (Linnaeus, 1758): Found at 143 sites in 119 squares; 384 indiv. recorded (Fig. 4). Widespread but, according to the BMP, seems to be more common in the E parts of the country. The presence of two species of *Leptidea* in Estonia was first confirmed by Kesküla and Pöyry (2003), so none of the earlier reports distinguished between

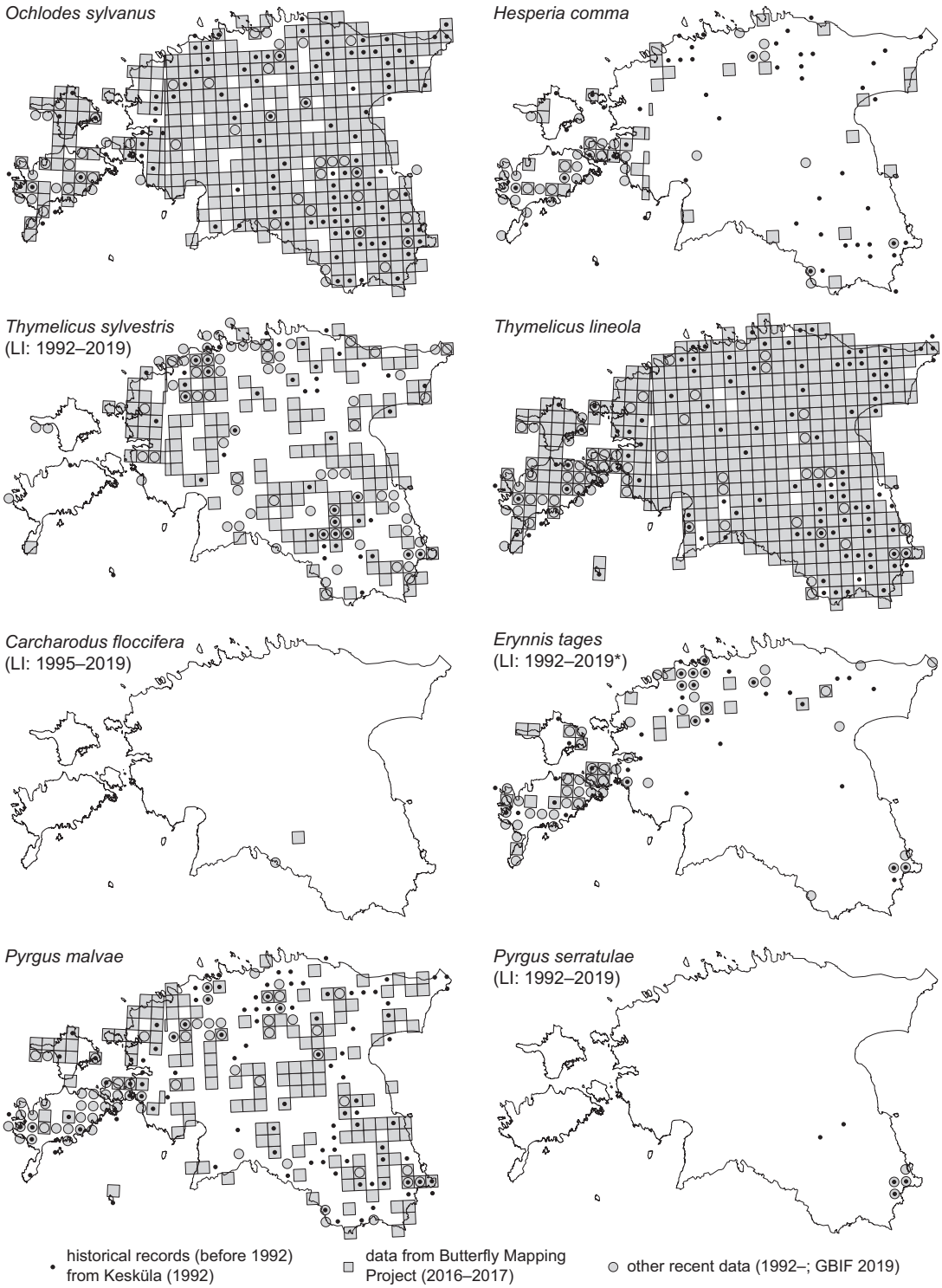

Fig. 3. Distribution of Estonian butterflies.'LI:' followed by the years indicates that distribution data were systematically collected and published in *Lepinfo* in the period indicated. * since 2002 the distribution data for *E. tages* have been collected by *Lepinfo* for the areas other than western Estonia (UTM squares L*5* and east of those).

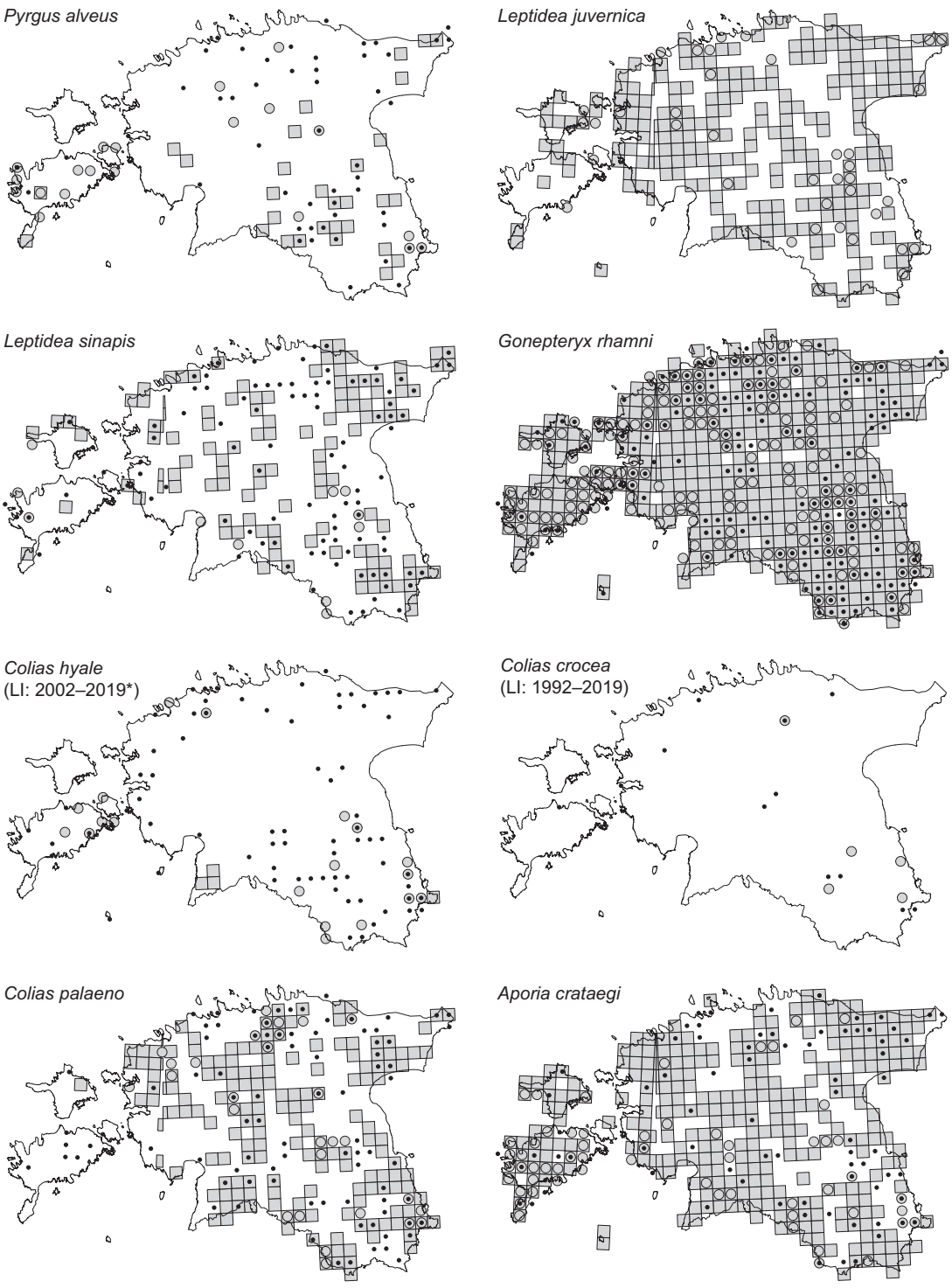

Fig. 4. Distribution of Estonian butterflies.'LI:' followed by the years indicates that distribution data were systematically collected and published in *Lepinfo* in the period indicated. * distribution data for *C. hyale* have been collected by Lepinfo for northern Estonia (UTM squares *F*5 and north of those).

L. sinapis and *L. juvernica*. For *Leptidea* spp. collectively, the data point at an increasing trend as Petersen (1924) characterized the butterfly as 'uncommon and absent in some areas'. LC.

Gonepteryx rhamni (Linnaeus, 1758): Found at 1034 sites in 481 squares; 12 526 indiv. recorded (Fig. 4). Widespread and numerous throughout the country (3rd most abundant species according to the BMP). No indication of change. LC.

Colias hyale (Linnaeus, 1758): Found at 4 sites in 4 squares; 5 indiv. recorded (Fig. 4). Earlier authors (e.g. Viidalepp & Remm 1996, Viidalepp & Möls 1963) characterized *C. hyale* as a species with no resident populations in Estonia. Recent observations made in spring suggest that *C. hyale* has overwintering populations at least in the extreme SE of Estonia. The abundance of *C. hyale* was certainly below average during the BMP years. LC.

Colias crocea (Geoffroy, 1785): Not recorded during the BMP. A rare immigrant, observed about 20 times in Estonia (Ruben 2015) (Fig. 4). Majority of the hitherto known Estonian specimens were found in 2013, but no subsequent records are available. NA.

Colias palaeno (Linnaeus, 1761): Found at 242 sites (incl. 55 out of 85 raised-bog sites), 174 squares; 1128 indiv. recorded (Fig. 4). A raised-bog species regularly present in suitable habitats. No indication of change in overall abundance. There were no BMP records from the island of Saaremaa, but the species has recently been recorded in that area as well (R. Melsas pers. comm). LC.

Aporia crataegi (Linnaeus, 1758): Found at 541 sites in 325 squares; 3921 indiv. recorded (Fig. 4). Widespread but rarely numerous. Abundance varies considerably among years. No indication of change. LC.

Pontia edusa (Fabricius, 1777): No BMP records. This species is not resident in the country and immigrants are observed in about 3–4 years out of 10 (Fig. 5). NA.

Pieris brassicae (Linnaeus, 1758): Found at 306 sites in 235 squares; 708 indiv. recorded (Fig. 5). Widespread and moderately numerous. No indication of change. LC.

Pieris rapae (Linnaeus, 1758): Found at 191 sites in 156 squares; 576 indiv. recorded (Fig. 5). Widespread and moderately numerous. No indication of change. LC.

Pieris napi (Linnaeus, 1758): Found at 1074 sites in 485 squares; 17 359 indiv. recorded (Fig. 5). One of the most abundant butterflies in the country (2nd according to BMP). No indication of change. LC.

Anthocharis cardamines (Linnaeus, 1758): Found at 245 sites in 188 squares; 653 indiv. recorded (Fig. 5). Widespread and relatively numerous. The BMP results from 2016 likely underestimated the abundance as the flight of *A. cardamines* peaked in mid-May of that year, i.e. before the BMP fieldwork started. No indication of change. LC.

Hamearis lucina (Linnaeus, 1758): Found at 61 sites in 50 squares; 331 indiv. recorded (Fig. 5). First recorded in 1924 (Petersen, 1924, 1927). Later, this species extended its range over the majority of the W part of the country, with expansion to the northern part of its current Estonian range being relatively recent (Marnot 2007). LC.

Lycaena helle (Denis & Schiffermüller, 1775). Not recorded during the BMP. There is just one Estonian record from 1905 (Petersen 1924) (Fig. 5). The species is not known to have had a resident population in Estonia. NA.

Lycaena alciphron (Rottemburg, 1775): Found at 34 sites in 32 squares; 61 indiv. recorded (Fig. 5). Relatively common in the SE and NE parts, but absent from the W part of the country. Petersen (1924) considered this species a rarity. Also later e.g. Viidalepp and Möls (1973) and Viidalepp and Remm (1996) reported it to be rare. Currently, such an assessment is definitely not valid for at least some parts of the country, allowing us to conclude that there was an increasing trend during the last century. LC.

Lycaena dispar (Haworth, 1802): Found at 131 sites in 108 squares; 227 indiv. recorded (Fig. 6). A relative newcomer to the Estonian fauna, first recorded in 1947 (Vilbaste 1959). Nowadays, the species is widespread throughout most of the country though not numerous. Scarcity of the species in W Esto-

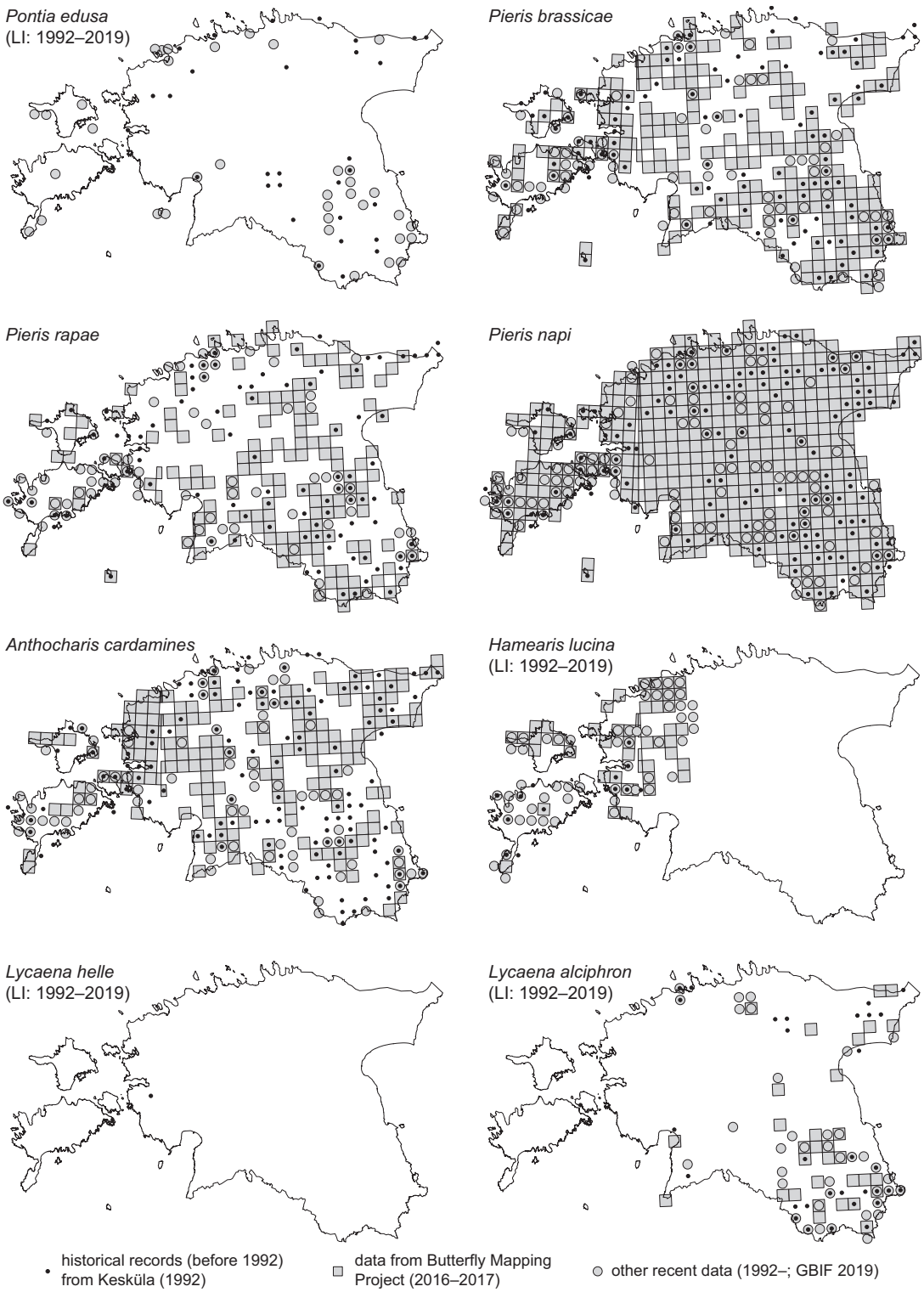

Fig. 5. Distribution of Estonian butterflies.'LI:' followed by the years indicates that distribution data were systematically collected and published in *Lepinfo* in the period indicated.

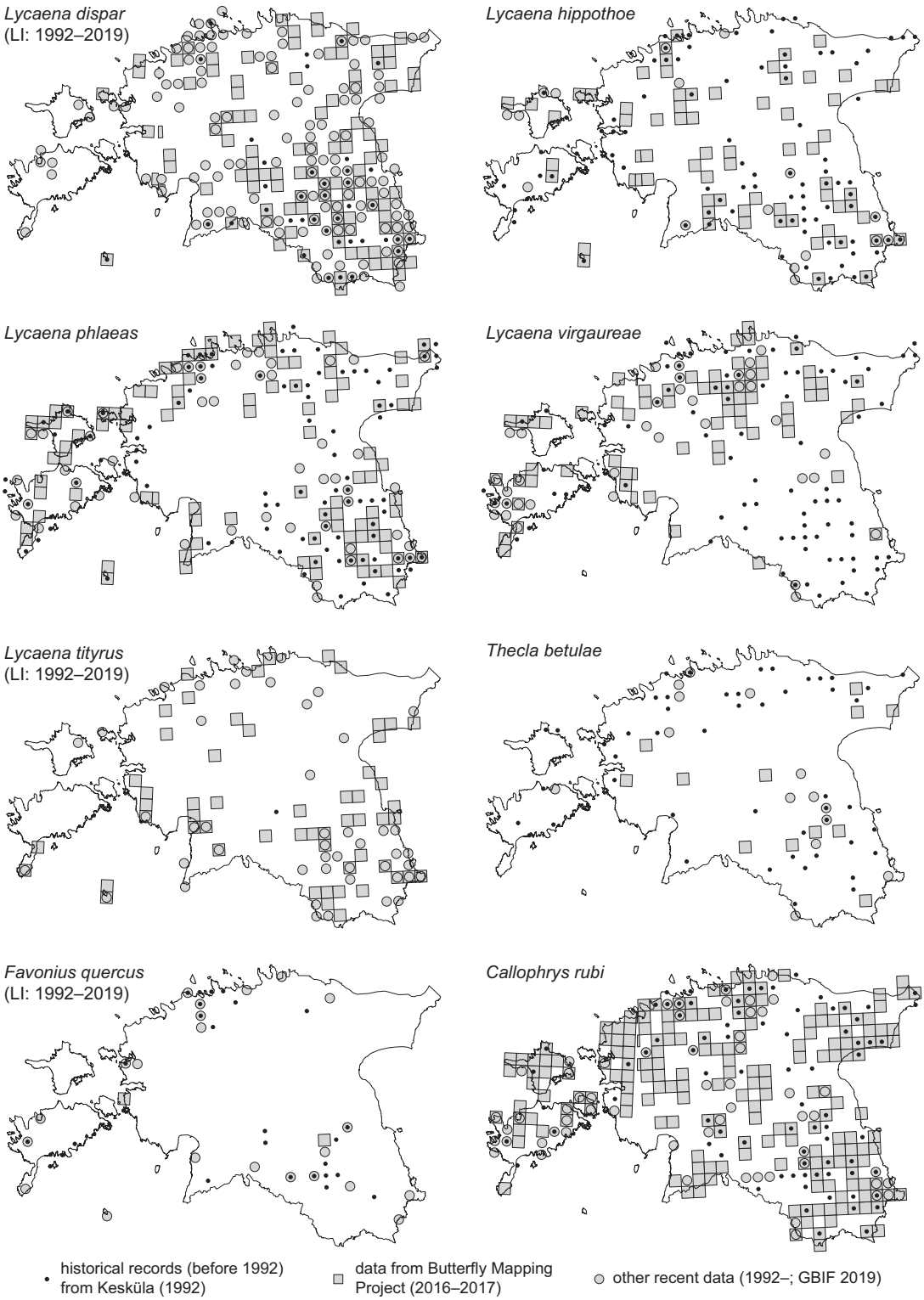

Fig. 6. Distribution of Estonian butterflies.'LI:' followed by the years indicates that distribution data were systematically collected and published in *Lepinfo* in the period indicated.

nia noted earlier (Šulcs & Viidalepp 1974, Lindman *et al.* 2015) was confirmed by the BMP. LC.

Lycaena hippothoe (Linnaeus, 1761): Found at 73 sites in 70 squares; 111 indiv. recorded (Fig. 6). Distributed throughout the entire country, but has never been considered common. No indication of change. LC.

Lycaena phlaeas (Linnaeus, 1761): Found at 123 sites in 102 squares; 300 indiv. recorded (Fig. 6). Widespread and moderately numerous throughout the country. No indication of change but the BMP results unexpectedly suggest existence of a large unoccupied area in central Estonia. Further studies are needed to confirm the validity of this observation. LC.

Lycaena virgaureae (Linnaeus, 1758): Found at 83 sites in 69 squares; 295 indiv. recorded (Fig. 6). This species was considered common by earlier sources, but the BMP results indicate that it has clearly retreated in the S parts of the country. LC.

Lycaena tityrus (Poda, 1761): Found at 66 sites in 57 squares; 342 indiv. recorded (Fig. 6). A newcomer in the Estonian fauna. Disregarding a doubtful record from 1942 (*see* above), the species was first discovered in Estonia in 1996 (Sarv *et al.* 1999). In 1998 the existence of a permanent population in SE Estonia was confirmed, as numerous individuals representing both spring and summer generation were recorded (Sarv & Õunap 2001). This species has been steadily spreading towards N and W since then, and the BMP found it to be distributed across the entire country. LC.

Thecla betulae (Linnaeus, 1758): Found at 12 sites in 12 squares; 14 indiv. recorded (Fig. 6). Widespread and rather numerous throughout the country. Scarcity of the BMP records can be explained by late (early to mid-August) peak of the flight which placed it outside the time frame of the BMP. No indication of change. LC.

Favonius quercus (Linnaeus, 1758): Found at 2 sites in 2 squares; 2 indiv. recorded (Fig. 6). Perhaps the hardest to detect Estonian butterfly, primarily due to the adults' habit to fly at the height of tree crowns. Petersen (1924) considered the species to be widespread in Estonia. Despite scarce BMP records, there is hardly sufficient evidence to question the validity of his conclusion. LC.

Callophrys rubi (Linnaeus, 1758): Found at 269 sites in 200 squares; 2033 indiv. recorded (Fig. 6). Widespread and numerous throughout the country. No indication of change. LC.

Satyrium pruni (Linnaeus, 1758): Found at 9 sites in 9 squares; 10 indiv. recorded (Fig. 7). Relatively rare but widespread species. No indication of change. LC.

Satyrium ilicis (Esper, 1779): Found at 12 sites in 8 squares; 17 indiv. recorded (Fig. 7). Considered rare and local since Petersen's (1924) studies, but sporadically this butterfly was abundant in W Estonia (Jürivete *et al.* 2016a), and present as far north as close to Tallinn (Mihkelson 1971). The BMP revealed a broader than expected distribution of the species on W Estonian mainland. LC.

Satyrium w-album (Knoch, 1782): Found at 9 sites in 9 squares; 17 indiv. recorded (Fig. 7). Petersen (1924) had listed just a few records and the species was considered rare also later. During recent decades, there has been a clear expansion of its area of occupation. The BMP records however remain scarce, likely due to limited detectability of *Satyrium* species in transect counts. LC.

Celastrina argiolus (Linnaeus, 1758): Found at 230 sites in 183 squares; 452 indiv. recorded (Fig. 7). Widespread and moderately numerous throughout the country, as confirmed also by the BMP despite the fact that the BMP started when the flight period of the first (more abundant) generation of the species was largely over. No indication of change. LC.

Phengaris alcon (Denis & Schiffermüller, 1775): Not recorded during the BMP. There are two old records of single specimens, from 1937 (Šulcs & Viidalepp 1974) and 1977 (Jürivete & Õunap 2008). The first resident population was discovered in Estonia as recently as in 2011 (Vilbas *et al.* 2016a, 2016b; Fig. 7). It was found in an area not popular among lepidopterists, so the age of the Estonian populations is not known. In Estonia, *P. alcon* feeds on *Gentiana cruciata*, belonging thus to the ecological form *rebeli* (Vilbas *et al.* 2016a). CR.

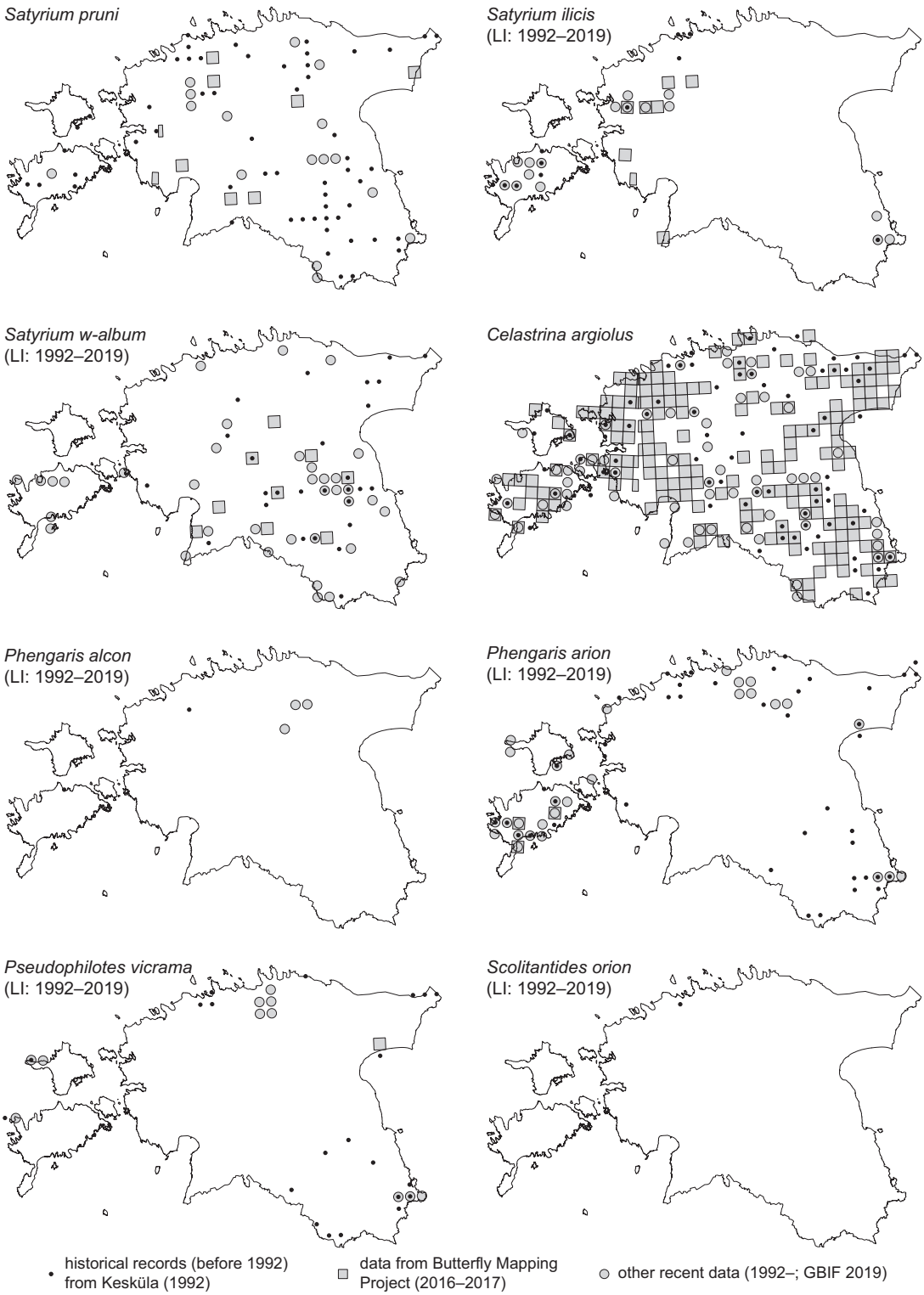

Fig. 7. Distribution of Estonian butterflies.'LI:' followed by the years indicates that distribution data were systematically collected and published in *Lepinfo* in the period indicated.

Phengaris arion (Linnaeus, 1758): Found at 4 sites in 3 squares; 30 indiv. recorded (Fig. 7). This species occurs in a few restricted areas in the country, with the largest number of populations known from the island of Saaremaa (Vilbas *et al.* 2015). During the last 100 years, the number of populations certainly decreased. EN.

Pseudophilotes vicrama (Moore, 1865): Found at 1 site in 1 square, 1 indiv. recorded (Fig. 7). During recent decades, this species had been known from only two populations (Põhja-Kõrvemaa Landscape Reserve and western Hiiumaa). However, in 2016 it was re-discovered in SE Estonia (Martin & Õunap 2019a) where it had not been recorded for almost 20 years (last observation dates back to 1998; *see* Sarv & Õunap 2001). The BMP record from the northern coast of lake Peipsi is an unexpected addition to the known Estonian distribution of *P. vicrama*. Apart from the BMP data, the species was recently recorded also in NW Saaremaa (Martin & Õunap 2019b) where it had not been observed since 1938 (GBIF 2019). Overall, there appears to be a negative trend at the scale of the century. VU.

Scolitantides orion (Pallas, 1771). Not recorded during the BMP. There is just one record of this species from 1886 (Fig. 7). The species is not known to have had populations in Estonia. NA.

Glaucopsyche alexis (Poda, 1761) Not recorded during the BMP. The species was recorded as new to Estonia in 1980 (Remm & Viidalepp 1981), and a permanent population was known to occur in the extreme SE of the country until 2006 (Fig. 8), with no records thereafter. RE.

Cupido argiades (Pallas, 1771): Found at 114 sites in 89 squares; 270 indiv. recorded (Fig. 8). More common in the SE half of the country. Recorded as new to Estonia in 1947 (Vilbaste 1959), it occurred in the country until 1952 (Šulcs & Viidalepp 1974) and again since 1972 (Viidalepp & Remm 1996, GBIF 2019). The species was not considered resident in Estonia by e.g. Viidalepp and Möls (1963), but currently there is little doubt about the resident status of at least the SE Estonian populations. LC.

Cupido minimus (Fuessly, 1775): Found at 147 sites in 103 squares; 2178 indiv. recorded (Fig. 8). A common and frequently abundant inhabitant of dry calcareous grasslands in N and W Estonia, with scattered records from elsewhere. No indication of change. LC.

Plebejus argus (Linnaeus, 1758): Found at 328 sites in 228 squares; 7968 indiv. recorded (Fig. 8). Widespread and numerous throughout the country. No indication of change. LC.

Plebejus idas (Linnaeus, 1761): Found at 138 sites in 117 squares; 1806 indiv. recorded (Fig. 8). Widespread and numerous throughout the country but generally less abundant than *P. argus*. No indication of change. LC.

Agriades optilete (Knoch, 1781): Found at 121 sites (incl. 33 out of 85 raised-bog sites) in 97 squares; 419 indiv. recorded (Fig. 8). Widespread and moderately numerous in suitable habitats (primarily, raised bogs and paludifying pine forests with *Vaccinium* undergrowth) throughout the country. No indication of change. LC.

Eumedonia eumedon (Esper, 1780): Found at 87 sites in 78 squares; 184 indiv. recorded (Fig. 8). Widespread throughout the country but not numerous, clearly less common than *A. artaxerxes*. The BMP indicated that the species is more widespread in S parts of the country. No indication of change. LC.

Cyaniris semiargus (Rottemburg, 1775): Found at 311 sites in 232 squares; 815 indiv. recorded (Fig. 8). Widespread and moderately numerous throughout the country. No indication of change. LC.

Aricia artaxerxes (Fabricius, 1793): Found at 249 sites in 195 squares; 664 indiv. recorded (Fig. 9). Widespread and moderately numerous throughout the country. As Petersen (1924) considered the species 'not common', there may have been an increasing trend during the last century. LC.

Lysandra bellargus (Rottemburg, 1775): Not recorded during the BMP. There are only three records of single specimens from Estonia from 1939 and 1948 (Viidalepp & Remm 1996) and from 2008 (Jürivete & Õunap 2015) (Fig. 9). The species is not known to have had a resident population in the country. NA.

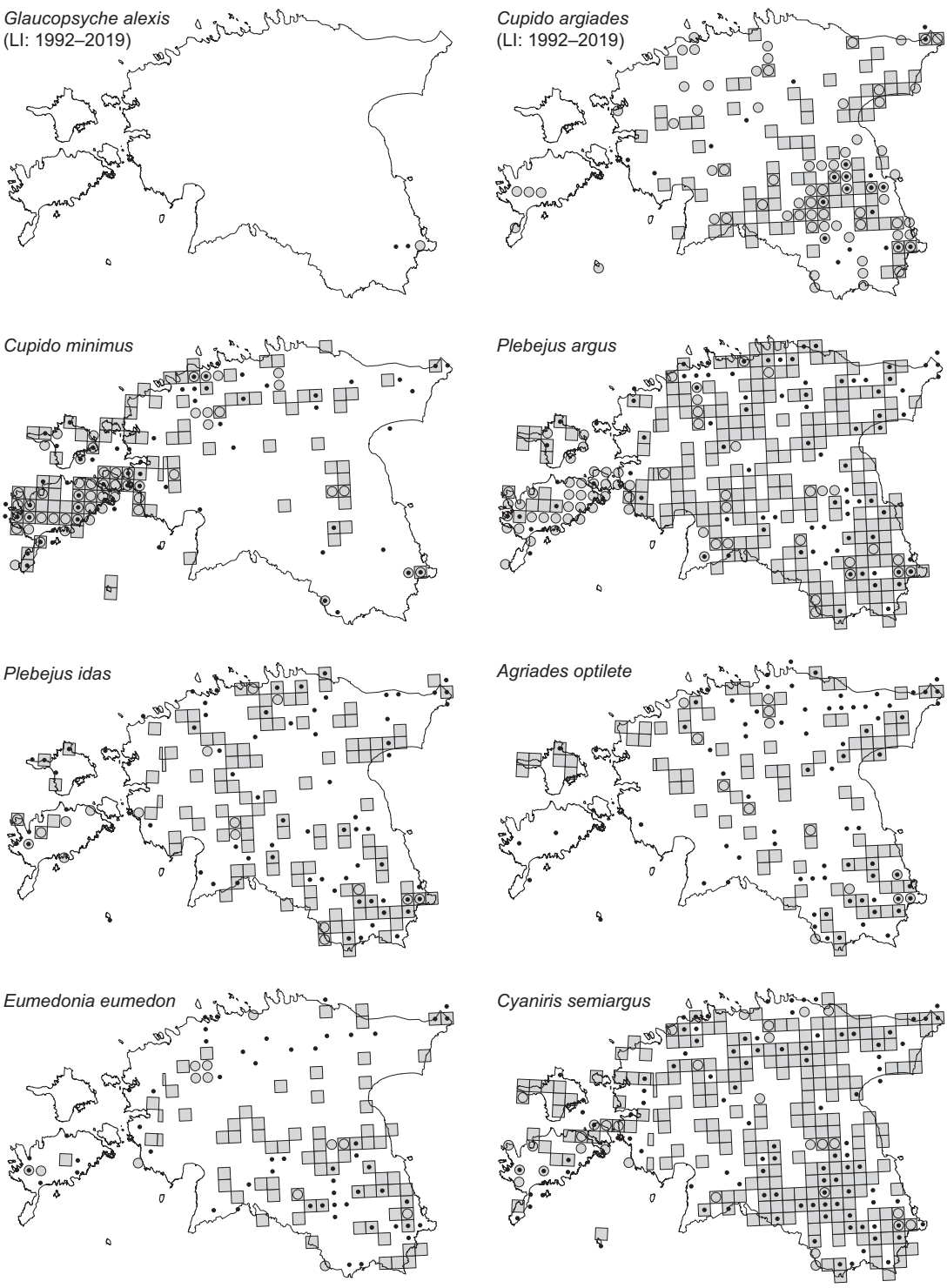

Fig. 8. Distribution of Estonian butterflies.'LI:' followed by the years indicates that distribution data were systematically collected and published in *Lepinfo* in the period indicated.

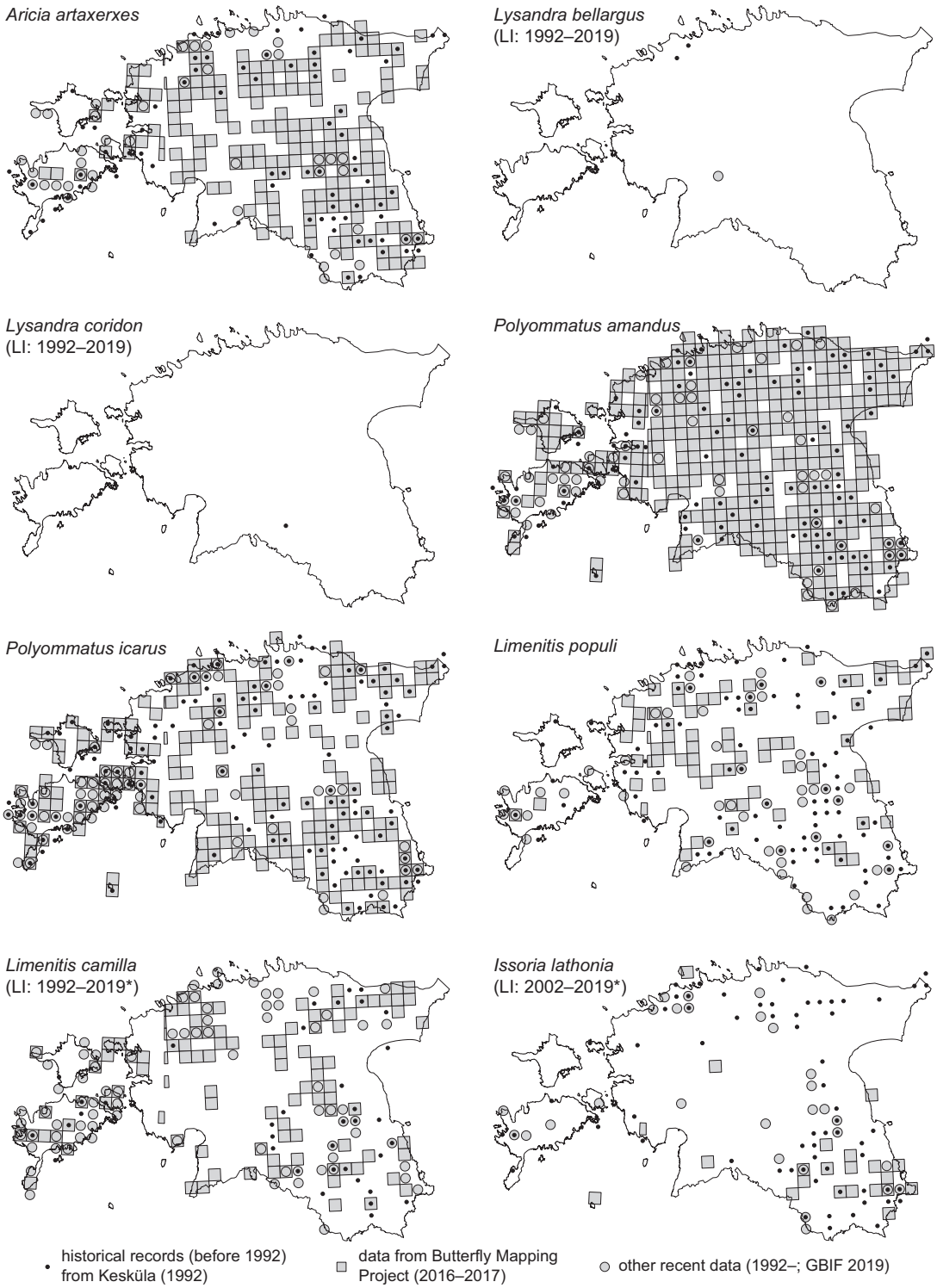

Fig. 9. Distribution maps of Estonian butterflies.'LI:' followed by the years indicates that distribution data were systematically collected and published in *Lepinfo* in the period indicated. * since 2002 distribution data for *L. camilla* and *I. lathonia* have been collected by Lepinfo for northern Estonia only (UTM squares *F*5 and north of those).

Lysandra coridon (Poda, 1761): Not recorded during the BMP. Only three specimens were recorded in Estonia: one in 1916 and two in 1943 (Viidalepp, 1961, Šulcs & Viidalepp 1974) (Fig. 9), with the latter two records being considered doubtful (*see* above). The species is not known to have had a resident population in Estonia. NA.

Polyommatus amandus (Schneider, 1792): Found at 556 sites in 369 squares; 2519 indiv. recorded (Fig. 9). Widespread and numerous throughout the country. No indication of change. LC.

Polyommatus icarus (Rottemburg, 1775): Found at 288 sites in 208 squares; 1127 indiv. recorded (Fig. 9). Widespread and numerous throughout the country. No indication of change. LC.

Limenitis populi (Linnaeus, 1758): Found at 86 sites in 76 squares; 158 indiv. recorded (Fig. 9). Widespread and moderately numerous throughout the country. The number of individuals reported by the BMP can be considered lower than expected. However, transect counts may not be the best way to detect the species, and the BMP may have underestimated its abundance. On the other hand, the abundance of *L. populi* varies considerably among years. Therefore, currently, there is no reliable indication of change. LC.

Limenitis camilla (Linnaeus, 1764): Found at 115 sites in 104 squares; 250 indiv. recorded (Fig. 9). Widely distributed throughout the country but not ubiquitous. With its first record from 1896 (Šulcs & Viidalepp 1974), the species was considered rare until the first decade of the 21th century (Jürivete & Õunap 2008). The current situation results from unquestionable expansion during the recent decades. LC.

Issoria lathonia (Linnaeus, 1758): Found at 23 sites in 22 squares; 48 indiv. recorded (Fig. 9). This species has been considered an immigrant with the abundance strongly varying among years (e.g. Viidalepp & Möls 1963). As it is regularly observed on the Piusa butterfly monitoring transect (57°50′22′′N, 27°28′20′′E) and its surroundings, it may well be resident in the SE parts of the country. No indication of change, with a possible exception of established resident populations in SE Estonia. LC.

Brenthis ino (Rottemburg, 1775): Found at 817 sites in 438 squares; 9374 indiv. recorded (Fig. 10). Widespread and numerous throughout the country. No indication of change. LC.

Argynnis paphia (Linnaeus, 1758): Found at 742 sites in 422 squares; 6485 indiv. recorded (Fig. 10). Widespread and numerous throughout the country. No indication of change. LC.

Argynnis laodice (Pallas, 1771): Found at 190 sites in 153 squares; 718 indiv. recorded (Fig. 10). Widespread and moderately numerous throughout the country, possibly scarcer on the island of Saaremaa. As Petersen (1924) listed only a few records, there apparently was an increasing trend during the last century. The BMP did not confirm the view of Šulcs and Viidalepp (1974) and Viidalepp and Remm (1996) that the species has an eastern distribution in the country. LC.

Speyeria aglaja (Linnaeus, 1758): Found at 686 sites in 403 squares; 4943 indiv. recorded (Fig. 10). Widespread and numerous throughout the country. No indication of change. LC.

Fabriciana niobe (Linnaeus, 1758): Found at 4 sites in 3 squares; 11 indiv. recorded (Fig. 10). Somewhat unexpectedly, during the BMP this species was encountered only on the island of Hiiumaa and close to the city of Tallinn. It was, however, present on a butterfly monitoring transect at Põhja-Kõrvemaa Lansdscape Reserve (59°21′57′′N, 25°42′33′′E) in 2018. From recent decades, there are records only from W, N and SE Estonia, while Petersen (1924) considered tis species to be distributed throughout the entire country though not being common everywhere. The species has thus been on a decline during the last century. The very few records from the BMP, especially when compared with those from the islands of Saaremaa and Muhu surveyed in 2007–2008 (Sang *et al.* 2010), suggest that there may be a decreasing trend within a shorter time scale as well. EN.

Fabriciana adippe (Denis & Schiffermüller, 1775): Found at 334 sites in 244 squares;

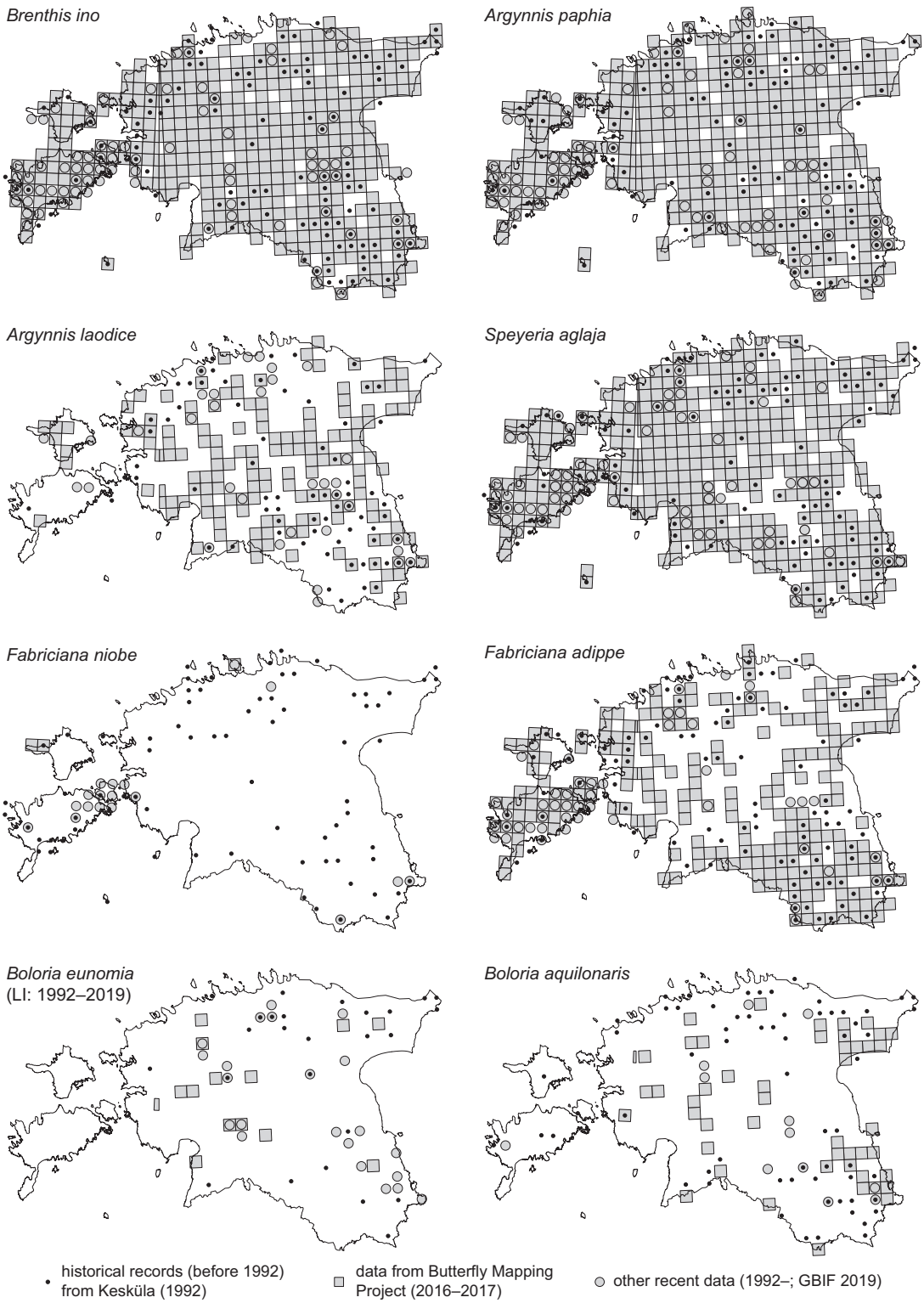

Fig. 10. Distribution of Estonian butterflies.'LI:' followed by the years indicates that distribution data were systematically collected and published in *Lepinfo* in the period indicated.

1394 indiv. recorded (Fig. 10). Widespread and numerous throughout the country. No indication of change. LC.

Boloria eunomia (Esper, 1800): Found at 15 sites (incl. 11 out of 85 raised-bog sites), 14 squares; 82 indiv. recorded (Fig. 10). A strict raised-bog specialist, usually present in suitable habitats but never abundant. No indication of change. LC.

Boloria aquilonaris (Stichel, 1908): Found at 60 sites (incl. 25 out of 85 raised-bog sites), 48 squares, 250 indiv. recorded (Fig. 10). Associated with transitional bogs, raised bogs and their surroundings. According to the BMP, more widespread in the E parts of the country. No evidence of change. LC.

Boloria selene (Denis & Schiffermüller, 1775): Found at 596 sites in 372 squares; 4537 indiv. recorded (Fig. 11). Widespread and numerous throughout the country. No indication of change. LC.

Boloria euphrosyne (Linnaeus, 1758): Found at 171 sites (incl. 68 out of 85 raised-bog sites) in 132 squares; 1435 indiv. recorded (Fig. 11). A butterfly frequently abundant on raised bogs and in their surroundings. No indication of change. LC.

Boloria dia (Linnaeus, 1767): Found at 11 sites in 9 squares; 60 indiv. recorded (Fig. 11). The species was first recorded in Estonia in 1975 (Šulcs *et al.* 1981), and has been regularly observed in the SE part of the country since then. The species' wide occurrence in the NE parts is a discovery attributable to the BMP. LC.

Boloria frigga (Thunberg, 1791): Found at 3 sites (incl. 3 out of 85 raised-bog sites) in 2 squares; 16 indiv. recorded (Fig. 11). A strict habitat specialist with recent records from 4 raised bogs in N and W Estonia. As the species has always been rare in Estonia, it is hard to make a reliable inference about the population trend. EN.

Boloria freija (Thunberg, 1791). Not recorded in the BMP. Last record is from 1947 (Viidalepp & Mikkola 2007). This former inhabitant of N and E Estonian raised bogs (Fig. 11) is now considered extinct in Estonia. RE.

Boloria titania (Esper, 1793): Found at 34 sites in 31 squares; 101 indiv. recorded (Fig. 11). The butterfly is widespread in the N half of the country but has clearly retreated from the S parts. The BMP confirmed that the species is, however, still present even in southernmost Estonia. LC.

Apatura iris (Linnaeus, 1758): Found at 81 sites in 74 squares; 143 indiv. recorded (Fig. 11). Distributed throughout the country but rarely abundant. As Petersen (1924) mentioned only a few records, an increasing trend at the scale of a century is beyond question. LC.

Apatura ilia (Denis & Schiffermüller, 1775): Found at 76 sites in 65 squares, 175 indiv. recorded (Fig. 11). With its first record from 1937, the species appears to have been resident in Estonia until late 1950s, and disappeared thereafter. A few specimens were captured in the mid-1970s, followed by another period of absence that lasted until 1995. The number of records drastically increased around the year 2000 (Kesküla 2002), and the species has been rather common since then. Its abundance appears to have decreased during recent years but, in any case, *A. ilia* is now widespread throughout the country, approximately equal in abundance to *A. iris*. LC.

Araschnia levana (Linnaeus, 1758): Found at 786 sites in 419 squares; 6000 indiv. recorded (Fig. 12). Widespread and abundant throughout the country, perhaps less common on the western islands. This species has undergone an obvious expansion: Petersen (1924) listed only a few records from the E parts of the country, and the species was still absent from W Estonia 50 years later (Šulcs & Viidalepp 1974). LC.

Vanessa cardui (Linnaeus, 1758): Found at 131 sites in 113 squares; 263 indiv. recorded (Fig. 12). A migratory species, whose abundance varies greatly among years. LC.

Vanessa atalanta (Linnaeus, 1758): Found at 217 sites in 170 squares; 449 indiv. recorded (Fig. 12). A migratory species observed yearly. LC.

Aglais io (Linnaeus, 1758): Found at 945 sites in 457 squares; 11 036 indiv. recorded (Fig. 12). One of the most abundant butterflies in the country (4th, according to BMP). Petersen (1924) considered it widespread but rare and predicted increase in abundance of the spe-

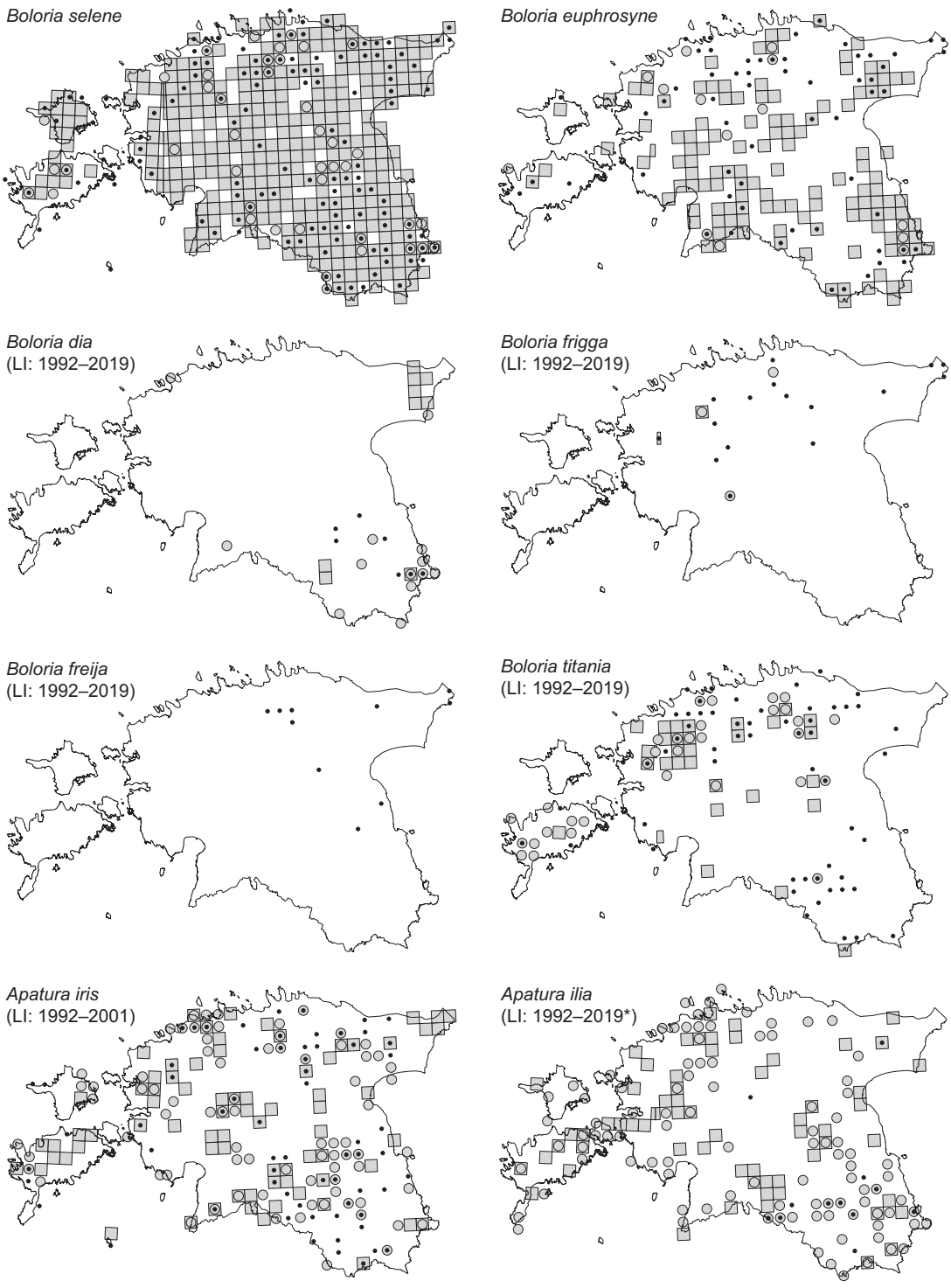

Fig. 11. Distribution of Estonian butterflies.'LI:' followed by the years indicates that distribution data were systematically collected and published in *Lepinfo* in the period indicated. * since 2012 distribution data for *A. ilia* have been collected by Lepinfo for northern Estonia (UTM squares *F*5 and north of those) only.

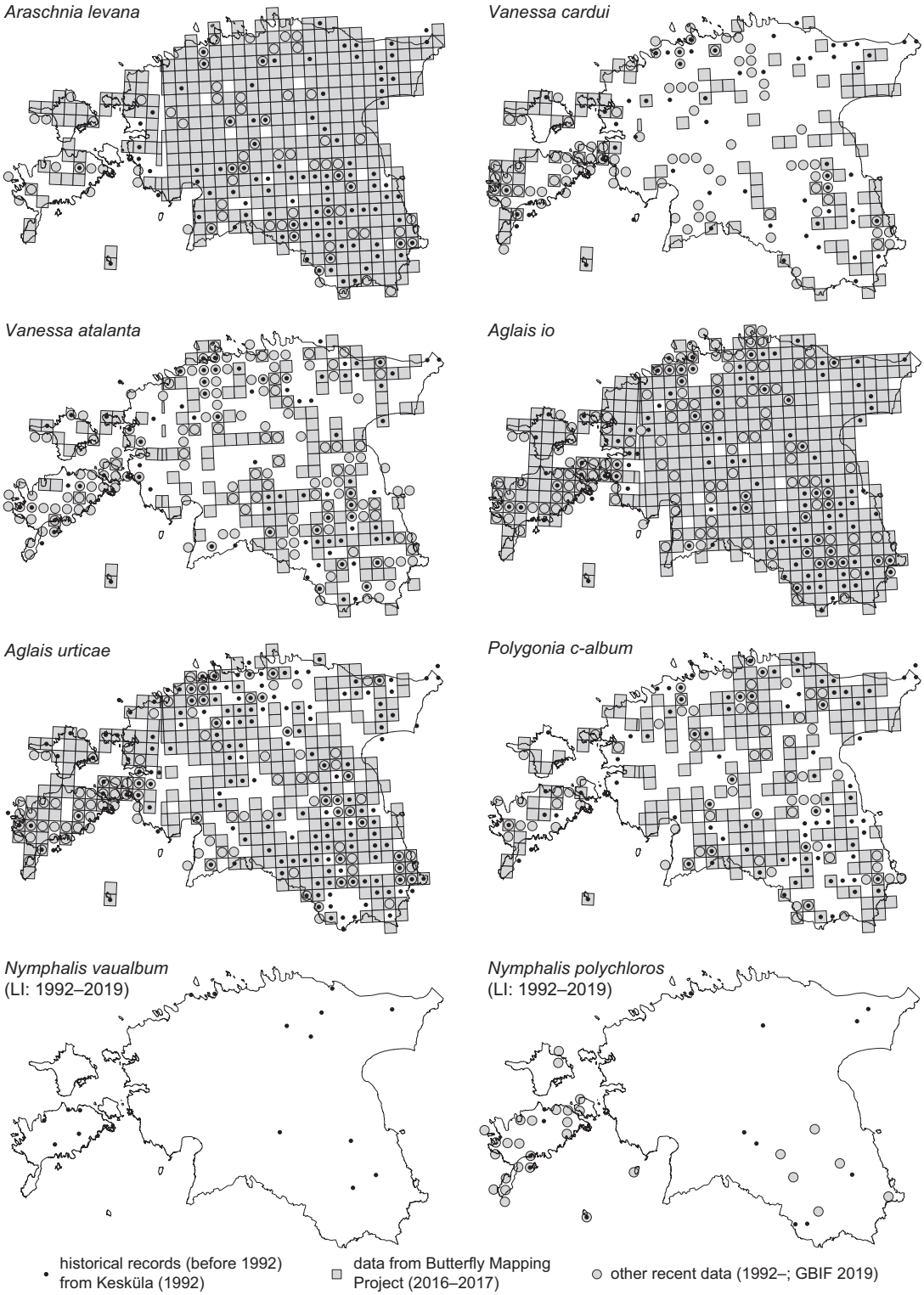

Fig. 12. Distribution of Estonian butterflies.'LI:' followed by the years indicates that distribution data were systematically collected and published in *Lepinfo* in the period indicated.

cies which took place around the mid-20th century (e.g. Veldre 1959). LC.

Aglais urticae (Linnaeus, 1758): Found at 449 sites in 313 squares; 1859 indiv. recorded (Fig. 12). Widespread and numerous throughout the country but showing decreasing trend during the last century. While Petersen (1924) considered this species the most common butterfly in the country, in the BMP it was placed on the 21st position, with the number of individuals recorded being lower than those of the top species by an order of magnitude. LC.

Polygonia c-album (Linnaeus, 1758): Found at 299 sites in 216 squares; 775 indiv. recorded (Fig. 12). Widespread and moderately numerous throughout the country. No indication of change. LC.

Nymphalis vaualbum (Denis & Schiffermüller, 1775): Not recorded during the BMP. Considered extinct in the country. The last Estonian record was from 1959 (Viidalepp 1962, Viidalepp & Remm 1996) while Petersen (1924) knew the species from a number of places, and even reported it not to have been rare in the vicinity of Tallinn (Fig. 12). RE.

Nymphalis polychloros (Linnaeus, 1758). Not recorded during the BMP. Šulcs and Viidalepp (1974) suggested that Estonia was within the northern fluctuation zone of *N. polychloros* with the species not occurring permanently in the country. During recent decades, the species was regularly present and sometimes numerous on the W Estonian islands (Fig. 12), therefore its complete absence from the BMP records was unexpected. However, it should also be considered that the BMP recording scheme may have been suboptimal for *N. polychloros*, as well as for *Nymphalis* spp. in general: these butterflies are best observed immediately after overwintering in April, a period not covered by the BMP. In contrast, the flight period of freshly eclosed individuals in July is short, and even then, the butterflies can be more easily attracted to sugar baits than be observed during transect counts. NT.

Nymphalis xanthomelas (Denis & Schiffermüller, 1775): Found at 39 sites in 34 squares; 86 indiv. recorded (Fig. 13). A species with a highly variable abundance. Likely there are few resident populations in the country but in the years of immigration events, and in the years that follow, its abundance may increase dramatically. A series of striking immigration events took place in 2012–2015, and we believe that in the years of the BMP the abundance of this species had not yet returned to its baseline level. LC.

Nymphalis antiopa (Linnaeus, 1758): Found at 67 sites in 62 squares; 117 indiv. recorded (Fig. 13). Widespread throughout the country though never abundant (*see* also a note under *N. polychloros*). No indication of change. LC.

Euphydryas aurinia (Rottemburg, 1775): Found at 74 sites in 69 squares; 307 indiv. recorded (Fig. 13). The species is not common in Estonia, but the overall distribution appears stable. Nevertheless, the suspected disappearance from the Otepää–Elva area (Martin 2012) during the recent few decades was confirmed by the BMP, and deserves attention with respect to conservation of the species. LC.

Euphydryas maturna (Linnaeus, 1758): Found at 73 sites in 68 squares; 142 indiv. recorded (Fig. 13). Its distribution seems to follow that of *Fraxinus excelsior*, the main pre-hibernation larval host plant of the species in Estonia (Lindman *et al.* 2018). Accordingly, *E. maturna* is widespread across the W parts but virtually absent in SE Estonia. The absence of BMP records from north-central Estonia (including the surroundings of Tallinn) calls for further studies of the status of the species in that area. LC.

Melitaea didyma (Esper, 1778). Not recorded during the BMP. Only three specimens have been reported from Estonia, two in 1943 (Viidalepp 1961) which we consider doubtful (*see* above), and one in 2009 (Õunap & Tartes 2014) (Fig. 13). The species is not known to have had a resident population in the country. NA.

Melitaea phoebe (Denis & Schiffermüller, 1775): Found at 3 sites in 3 squares; 8 indiv. recorded (Fig. 13). The species was first recorded in Estonia in 1955 (Reindorff 1971) and is known to occur regularly in the SE parts since then. There are two recent records

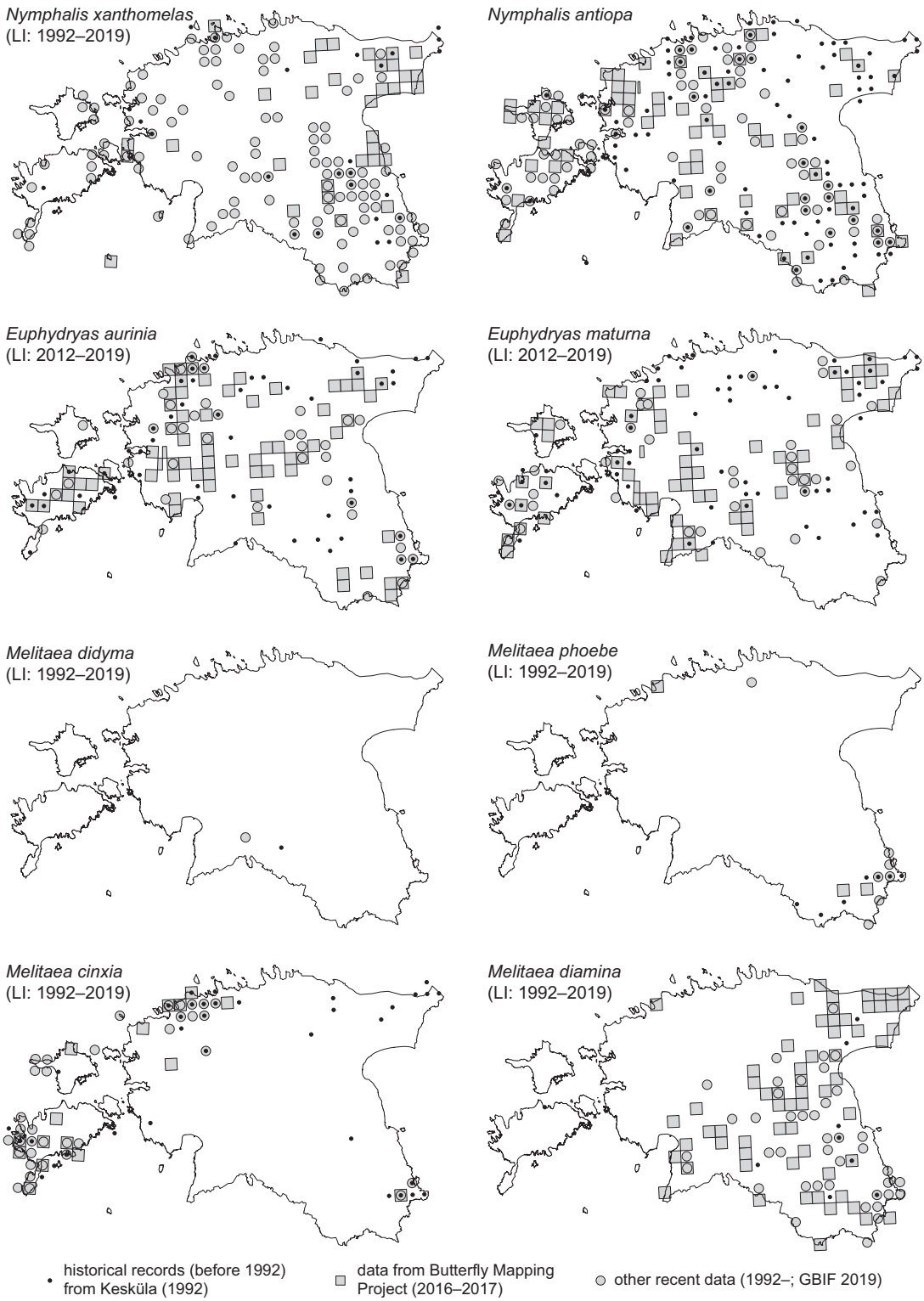

Fig. 13. Distribution of Estonian butterflies.'LI:' followed by the years indicates that distribution data were systematically collected and published in *Lepinfo* in the period indicated.

from N Estonia, the first from 2009 (Jürivete & Õunap 2011), and the second made during the BMP. LC.

Melitaea cinxia (Linnaeus, 1758): Found at 18 sites in 16 squares; 199 indiv. recorded (Fig. 13). The species inhabits calcareous meadows in the NW and on Saaremaa where it can be locally rather abundant, as well as sandy areas of SE Estonia. The species is likely extinct from the NE parts, as the most recent record from that region dates back to 1976 (GBIF 2019). EN.

Melitaea diamina (Lang, 1789): Found at 75 sites in 62 squares; 190 indiv. recorded (Fig. 13). The species is now widespread in the SE half of the country. It was first recorded in 1942 (Viidalepp 1961) and was considered rare until the first decade of the 21st century (Jürivete & Õunap 2008). The species thus underwent a clear expansion during the recent decades. LC.

Melitaea athalia (Rottemburg, 1775): Found at 578 sites in 353 squares; 3817 indiv. recorded (Fig. 14). Widespread and numerous throughout the country. No indication of change. LC.

Melitaea aurelia (Nickerl, 1850): Found at 9 sites in 9 squares; 50 indiv. recorded (Fig. 14). In Estonia, this is primarily a species of dry calcareous meadows in the west though it used to occur also in the SE parts. The most recent records from the southeast, however, date back to 2006 (Bichele & Õunap 2009), and this species may now be extinct in that part of the country. It has been considered common on the island of Saaremaa so that the relatively few records from the BMP raise concerns about the decline of the species within the short time scale. EN.

Coenonympha pamphilus (Linnaeus, 1758): Found at 262 sites in 181 squares; 1883 indiv. recorded (Fig. 14). Widespread and numerous throughout the country. No indication of change. LC.

Coenonympha tullia (Müller, 1764): Found at 21 sites (incl. 12 out of 85 raised-bog sites) in 21 squares; 53 indiv. recorded (Fig. 14). An uncommon inhabitant of various bogs. Petersen (1924) considered the species to occur 'everywhere on swampy meadows and bogs' which appears not to correspond to the current situation. Nevertheless, even nowadays this species can be locally abundant on transitional bogs, it is scarcer on raised bogs, and seldom occurs outside these habitat types. However, as there were not enough BMP study sites in habitats preferred by the species, the BMP data do not allow to draw conclusions regarding the temporal trend. LC.

Coenonympha glycerion (Borkhausen, 1788): Found at 665 sites in 416 squares; 5756 indiv. recorded (Fig. 14). Widespread and numerous throughout the country. No indication of change. LC.

Coenonympha hero (Linnaeus, 1760): Found at 163 sites in 137 squares; 701 indiv. recorded (Fig. 14). Widespread and moderately numerous throughout the country. For the ecology of the species in Estonia, *see* Tiitsaar *et al.* (2016). No indication of change. LC.

Coenonympha arcania (Linnaeus, 1760): Found at 123 sites in 77 squares; 765 indiv. recorded (Fig. 14). For many decades, the species has been rather common in SE Estonia, with an abrupt distribution boundary at the Emajõgi. During the BMP, the presence of the species outside the 'traditional' area was discovered, which is likely due to recent expansion. LC.

Lopinga achine (Scopoli, 1763): Found at 97 sites in 81 squares; 516 indiv. recorded (Fig. 14). Widespread but more common in W Estonia. For the ecology of the species in Estonia, *see* Lindman *et al.* (2013). No indication of change. LC.

Pararge aegeria (Linnaeus, 1758): Found at 18 sites in 17 squares; 36 indiv. recorded (Fig. 15). The species is not considered rare in Estonia, so that the low number of BMP records, especially from the S parts of the country, is somewhat surprising and may indicate a recent decreasing trend. On the other hand, considerable number of occurrences may have been missed as the BMP was focused on open habitats. LC.

Lasiommata maera (Linnaeus, 1758): Found at 346 sites in 262 squares; 1335 indiv. recorded (Fig. 15). Widespread and numerous throughout the country. No indication of change. LC.

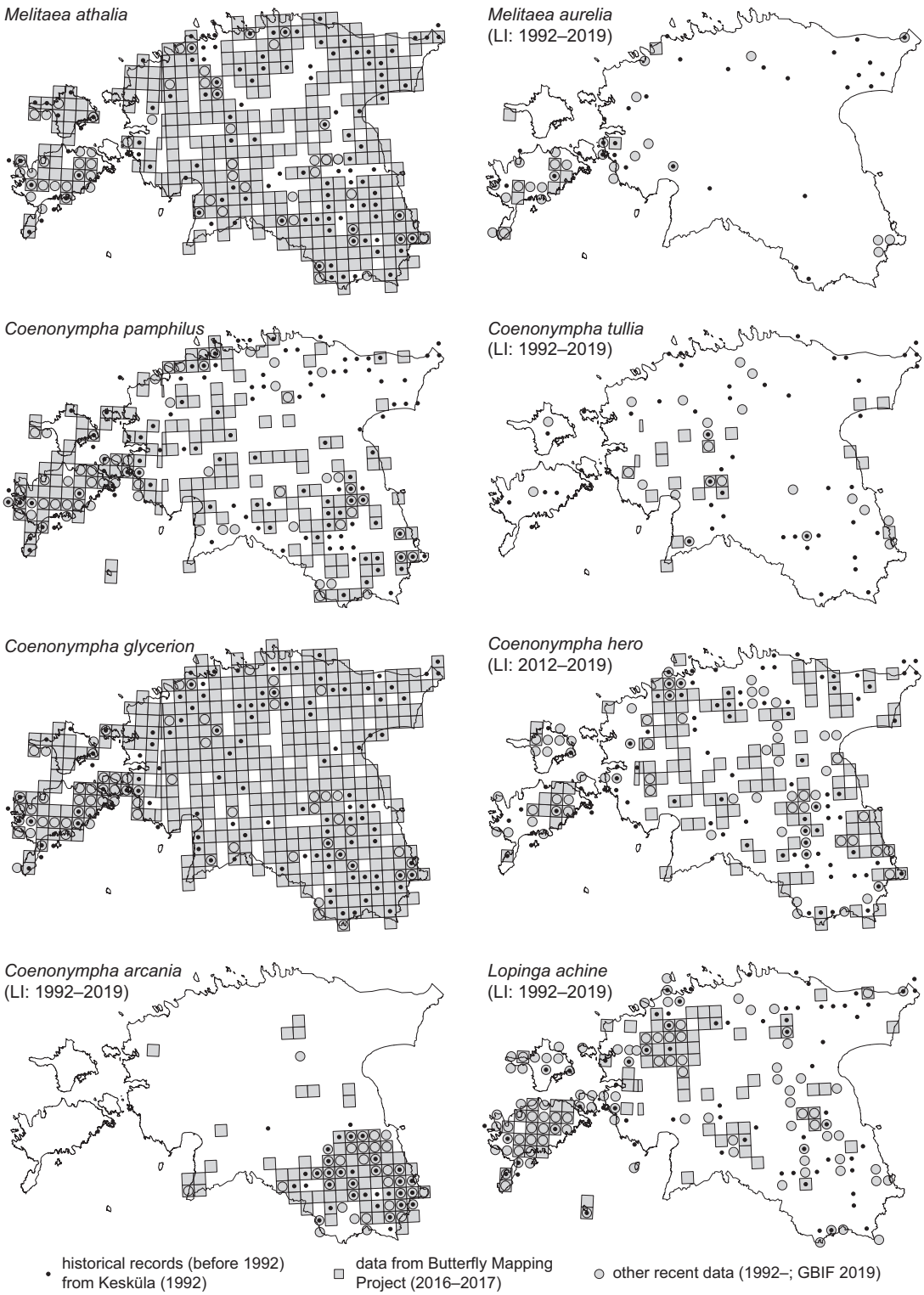

Fig. 14. Distribution of Estonian butterflies.'LI:' followed by the years indicates that distribution data were systematically collected and published in *Lepinfo* in the period indicated.

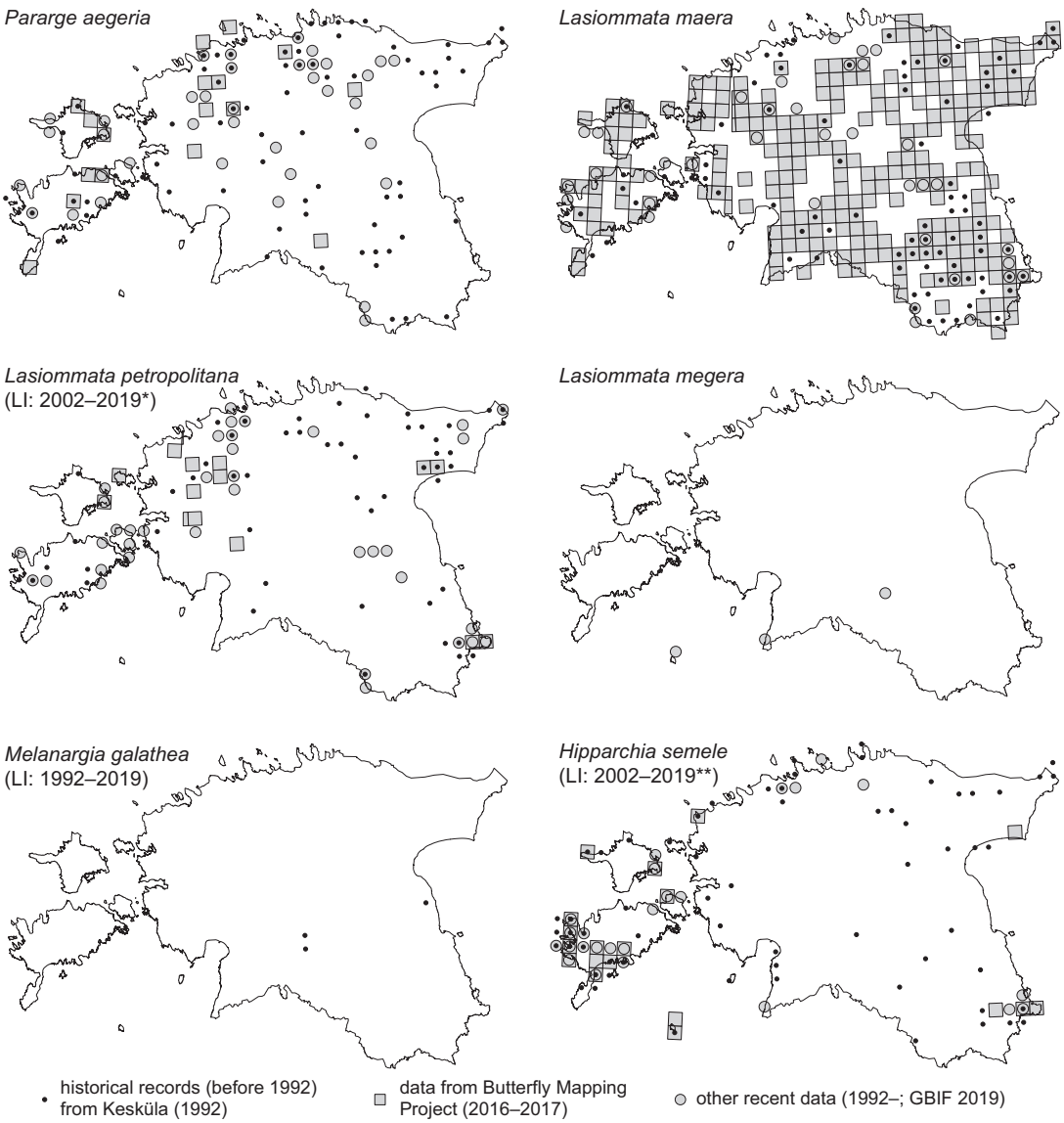

Fig. 15. Distribution of Estonian butterflies.'LI:' followed by the years indicates that distribution data were systematically collected and published in *Lepinfo* in the period indicated. * distribution data for *L. petropolitana* have been collected by Lepinfo for the areas other than western Estonia (UTM squares L*5* and east of those); ** distribution data for *Hipparchia semele* have been collected for the areas other than western Estonia (L*5* and east of those), and northern Estonia (*F*4 and south of those).

Lasiommata petropolitana (Fabricius, 1787): Found at 17 sites in 15 squares; 33 indiv. recorded (Fig. 15). Distributed in N, W and extreme SE Estonia. Even if a decreasing trend can be suspected, the evidence is insufficient to make such a conclusion. LC.

Lasiommata megera (Linnaeus, 1767). Not recorded during the BMP. The species is the most recent addition to the Estonian butterfly fauna. The first two individuals were both recorded on 8 August 2018: the first in Treimani on the SW coast of mainland Estonia (A. Truuverk pers. comm.), and the second in the northern part of the island of Ruhnu (T. Ruben pers. comm.), with a few further records made in 2019 (Fig. 15). NE.

Melanargia galathea (Linnaeus, 1758): Not recorded during the BMP. There are just three reports from Estonia, from the years 1943 and 1944 (Viidalepp 1961) which we consider doubtful (*see* above), and 1977 (Fig. 15). Here we publish the data of the most recent collection for the first time: Tõruvere (58°38´N, 27°05´E), 20.VI.1977, J. Uudelepp leg., E. Neemaru det., coll. TAMZ, specimen ID: TAMZ0112320. The species is not known to have had a resident population in Estonia. NA.

Hipparchia semele (Linnaeus, 1758): Found at 28 sites in 19 squares; 348 indiv. recorded (Fig. 15). Locally common in sandy coastal habitats. Being considered widespread by Petersen (1924), this species appears to have disappeared from the Estonian inlands, with the exception of the extreme SE parts and a few localities in the north. LC.

Oeneis jutta (Hübner, 1806): Found at 14 sites (incl. 13 out of 85 raised-bog sites) in 13 squares; 81 indiv. recorded (Fig. 16). Found exclusively on raised bogs, primarily in the E part of the country. No indication of overall change, though most likely locally extinct on a number of drained raised bogs. LC.

Hyponephele lycaon (Kühn, 1774): Found at 52 sites in 36 squares; 357 indiv. recorded (Fig. 16). Often numerous in sandy habitats on the coast, local and generally rare inland. A slight decreasing trend in the inland populations can be suspected. VU.

Aphantopus hyperantus (Linnaeus, 1758): Found at 1134 sites in 504 squares; 36 309 indiv. recorded (Fig. 16). The most widespread and most abundant butterfly according to the BMP results. No indication of change. LC.

Maniola jurtina (Linnaeus, 1758): Found at 446 sites in 305 squares; 3976 indiv. recorded (Fig. 16). Widespread and numerous throughout the country. No indication of change. LC.

Erebia embla (Thunberg, 1791): Not recorded during the BMP. This species was recorded as new to Estonia in 1937 (Šulcs & Viidalepp 1974), and few specimens have thereafter been found from the S and SE parts of the country (Fig. 16). There are also 21th century records (most recent from 2019) from SE Estonia confirming the existence of at least one small permanent population. All known Estonian specimens were recorded in odd years. EN.

Erebia ligea (Linnaeus, 1758): Found at 102 sites in 79 squares; 471 indiv. recorded (Fig. 16). The species has been considered widespread and numerous in Estonia. The scarcity of BMP records in the S half of the country may indicate a decreasing trend in this area. The absence of BMP records from the western islands must be explained by alternate-year flight of the butterfly. In particular, during the BMP, the island of Saaremaa was visited only in 2016 (Appendix 1), while *E. ligea* is more numerous in odd years. The alternate-year flight appears to be particularly evident on the islands and in the W part of the country (authors' pers. obs.). LC.

Discussion

Ninety-five out of 98 species supposedly forming resident populations in Estonia were represented among the over 180 000 individuals recorded in the course of Estonian Butterfly Mapping Project (2016–2017), in addition to two immigrants (*V. atalanta* and *V. cardui*). This indicates that the approach chosen — a semirandom preselection of study sites, as opposed to visiting previously known hotspots of butterfly diversity — still resulted in almost complete coverage of the Estonian fauna. The failure to record two of the missed resident species — *Erebia embla* and *Phengaris alcon* — was expected as these species are known to be represented in the country by one or two very small populations only and the respective sites were not among those visited during BMP. The third missing species, *Nymphalis polychloros*, is characterised by fluctuating abundance and may have been in a low phase during the BMP years, complemented by the limited suitability of the transect count method for recording *Nymphalis* spp. (*see* above). No new species for the fauna of the country were discovered in the course of BMP despite an unprecedented search effort, and the number of other 'surprising' outcomes (discussed in species accounts) remained relatively low. This indicates

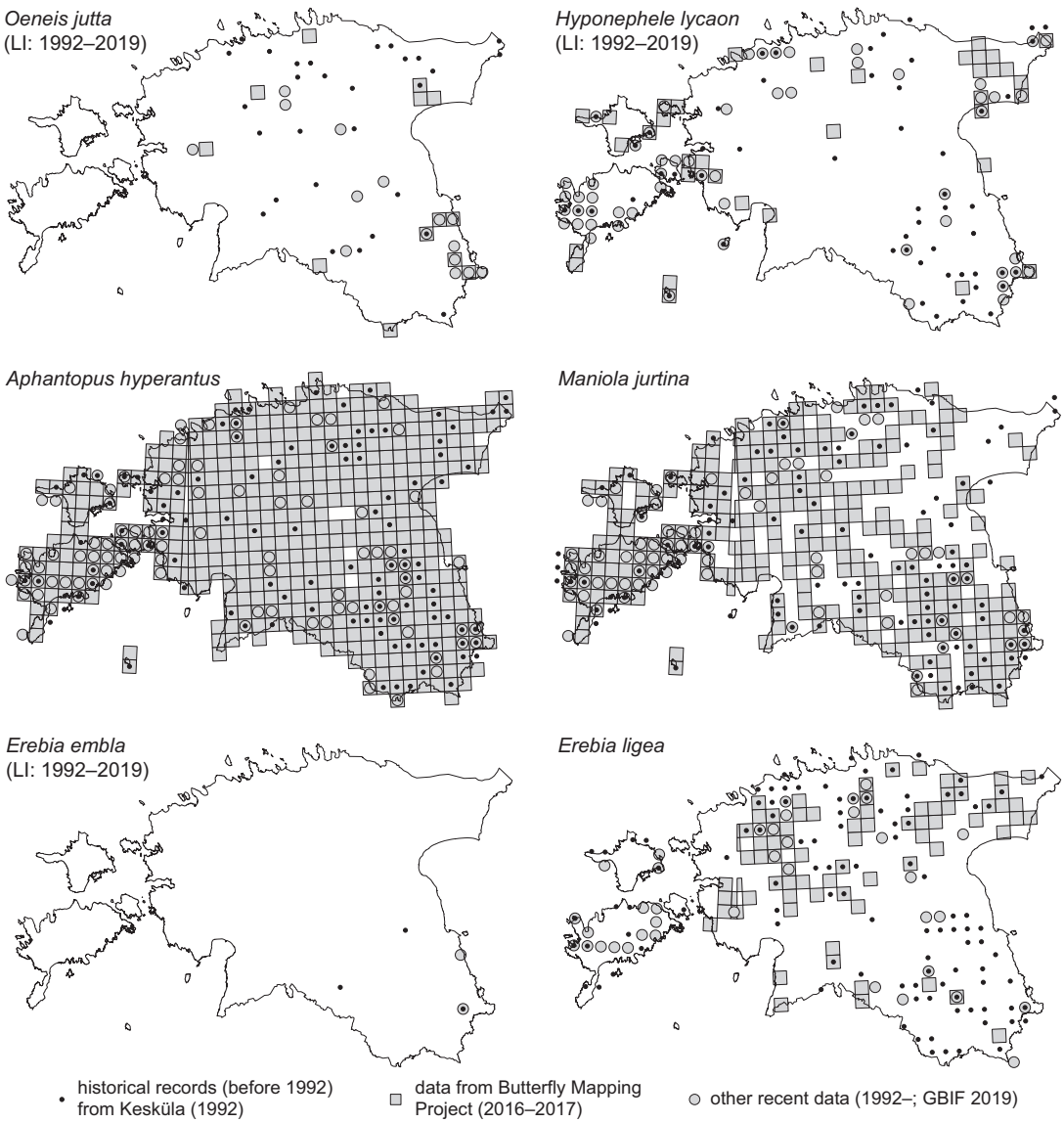

Fig. 16. Distribution of Estonian butterflies.'LI:' followed by the years indicates that distribution data were systematically collected and published in *Lepinfo* in the period indicated.

that, overall, we can consider the Estonian butterfly fauna to be well known.

The three observation rounds (focussing on early June, early July, early August) appeared to be sufficient to cover the entire phenological spectrum of Estonian butterflies. There are a few species whose adult flight peaked earlier than the first round (*Anthocharis cardamines*, *Celastrina argiolus*, *Callophrys rubi*), but despite this, all these species were encountered in considerable numbers. The only species flying 'too late' is *Thecla betulae*. In order to also cover these outliers, the number of recording rounds may be increased to four in similar studies in the future.

We see the primary value of the accumulated data set as providing a reference point for future studies. The methodology of site selection and field observations is repeatable, so any similar project conducted sometime in the coming years will provide quantitative evidence of

changes in distribution, abundance and species composition of Estonian butterflies. As there is no comparable data set from earlier years, we deliberately abstain from any quantitative analyses comparing the present and the past of the Estonian butterfly fauna. Nevertheless, there are major unquestionable changes in distribution patterns and abundance of particular species. Even if comparing verbal statements of the earliest sources with the quantitative data of BMP is inevitably not straightforward, we are confident that changes in species abundance that exceed an order of magnitude cannot fail to be revealed by this method. Changes which appear reliable were discussed in species accounts above and are summarized below.

Since Petersen published his faunistic works roughly a century ago (1902, 1924), at least 14 species can now be added to the list of butterfly species having populations in Estonia, with BMP confirming their resident status. These include *Pyrgus serratulae*, *Leptidea juvernica*, *Hamearis lucina*, *Lycaena dispar*, *L. tityrus*, *Cupido argiades*, *Phengaris alcon*, *Limenitis camilla*, *Issoria lathonia*, *Boloria dia*, *Apatura ilia*, *Melitaea phoebe*, *M. diamina* and *Erebia embla*. The newcomer status of *M. phoebe* and *P. alcon* is nevertheless difficult to assess due to the small sizes of the current populations (see above); if the situation has been similar also earlier, the species may have been overlooked. On the other hand, while the northern taiga species *E. embla* was not known in Petersen's times, its newcomer status appears highly unlikely and the species was most probably overlooked by Petersen.

A number of additional species, in particular *Parnassius mnemosyne*, *Heteropterus morpheus*, *Thymelicus sylvestris*, *Lycaena alciphron*, *Satyrium ilicis*, *Argynnis laodice*, *Araschnia levana* and *Coenonympha arcania* have considerably extended their distribution within the country. For at least *H. morpheus*, *B. dia, M. diamina* and *C. arcania*, the results of BMP have played a crucial role in revealing the range expansion that has occurred during recent decades, and that had not been fully assessed before (*see* Õunap & Tartes 2014). Furthermore, comparing the results of BMP with the assessments of abundance found in the literature allows us to conclude that *Aglais io* and *Thymelicus lineola* have become more numerous within the last century, and *Apatura* spp., *Limenitis camilla* and *M. diamina* over the course of the last few decades. The same appears to be the case for the just recently recognized *Leptidea juvernica* (Bichele 2005).

As for the reasons behind the described positive changes, climate warming appears to be the likely driver for at least *H. morpheus*, *T. sylvestris*, *L. tityrus*, *L. alciphron*, *C. argiades*, *L. camilla*, *Apatura* spp. and *B. dia*. These species have been continuously distributed in the areas south of Estonia, and the northward shift of the northern limit of their range — most prominent in the recent few decades — is paralleled elsewhere in the region (e.g. Pöyry *et al.* 2009, Betzholtz *et al.* 2013). The colonisation of Estonia by *A. levana* and *L. dispar* is a part of a positive trend across the entire ranges of these species (Betzholtz *et al.* 2013, Park *et al.* 2014, Lindman *et al.* 2015). To explain the expansion of the distribution of *P. mnemosyne* in Estonia, it has been proposed that this species has probably benefitted from an increase in suitable habitats like semi-natural grassland patches on the banks of rivers surrounded by forests or riparian tree lines (Meier *et al.* 2005). Such habitats are suitable for both adults of *P. mnemosyne*, and the food plant of their monophagous larvae, *Corydalis solida* (Meier *et al.* 2005).

Three formerly resident butterfly species can be considered extinct in Estonia. Two of the extinct species were last recorded in the mid-20th century. One of them, *Nymphalis vaualbum*, shows a negative trend across Europe (Kudrna *et al.* 2011, van Swaay *et al.* 2011). Another one, *B. freija*, may have suffered from irrigation of raised bogs in the mid-20th century. Nevertheless, given the early flight period of the species (May) and poor accessibility of its raised-bog habitat, it cannot be excluded that there may still be overlooked populations of *B. freija* in Estonia. The third species now considered extinct, *Glaucopsyche alexis*, had very small populations in the extreme south-eastern part of the country, which have most likely vanished due to habitat degradation. Nevertheless, *G. alexis* has also disappeared from Latvia within the last few decades (N. Savenkov pers. comm.), which suggests broader drivers behind this decline.

Lycaena virgaureae, *Phengaris arion*, *Pseudophilotes vicrama*, *Boloria titania*, *Argynnis*

niobe, *Melitaea cinxia*, *M. aurelia*, *Hipparchia semele* and *Erebia ligea* are the species for which a range contraction has been observed. *E. ligea* and *B. titania* are boreal forest species, which, in Estonia, are close to the southern limit of their lowland distribution in Europe (Kudrna *et al.* 2011). BMP revealed that these species have become less common in southern but not in northern Estonia, consistent with the expected negative impact of climate warming on such species. Notably, the rest of these declining species are specialists of dry meadows, a habitat type that is rapidly decreasing in Estonia due to abandonment of traditional agricultural practices (Pärtel *et al.* 1999, Helm *et al*. 2006, Sang *et al.* 2010). The results of BMP should thus be seen as a serious warning signal indicating that respective changes in landscape structure have started to affect biological diversity. We cannot currently propose a reason why *L. virgaureae* has declined in southern rather than northern Estonia; neither can we contribute to explaining the decline in the abundance of *Aglais urticae* (observed also elsewhere in Europe, Gripenberg *et al.* 2011, Audusseau *et al.* 2017).

Notably, there is no obvious decline in raised-bog species — *Colias palaeno*, *Boloria eunomia*, *B. frigga*, *B. aquilonaris*, *Oeneis jutta* — which constitute the majority of the northern faunal element among Estonian butterflies. It appears likely that these species are primarily connected to their specific (northern) habitat rather than directly to climatic parameters, and the negative effects of climate warming will thus affect them through habitat degradation, and therefore with a considerable delay. On the even more positive side, the results of BMP confirm the conclusions of ecological studies (Viljur & Teder 2016, 2018), which show that current forestry practices are comfortably compatible with the requirements of forest butterflies (M.-L. Viljur *et al*. unpubl. data), while the managed forest landscapes provide alternative habitats for most grassland species.

In summary, we believe that as an outcome of a systematic country-scale butterfly mapping project, we have been able to provide a quantitative characterization of the current state of the Estonian fauna, which is usable as a reference point for any similar projects in the future. Comparing the results with historical records, we conclude that the Estonian butterfly fauna has moderately changed on a century-long timescale, with positive trends in species' distribution and abundance dominating over negative ones. Some, but not all, of these changes can be associated with ongoing climate warming, while the primary conservation concern is the decline of dry-meadow specialists. We therefore suggest that maintenance and restoration of seminatural meadows is what conservation practices should be focused on.

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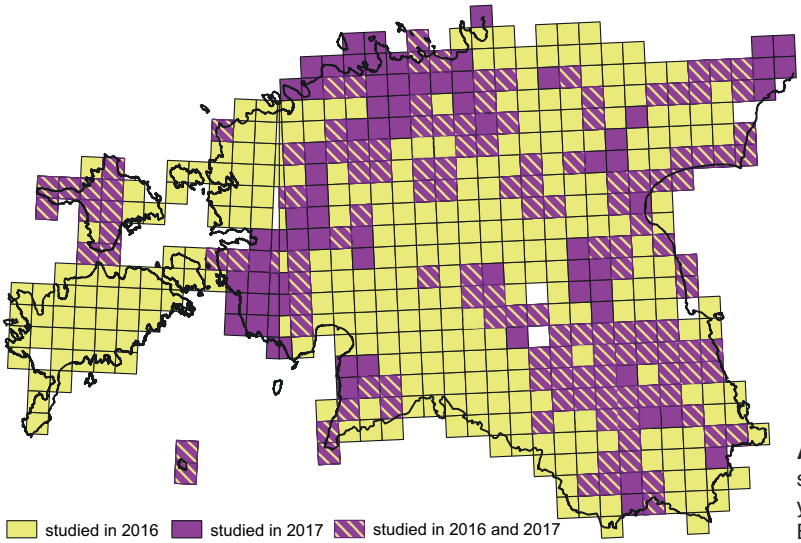

Appendix 1. 10 × 10 km UTM squares studied in one of the years (2016 or 2017) of the BMP, or both of them.

Appendix 2. Species for which proof was required either in the form of a photograph (ph) or a voucher specimen (indiv.). Photographs instead of specimens were requested for protected or rare species.

Boloria freija (ph or indiv.), *Boloria frigga* (ph), *Carcharodus floccifera* (ph or indiv.), *Coenonympha hero* (ph), *Colias crocea* (ph or indiv.), *Erebia embla* (ph), *Euphydryas maturna* (ph), *Euphydryas aurinia* (ph), *Fabriciana niobe* (ph or indiv.), *Hyponephele lycaon* (ph or indiv.), *Iphiclides podalirius* (ph or indiv.), *Lasiommata petropolitana* (ph or indiv.), *Leptidea* spp. (indiv.), *Lopinga achine* (ph), *Lycaena dispar* (ph), *Lycaena helle* (ph or indiv.), *Lysandra bellargus* (ph or indiv.), *Lysandra coridon* (ph or indiv.), *Melanargia galathea*, *Melitaea aurelia* (ph or indiv.), *Melitaea didyma* (ph or indiv.), *Melitaea phoebe* (ph or indiv.), *Nymphalis polychloros* (ph or indiv.), *Nymphalis vaualbum* (ph or indiv.), *Nymphalis xanthomelas* (ph or indiv.), *Parnassius mnemosyne* (ph), *Phengaris alcon* (ph), *Phengaris arion* (ph), *Plebejus* spp. (indiv.), *Pseudophilotes vicrama* (ph), *Pyrgus serratulae* (ph or indiv.), *Satyrium ilicis* (ph or indiv.), *Scolitantides orion* (ph or indiv.), *Thymelicus sylvestris* (indiv.).

Appendix 3. Recorded species arranged in order of decreasing abundance. Numbers of sites, numbers of 10 × 10 km UTM squares, and total numbers of individuals are given for each species.

Species	Number of sites	Number of UTM squares	Number of individuals
Aphantopus hyperantus	1134	504	36309
Pieris napi	1074	485	17359
Gonepteryx rhamni	1034	481	12526
Aglais io	945	457	11036
Thymelicus lineola	973	472	10439
Brenthis ino	817	438	9374
Plebejus argus	328	228	7968
Argynnis paphia	742	422	6485
Araschnia levana	786	419	6000
Coenonympha glycerion	665	416	5756
Speyeria aglaja	686	403	4943
Boloria selene	596	372	4537
Maniola jurtina	446	305	3976
Aporia crataegi	541	325	3921
Melitaea athalia	578	353	3817
Ochlodes sylvanus	670	404	3188

continued

Appendix 3. Continued.

Species	Number of sites	Number of UTM squares	Number of individuals
Polyommatus amandus	556	369	2519
Cupido minimus	147	103	2178
Callophrys rubi	269	200	2033
Coenonympha pamphilus	262	181	1883
Aglais urticae	449	313	1859
Plebejus idas	138	117	1806
Boloria euphrosyne	171	132	1435
Fabriciana adippe	334	244	1394
Lasiommata maera	346	262	1335
Colias palaeno	242	174	1128
Polyommatus icarus	288	208	1127
Leptidea juvernica	323	245	1005
Thymelicus sylvestris	204	160	932
Heteropterus morpheus	259	177	853
Cyaniris semiargus	311	232	815
Polygonia c-album	299	216	775
Coenonympha arcania	123	77	765
Argynnis laodice	190	153	718
Pieris brassicae	306	235	708
Coenonympha hero	163	137	701
Aricia artaxerxes	249	195	664
Anthocharis cardamines	245	188	653
Carterocephalus palaemon	233	187	642
Pieris rapae	191	156	576
Lopinga achine	97	81	516
Pyrgus malvae	199	161	472
Erebia ligea	102	79	471
Celastrina argiolus	230	183	452
Vanessa atalanta	217	170	449
Agriades optilete	121	97	419
Leptidea sinapis	143	119	384
Hyponephele lycaon	52	36	357
Hipparchia semele	28	19	348
Lycaena tityrus	66	57	342
Hamearis lucina	61	50	331
Papilio machaon	164	137	315
Euphydryas aurinia	74	69	307
Lycaena phlaeas	123	102	300
Lycaena virgaureae	83	69	295
Carterocephalus silvicola	153	135	290
Cupido argiades	114	89	270
Vanessa cardui	131	113	263
Boloria aquilonaris	60	48	250
Limenitis camilla	115	104	250
Lycaena dispar	131	108	227
Melitaea cinxia	18	16	199
Melitaea diamina	75	62	190
Eumedonia eumedon	87	78	184
Apatura ilia	76	65	175
Limenitis populi	86	76	158
Apatura iris	81	74	143
Euphydryas maturna	73	68	142
Hesperia comma	36	36	123
Nymphalis antiopa	67	62	117
Lycaena hippothoe	73	70	111

continued

Appendix 3. Continued.

Species	Number of sites	Number of UTM squares	Number of individuals
Boloria titania	34	31	101
Parnassius mnemosyne	17	17	92
Nymphalis xanthomelas	39	34	86
Boloria eunomia	15	14	82
Oeneis jutta	14	13	81
Erynnis tages	29	26	74
Lycaena alciphron	34	32	61
Boloria dia	11	9	60
Coenonympha tullia	21	21	53
Melitaea aurelia	9	9	50
Issoria lathonia	23	22	48
Pyrgus alveus	30	30	44
Pararge aegeria	18	17	36
Lasiommata petropolitana	17	15	33
Phengaris arion	4	3	30
Satyrium ilicis	12	8	17
Satyrium w-album	9	9	17
Boloria frigga	3	2	16
Thecla betulae	12	12	14
Fabriciana niobe	4	3	11
Satyrium pruni	9	9	10
Melitaea phoebe	3	3	8
Colias hyale	4	4	5
Favonius quercus	2	2	2
Carcharodus floccifera	1	1	1
Pseudophilotes vicrama	1	1	1

Appendix 4. Threatened butterflies in Estonia according to the 2017 evaluation report (first author's unpubl. data). The regional evaluation criteria met are presented as codes (*see* IUCN 2012b) followed by explanations.

Species	Conservation status	Code	Explanation
Phengaris alcon	Critically endangered	CR EN C2(i); D	Very small population size estimated from host-plant and egg counts, and no subpopulation is estimated to include more than 50 mature individuals.
Phengaris arion	Endangered	EN EN B2b(iii)	Continuing decline in species area of occupancy together with decline in habitat area and quality.
Fabriciana niobe	Endangered	EN EN B2b(iii)	Continuing decline in species area of occupancy together with decline in habitat area and quality.
Melitaea aurelia	Endangered	EN EN B2b(iii)	Continuing decline in species area of occupancy together with decline in habitat area and quality.
Boloria frigga	Endangered	EN VU D2	Population with very restricted area (less than 20 km^2), with very few localities known. Local estimates increased because species is decreasing or lacking in neighbouring countries, and migration likelihood between populations is extremely low.

continued

Appendix 4. Contimued.

Species	Conservation status	Code	Explanation
Melitaea cinxia	Endangered	EN EN B2b(iii)	Continuing decline in species area of occupancy together with decline in habitat area and quality.
Erebia embla	Endangered	EN VU D2	Population with very restricted area (known area less than 10 ha) with only one current population known. Local estimates increased because species is decreasing or lacking in neighbouring countries and migration likelihood between populations is extremely low.
Pseudophilotes vicrama	Vulnerable	VU A2b; D2	Population-size index decreased and populations were very restricted in area and number of known populations is low.
Pyrgus serratulae	Vulnerable	VU D2	Restricted population area with very small number of known populations (fewer than five).
Hyponephele lycaon	Vulnerable	VU EN A2b; B2b(iii)	Observed population-size index reduction during the last 10 years together with decreasing habitat area and quality.
Erynnis tages	Near threatened	NT LC	Habitat quality and area is decreasing but there is sufficient information about the changes in the area of occupancy. Species is decreasing but not enough to be qualified as vulnerable or threatened.
Colias hyale	Near threatened	NT VU D2	Species estimated to be vulnerable due to restricted area (less than 20 km^2) and fewer than five localities known; however as migration from the south is common category was lowered.
Nymphalis polychloros	Near threatened	NT LC	Species is decreasing but not enough to be qualify as threatened.