REVIEW

Updated occurrence and bionomics of potential malaria vectors in Europe: a systematic review (2000–2021)

Michela Bertola[1], Matteo Mazzucato[1], Marco Pombi[2]* and Fabrizio Montarsi[1,2]

Abstract

Despite the eradication of malaria across most European countries in the 1960s and 1970s, the anopheline vectors are still present. Most of the malaria cases that have been reported in Europe up to the present time have been infections acquired in endemic areas by travelers. However, the possibility of acquiring malaria by locally infected mosquitoes has been poorly investigated in Europe, despite autochthonous malaria cases having been occasionally reported in several European countries. Here we present an update on the occurrence of potential malaria vector species in Europe. Adopting a systematic review approach, we selected 288 papers published between 2000 and 2021 for inclusion in the review based on retrieval of accurate information on the following *Anopheles* species: *An. atroparvus*, *An. hyrcanus* sensu lato (s.l.), *An. labranchiae*, *An. maculipennis* sensu stricto (s.s.), *An. messeae/daciae*, *An. sacharovi*, *An. superpictus* and *An. plumbeus*. The distribution of these potential vector species across Europe is critically reviewed in relation to areas of major presence and principal bionomic features, including vector competence to *Plasmodium*. Additional information, such as geographical details, sampling approaches and species identification methods, are also reported. We compare the information on each species extracted from the most recent studies to comparable information reported from studies published in the early 2000s, with particular reference to the role of each species in malaria transmission before eradication. The picture that emerges from this review is that potential vector species are still widespread in Europe, with the largest diversity in the Mediterranean area, Italy in particular. Despite information on their vectorial capacity being fragmentary, the information retrieved suggests a re-definition of the relative importance of potential vector species, indicating *An. hyrcanus* s.l., *An. labranchiae*, *An. plumbeus* and *An. sacharovi* as potential vectors of higher importance, while *An. messeae/daciae* and *An. maculipennis* s.s. can be considered to be moderately important species. In contrast, *An. atroparvus* and *An. superpictus* should be considered as vectors of lower importance, particularly in relation to their low anthropophily. The presence of gaps in current knowledge of vectorial systems in Europe becomes evident in this review, not only in terms of vector competence but also in the definition of sampling approaches, highlighting the need for further research to adopt the appropriate surveillance system for each species.

Keywords: *Anopheles maculipennis* s.l., *Anopheles hyrcanus* s.l., *Anopheles plumbeus*, *Anopheles superpictus*, Malaria transmission, Vector ecology, Vector behavior, Vector competence, Distribution map

Background

Despite major efforts of researchers and funding institutions to tackle malaria, the most deadly of known parasitic diseases, the global burden of this life-threatening disease remains dramatic. However, great strides in

*Correspondence: marco.pombi@uniroma1.it

[2] Dipartimento di Sanità Pubblica e Malattie Infettive, Università di Roma "Sapienza", P.le Aldo Moro 5, 00185 Roma, Italy
Full list of author information is available at the end of the article

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combatting malaria were made in the last century, with the disease eradicated from several regions of the world, in particular in temperate areas, thanks to joint efforts at scientific, social and political levels. This disease, caused by five different species of *Plasmodium* parasites, remains a major healthcare challenge in tropical regions, particularly in sub-Saharan Africa, where *Plasmodium falciparum* and *Plasmodium vivax* are responsible for most of the morbidity.

Despite the eradication of malaria across most European countries in the 1960s and 1970s, the anopheline vectors of this disease are still present in Europe [1]. To date, most of the malaria cases reported in Europe have been infections acquired in endemic areas by travelers. However, the possibility of acquiring malaria by locally infected mosquitoes has been poorly investigated, despite autochthonous malaria cases occasionally being reported in several European countries [2].

In terms of malaria vectors in Europe, while several publications and reviews are available on the presence, density and distribution of *Anopheles* species competent for malaria transmission, most contain detailed information on countries where malaria is endemic [3–5]. To help researchers study malaria transmission, maps of the global distribution of malaria vector species have been created [6–9], most of which focus on tropical endemic areas.

Several potential *Anopheles* malaria vectors have been identified at various locations throughout Europe, but data on these species are less structured and often collected within the framework of monitoring plans focused on other mosquito species. Precise data on the presence of *Anopheles* mosquitoes is limited, with complete information available only for some European countries.

A comprehensive picture of *Anopheles* distribution at the European level was provided in three reviews [10–12]. Subsequent to the publication of these reviews, the last study that reviewed the occurrence and geographic distribution of the dominant vector species of human malaria (DVS; with "dominant" defining a vector species that has been identified as the main, dominant or important vector in at least one region) was published in 2010 by Sinka et al. [4] within the framework of the Malaria Atlas Project (MAP) [13]. Recent publications, mostly driven by the use of the more novel molecular diagnostic techniques applied in recent years [14], provide the basis for a novel critical review of the occurrence of *Anopheles* species, in particular a review of those species not included in the category of DVS but potentially involved in malaria transmission that have not previously been considered.

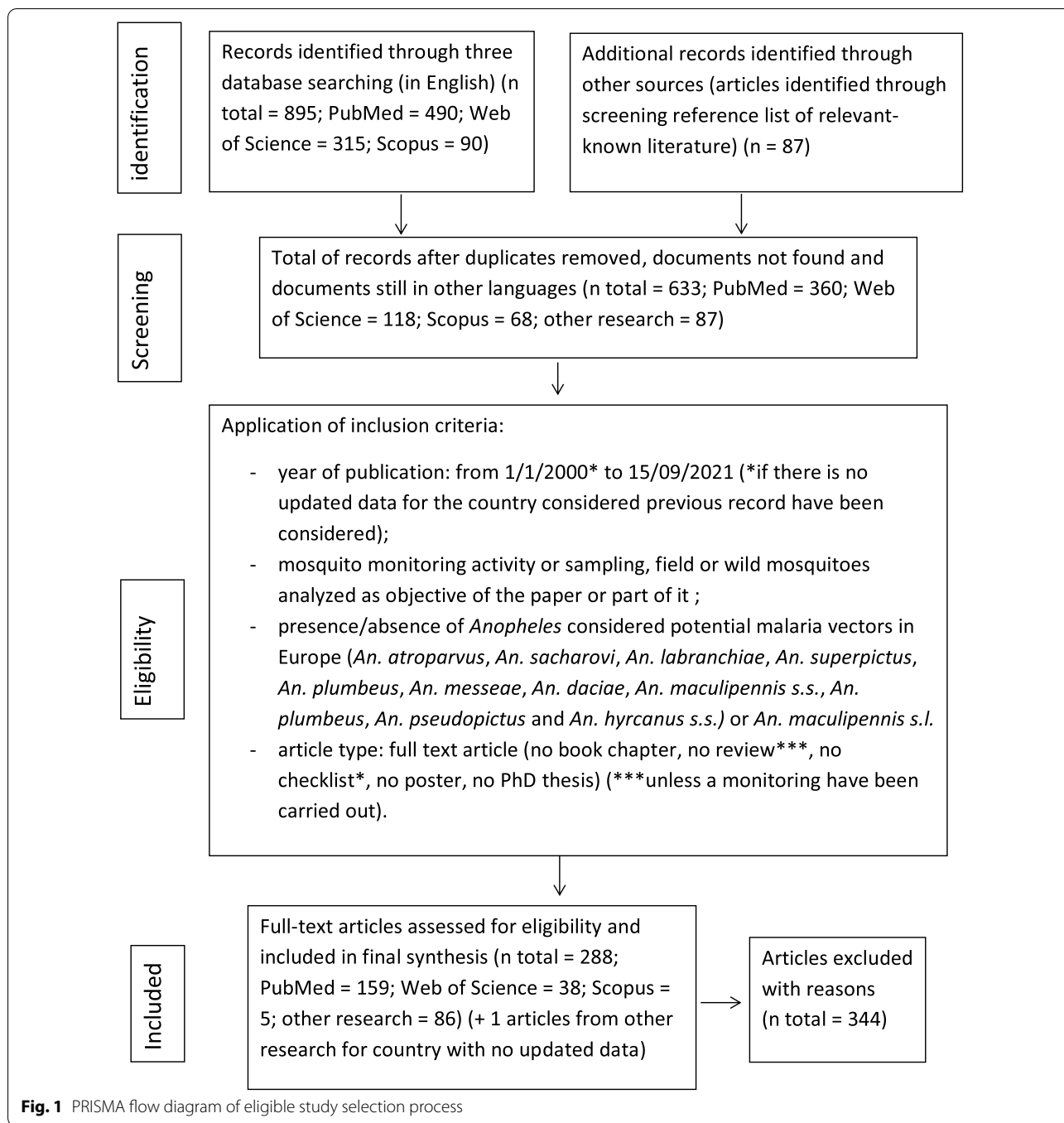We present here an updated systematic review on the occurrence of potential mosquito malaria vectors in Europe, with a specific focus on studies published in the last 20 years, with the aim to provide a critical revision of the species that should be considered of major importance for local malaria transmission. The accurate selection of peer-reviewed literature available since 2000 has allowed the retrieval of information on the occurrence of *Anopheles* target species in European countries, highlighting the areas of major interest, and critical descriptions of major aspects of species ecology, behavior and vector competence. The most important *Anopheles* species potentially involved in local transmission events are critically reviewed in terms of their epidemiological relevance and presence in Europe.

Methods

The information retrieved from published literature for this review was collected following the reporting guidelines of the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) Statement for systematic reviews and Meta-Analyses [15] (Fig. 1).

Eligibility criteria of literature search

Across the world, 41 mosquito species (and species complexes) are considered to be "main" or "potential" human malaria vectors [16]. Based on two major reviews [4, 16], the DVS considered in this review are *Anopheles atroparvus*, *Anopheles sacharovi*, *Anopheles labranchiae*, *Anopheles messeae/daciae* and *Anopheles superpictus*. Additionally, we included *Anopheles plumbeus* and European species belonging to the Hyrcanus Group (hereafter referred to as *Anopheles hyrcanus* sensu lato [s.l.]) in this review based on the findings of recent studies indicating their potential role as malaria vectors in some geographic areas. Lastly, *Anopheles maculipennis* sensu stricto (s.s.) is also taken into consideration; although this species is considered to be a secondary malaria vector, its wide distribution and local abundance make it a potential malaria vector in some areas. The criteria of selection of species are based on their occurrence, abundance, biology, evidence or suspicion of involvement in malaria transmission (also at a local level) and vectorial competence. To retrieve a more complete set of data, the taxonomic definition *An. maculipennis* s.l. was also searched. Some authors formally state that *An. daciae* is a new species [17], while others consider it to be a genetic polymorphism within *An. messeae* taxon [18]. Taking into account that this question is still being debated and that data on each taxon are still scarce and difficult to unequivocally address, we did not separate these two taxa in this review, and refer to them as *An. messeae/daciae.* In addition, *An. hyrcanus* is a taxonomic group of closely related *Anopheles* species that are difficult to distinguish, some of which are considered to be malaria vectors. Due

Identification

Records identified through three database searching (in English) (n total = 895; PubMed = 490; Web of Science = 315; Scopus = 90)

Additional records identified through other sources (articles identified through screening reference list of relevant-known literature) (n = 87)

Screening

Total of records after duplicates removed, documents not found and documents still in other languages (n total = 633; PubMed = 360; Web of Science = 118; Scopus = 68; other research = 87)

Eligibility

Application of inclusion criteria:

- year of publication: from 1/1/2000* to 15/09/2021 (*if there is no updated data for the country considered previous record have been considered);
- mosquito monitoring activity or sampling, field or wild mosquitoes analyzed as objective of the paper or part of it ;
- presence/absence of *Anopheles* considered potential malaria vectors in Europe (*An. atroparvus*, *An. sacharovi*, *An. labranchiae*, *An. superpictus*, *An. plumbeus*, *An. messeae*, *An. daciae*, *An. maculipennis s.s.*, *An. plumbeus*, *An. pseudopictus* and *An. hyrcanus s.s.*) or *An. maculipennis s.l.*
- article type: full text article (no book chapter, no review***, no checklist*, no poster, no PhD thesis) (***unless a monitoring have been carried out).

Included

Full-text articles assessed for eligibility and included in final synthesis (n total = 288; PubMed = 159; Web of Science = 38; Scopus = 5; other research = 86) (+ 1 articles from other research for country with no updated data)

Articles excluded with reasons (n total = 344)

Fig. 1 PRISMA flow diagram of eligible study selection process

to the uncertainty in the description of these species in the literature, we refer to them here as *An. hyrcanus* s.l. [19, 20].

In this review we focus on malaria vectors in Europe, but we also include additional countries based on a compromise between the geographical and political borders of Europe. Therefore, we have included Turkey, Azerbaijan, Georgia and Armenia, as well as European Russia, in this review, but excluded Kazakhstan. Data on Cyprus have been collected referring to the whole island (not considering political boundaries). Islands not located in the Mediterranean Sea and overseas territories are excluded. Countries with a limited surface, such as Lichtenstein, Andorra, San Marino, Vatican City State and the Principality of Monaco were also not included, since no data are available for any of these.

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Due to the heterogeneity in sampling methods and geographic details of occurrence available in the retrieved literature, data on mosquito abundance are not taken into account, and only presence/absence data are included.

In order to represent the most current possible representation of *Anopheles* vector presence, only studies published between 2000 and 2021 were considered. However, articles published within this time frame but reporting samplings made prior to the study period were included in the review. Articles published before 2000, if available, were taken into account only for countries for which more recent literature was not available.

Only full-text articles providing original research and data were screened; book chapters, conference abstracts, checklists, posters, PhD theses, among others (gray literature) were excluded. Reviews were also excluded, unless original data were reported.

Information sources

Three online databases (PubMed [21], Web of Science [22] and Scopus [23]) were searched for relevant scientific literature. Additionally, cited references cited in the retrieved articles were checked (other research).

Search strategy

The systematic research and review were performed on studies published from January 2000 to September 2021. The search was conducted in English using the following keywords: "*Anopheles*" and "*messeae*" or "*maculipennis*" or "*daciae*" or "*messeae/daciae*" or "*atroparvus*" or "*labranchiae*" or "*sacharovi*" or "*superpictus*" or "*pseudopictus*" or "*hyrcanus*" or "*plumbeus*", in association with any one of the 45 countries considered: Albania, Armenia, Austria, Azerbaijan, Belarus, Belgium, Bosnia-Herzegovina, Bulgaria, Croatia, Cyprus, Czech Republic, Denmark, Estonia, Finland, France, Georgia, Germany, Greece, Hungary, Iceland, Ireland, Italy, Kosovo, Latvia, Lithuania, Luxembourg, Macedonia, Malta, Moldova, Montenegro, Netherlands, Norway, Poland, Portugal, Romania, Russia, Serbia, Slovakia, Slovenia, Spain, Sweden, Switzerland, Turkey, Ukraine, UK.

Study selection

As the first step, one of the authors of this review performed the literature search, removing duplicates (same articles obtained more than once during different searches), full-text documents not published in English and separating the retrieved articles into two groups according to the year of publication (before or after 2000). As the second step, the same author, who had read all the retrieved articles, performed the eligibility assessment; only those articles which met the above-mentioned

eligibility criteria were selected and used in this review. Then, a second author checked and repeated the process to evaluate agreement within the papers screened by the first author. Disagreements between authors were resolved by a third author. At the end of the study selection process, a final list of selected articles was obtained.

Data collection process

Following the eligibility assessment, a database reporting the following information from each selected article was created: bibliographical details (title, authors, journal, year of publication, DOI and database source), European countries considered, species occurrence, monitoring/field activity, year of monitoring activity, identification method(s) and sampling technique(s) (specifying if outdoor or indoor) (see Additional file 1).

In particular, adult mosquito capture methods were classified as: (i) active manual (aspiration, use of nets); (ii) mechanical visual (traps using visual attractants such as light, colors, shapes); (iii) mechanical olfactory (traps using olfactory attractants, such as CO_2, olfactory lures or water); (iv) human-baited (human landing catches or human-baited traps); (v) animal-baited (animal-baited traps). Only one capture method for larval collection is defined, namely dipping/hand collection; larvae or eggs collected by ovitraps are also specified separately.

Information on the ecology and behavior of the potential malaria vectors was also extracted for each species. In particular, breeding sites and feeding behavior were summarized in categories and displayed in tables. This review does not include any information relating to insecticide resistance since it is a topic not well addressed for the European *Anopheles* species.

After the selection process, two authors separately read all of the articles and checked whether all of the information had been correctly extracted. The other two authors double-checked and verified the accuracy of the information reported. Any disagreements between reviewers were resolved.

Geographical analysis

Geo-referenced data reported in the maps (Figs. 2–10) were classified into the three categories according to their availability: (i) GPS coordinates (of each collection site); (ii) area-zone (when multiple sites were sampled in a specific area or the name of this area was mentioned); (iii) country (when the geographic information was not specified for the country sampled).

Data on the area/zone of EU member countries, candidate countries and members of the European Free Trade Association are classified according to the Nomenclature of Territorial Units for Statistics (NUTS), which has three levels (NUT1, NUTS2, NUTS3) [24]. This classification
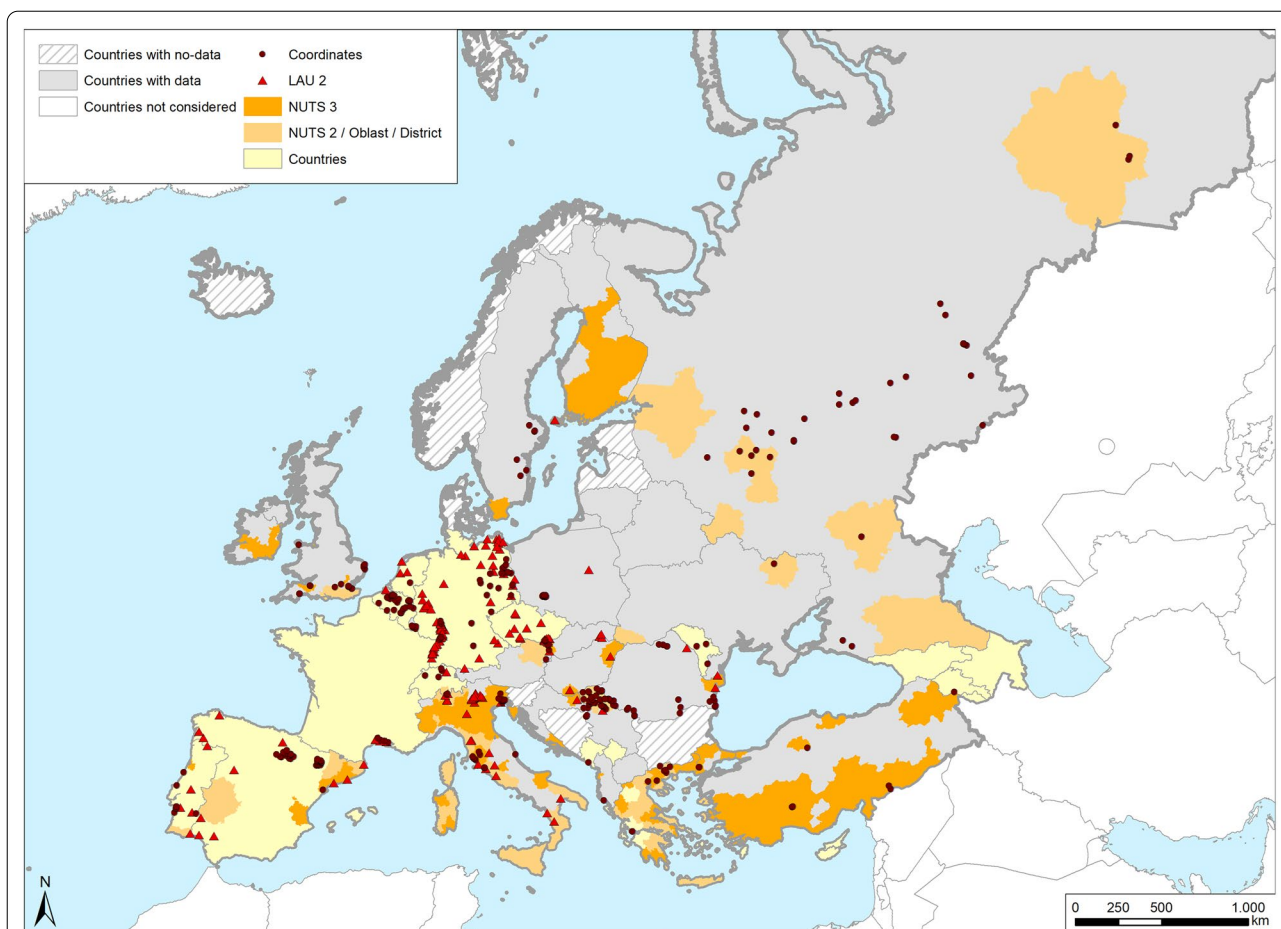
Fig. 2 Occurrence map of potential malaria vector species in Europe at different geographical levels (see legend at upper-left of figure) according to retrieved literature (January 2000–September 2021). *Abbreviations*: LAU, Local Administrative Units; NUTS 1, 2 3, Nomenclature of Territorial Units for Statistics levels 1, 2, 3, respectively; Oblast, alternative Nominal code for Russia and Ukraine

establishes a correspondence between the NUTS levels and the national administrative units. Local Administrative Units (LAU) were also used when it was possible to trace the municipality of the collection and circumscribe a more precise area within NUTS3 level. In cases where the areas involved different territorial units, they have been split into single territorial units to better show data in maps.

For countries with no NUTS classification (Armenia, Azerbaijan, Kosovo, Moldova, Montenegro and Cyprus), the widest geographic level was conservatively adopted (country level). For Russia and Ukraine, the Nominal Code named Oblast has been used as an alternative to NUTS classification. It was not possible to find the Nominal Code of the Republic of Dagestan (Russia); therefore, we enlarged the area to the North Caucasus Federal District and that Nominal Code was used.

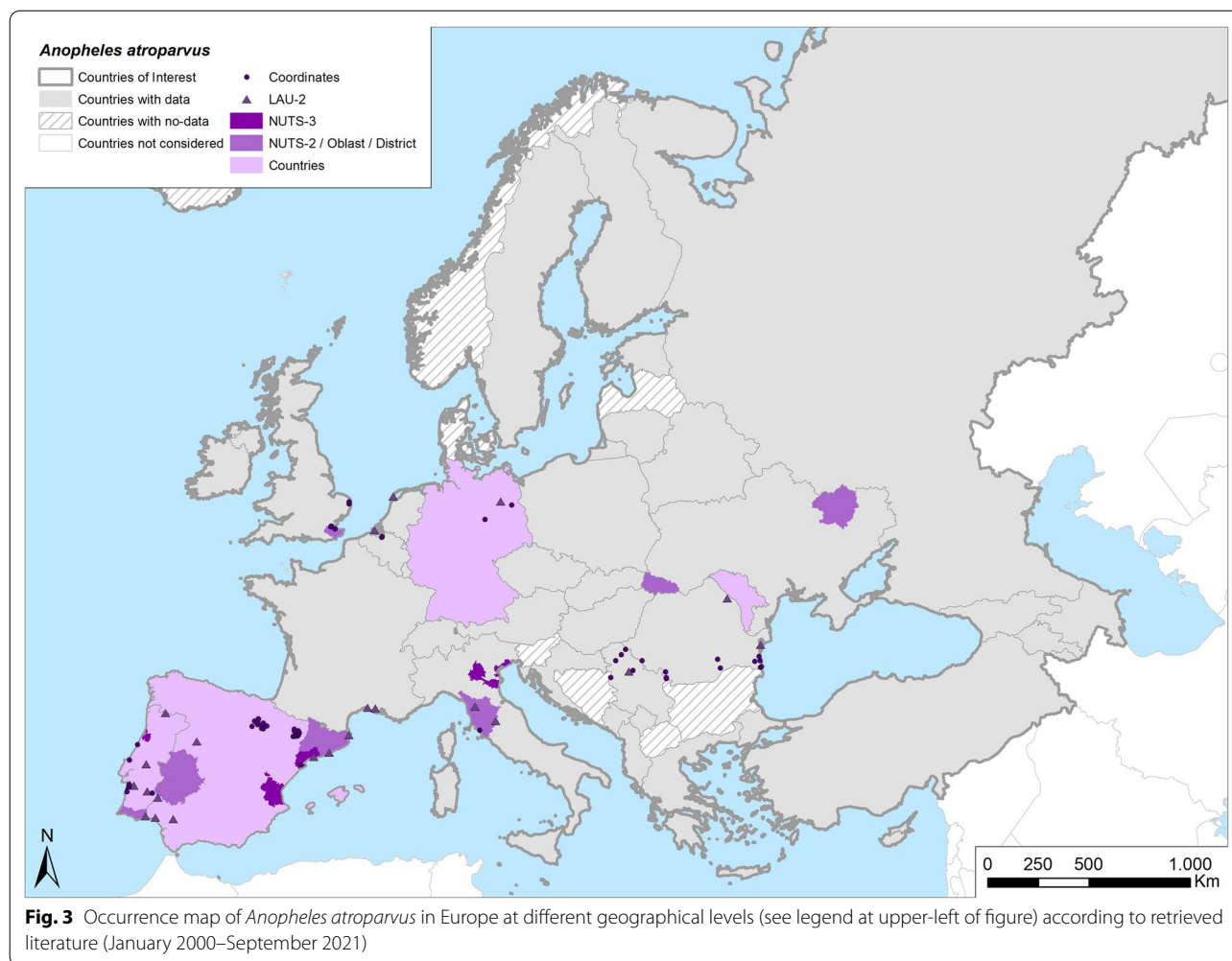When the presence of an *Anopheles* species has not been assigned to a specific site, all of the sites monitored were considered to be negative for that species (marked as Not Assigned "NA" Additional file 1), and the species occurrence reported at an upper geographical level.

Based on the above-mentioned classification, we created a European occurrence map for all potential malaria vector species (Fig. 2) and for each species separately (Figs. 3–10) based on the retrieved literature.

Maps and spatial data manipulation were carried out using ESRI ArcMap (ArcGIS Desktop: Release 10.5.1; Environmental Systems Research Institute, Redlands, CA, USA; copyright 1999–2017).

Data items and risk of bias in individual studies
Articles with unclear or questionable information were excluded; for example, articles on the occurrence of potential malaria vectors not supported by data. Only articles containing original data are recorded in the database. Therefore, articles reporting modeling based on data obtained from other studies were not included.

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Fig. 3 Occurrence map of *Anopheles atroparvus* in Europe at different geographical levels (see legend at upper-left of figure) according to retrieved literature (January 2000–September 2021)

Summary of extracted data

The search of the three databases resulted in the identification of 982 publications (Fig. 1), 490 in PubMed, 315 in Web of Science and 90 in Scopus, with subsequent review of the citations from retrieved articles identifying a further 87 studies. Of these, 633 papers (531 published after 2000 and 102 published before 2000) remained after the removal of duplicate studies and articles not published in English.

Of the 531 articles published after 2000, 288 fulfilled the inclusion criteria; the other publications were discarded due to: (i) no potential malaria vectors found in the monitoring activity of the considered country; (ii) no original data presented in the study; (iii) studies focused on other topics and/or presentation of data/monitoring activity was unclear. Of the 102 full-text articles published before 2000, only one fulfilled the inclusion criteria; for the other 101 articles, more recent data were available for the country considered.

The occurrence of potential malaria vectors in European countries is shown in Fig. 2 and summarized in Table 1; in 33 of the 45 screened European countries, at least one potential malaria vector was reported. The largest amount of data came from Italy (32 references), which is the only country reporting the presence of all of the *Anopheles* species investigated in this review. In contrast, only one or two studies were reported for 12 countries, in particular from countries in the Eastern part of Europe. Data from Belarus, Estonia and Lithuania reported the presence of specimens belonging to the *An. maculipennis* complex. No data were found for Bosnia-Herzegovina, Bulgaria, Denmark, Iceland, Latvia, Macedonia, Malta, Norway and Slovenia.

Anopheles plumbeus was the most recorded species and was found in 29 European countries; however, this species was generally reported in low numbers, within the framework of entomological surveys focused on other mosquito species. Among the other targeted

Anopheles, An. messeae/daciae and *An. maculipennis* s.s. are widespread in Europe (found in 21 and 22 countries, respectively), with the former particularly present in central and northern Europe. Findings on *Anopheles hyrcanus* s.l. and *An. atroparvus* are scattered across Europe (detected in 16 and 12 countries, respectively). As already reported in the literature, the presence of *An. sacharovi* and *An. superpictus* in south-eastern Europe was confirmed; similarly, the least prevalent of the mosquito species studied here, *An. labranchiae*, was reported only in Romania, Italy,and Corsica (France) (Table 1).

Specifically, *Anopheles* target species were found in 54.9% of the 1925 geographic records retrieved in the systematic review. *Anopheles messeae/daciae* was the most reported of these($n = 383$, 36.3%), followed by *An. maculipennis* s.s. ($n = 365$, 34.6%) and *An. sacharovi* ($n = 204$, 19.3%). The least prevalent species were *An. superpictus* and *An. labranchiae* ($n = 33$, 3.1% and $n = 27$, 2.6%, respectively) (Additional file 1).

Information retrieved on the collected samples indicated that adult mosquito catches was performed in 161 studies, larval/pupal collections in 35 studies and a combination of egg, larvae and adult collections were performed in 93 studies (Additional file 1).

Sampling methods were described in 278 of 288 papers, and the most common sampling method reported among all studies was adult mosquito catches using traps baited with CO_2, octenol or other lures (mechanical olfactory method; 115/254, 45.3% of studies). Only 28.8% of the 278 articles selected for inclusion in this review reported samplings planned specifically for *Anopheles* collection; the others referred to monitoring activities for detection of other mosquito species or surveillance planning for arboviral diseases. Considering only those papers which specifically aimed at human malaria vector surveillance and/or collection, the most used method to collect *Anopheles* species was manual collection (40/80, 50%) (Additional file 1).

Molecular identification was reported in 94 articles (32.5% of the total), with the primary aim to identify the species belonging to the *An. maculipennis* complex. Molecular diagnostics were also used to identify *An. plumbeus* and *An. hyrcanus* s.l. (2 and 4 records, respectively). In terms of the technique/method applied, the use of PCR methodology targeting the internal transcribed spacer 2 (ITS2) of ribosomal DNA was the most used approach in our dataset and was applied in 81/94 studies. Less commonly used methods included assays on other gene targets, such as fragments of the mitochondrial cytochrome oxidase I (*cox1*) gene (23 records), *28S* ribosomal DNA (3 records) or other genes.

Updates on the occurrence and bionomics of the potential vector species

Based on the information retrieved from systematic review of the three databases, in the following sections we provide an update of the occurrence and bionomics of each potential malaria vector species investigated in this review. For each species, we make a critical comparison: the data acquired from recent references screened in this review are summarized (Tables 2 and 3) and compared with information reported in the literature before 2000.

Anopheles atroparvus Van Thiel 1972
Occurrence
Anopheles atroparvus is widely distributed in Europe, with a distribution ranging from Portugal to the UK and Ukraine (Table 1; Fig. 3). Based on the data presented in this systematic review, this potential malaria vector is still abundant with medium–high densities in the Iberian Peninsula (for which it was historically considered the main malaria vector) and along the coastal region of northern Europe, in confirmation with older literature records [10, 11]. In Portugal, *An. atroparvus* is still reported throughout the country but particularly in the south and central areas [25, 26], with a spatial distribution pattern overlapping previously recorded malarial transmission areas [27]. In contrast, its occurrence is now sporadic in Mediterranean regions: in Italy, it was recorded in scattered sites of northern and central Italy [28–32]; in France, its occurrence is reduced as compared to the 1940s and 1950s [33, 34]. It has been suggested that one or more factors may have affected its current presence, such as changing land use, pollution, use of control methods (e.g. insecticides or predatory fishes in rice fields), lack of suitable larval habitats and feeding and resting sites [35, 36]. *Anopheles atroparvus* also shows a marked decrease in occurrence in central European countries: it has not been recorded since 2000 in the Czech Republic [37, 38] and Slovakia [39, 40], but is still present in Germany [41–44].

Breeding sites
Anopheles atroparvus has been traditionally described as a species more tolerant to salinity as compared to the other species of the complex (*An. maculipennis* s.l.), with a preference for brackish water breeding sites. However, it has also been reported in freshwater larval habitats, such as temporary pools, puddles, irrigation channels, river margins and rice fields. The retrieved literature contained reports of this species still being found in

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coastal areas, confirming the link with habitats characterized by a certain degree of salinity, in particular along the coast of Portugal, the Netherlands and Germany [27, 43–46]. The current occurrence of *An. atroparvus* seems also to be related to the presence of water supplies for agricultural purposes, which is particularly abundant in rice-growing areas; according to the retrieved data, in the absence of mosquito control activities rice crops were strongly colonized by this species [26, 46–48]. Irrigation channels are the breeding sites where *An. atroparvus* larvae were most frequently reported, followed by rice fields and large water basins (e.g. lagoons, marshes, swamps), both permanent and temporary, containing brackish or freshwater. Interestingly, in one study *An. atroparvus* larvae were also found in used tires [49]. This species was generally recorded in rural sites, away from populated areas [50, 51] but some authors reported its occurrence also near human settlements [36] (Table 2).

Resting/overwintering behavior

Anopheles atroparvus is reported to hibernate as adult females and is known to have a different overwintering behavior as compared to other species of *An. maculipennis* s.l. It has been described to occasionally feed on blood if the shelters were relatively warm, but without egg production [4]. No other recent observations were found regarding this behavior, but it was assumed that its occurrence might be related to the presence of suitable winter resting sites where winter feeding is still possible, such as farms and animal shelters/nests [35, 44].

Feeding behavior

Anopheles atroparvus has been considered to be zoophilic or more specifically mammalophilic [80], with anecdotal reports of feeding events on humans [52]. This statement is in contrast with the definition of this species as a major malaria vector in some areas. For this reason, recent studies have attempted to clarify this aspect. Brugman et al. [53–55] reported the collection of a small number of *An. atroparvus* females during human landing catches conducted in the UK. Human blood was also found in a single field-collected female [56], while most studies have reported collections of mosquitoes that fed on a wide range of farming or wild animals [56–58]. Noteworthy, three articles reported detecting mosquitoes that had several blood meals on birds (chickens, stove doves and 1 blackbird) [54, 59, 60]. Little evidence is available before 2000 that clarified if *An. atroparvus* is endo- or exo-phagic, and only a single recent study

reported that this species fed on animals located outdoors using human-made shelters for indoor resting after feeding [61] (Table 3).
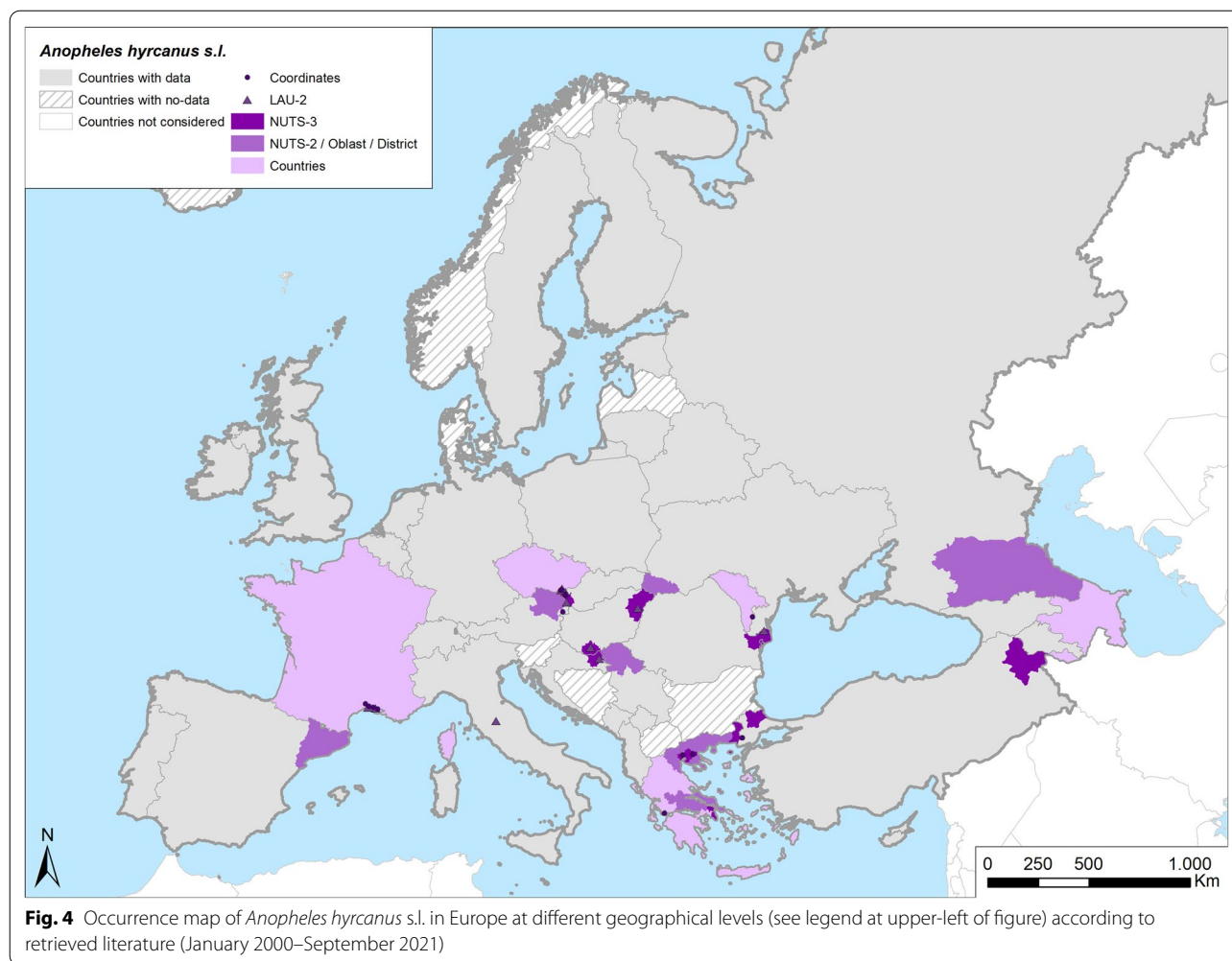
Vector competence

Few older studies investigated the vector competence of *An. atroparvus* for tropical *Plasmodium*, but in all of these studies the authors concluded that this species was unable to transmit tropical strains of both Asian and African *Plasmodiium falciparum* [62–65], while in the past it was competent in supporting European strains [66]. However, this species has been demonstrated to be competent for non-local *Plasmodium vivax* and *Plasmodium malariae* strains [64]. In addition, it has been speculated that *An. atroparvus* was involved as a vector in an autochthonous case of *Plasmodium ovale* that occurred in central Spain, although the possibility of an airport malaria case was also considered due to the proximity of the patient's residence to two international airports [67] (Table 4). In conclusion, all of the recent findings confirm that, given the mostly zoophilic nature of *An. atroparvus*, its role as a potential malaria vector can be considered low (Table 5).

Anopheles hyrcanus **s.l.**

Anopheles hyrcanus is considered to be a mosquito group that includes about 30 species distributed throughout the Palearctic and Oriental regions. In the last few years, the classification of these species has been subjected to debate. *Anopheles hyrcanus* s.s. Pallas, 1771 and *An. pseudopictus* Grassi, 1899 were formerly considered to be two distinct species occurring in Europe [19], but results from more recent studies based on genetic analyses suggest that *An. hyrcanus* s.s. and *An. pseudopictus* actually belong to the same taxon [20]. Therefore, we refer to *An. hyrcanus* s.l. when describing the bionomic features of this mosquito.

Occurrence

In France, *An. hyrcanus* s.l. is still as abundant as in the past, and it is currently considered to be the main malaria vector species [30, 33, 34, 68–70]. In Turkey, this species has been well described only in the last few years [20, 71–73]. Several studies, particularly those conducted after 2000, had the specific aim of identifying *An. hyrcanus* s.l., notably studies in Croatia, Hungary, Austria, Czech Republic and Slovakia [74]. A single study also reported the presence of *An. hyrcanus* s.l. in the Dagestan Lowland of Russia [75] (Table 1; Fig. 4).

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Fig. 4 Occurrence map of *Anopheles hyrcanus* s.l. in Europe at different geographical levels (see legend at upper-left of figure) according to retrieved literature (January 2000–September 2021)
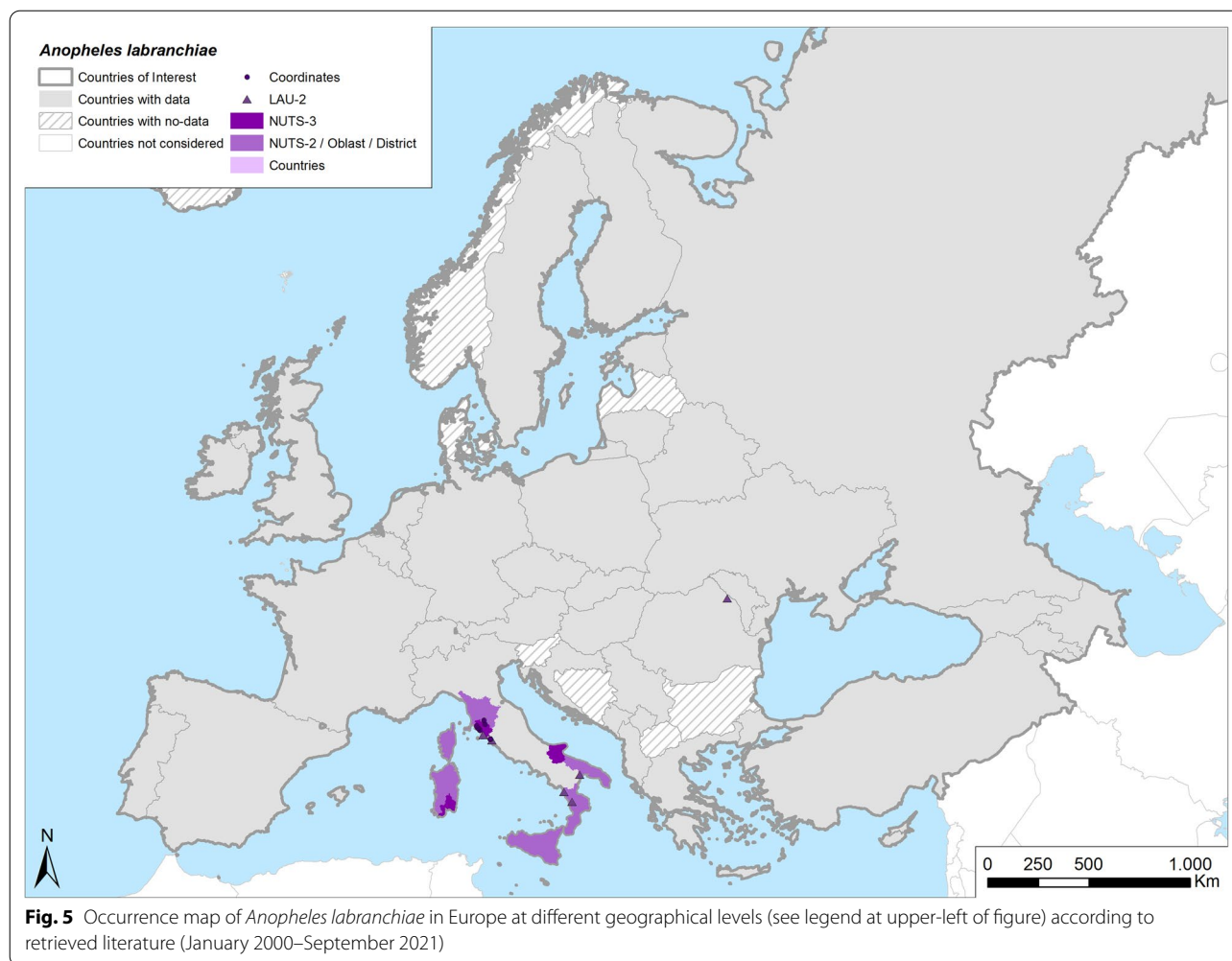
Breeding sites

Traditionally, the preferred breeding sites for larval development in *An. hyrcanus* s.l. have been reported to be sun-heated stagnant water bodies rich in aquatic vegetation and vertical structures, such as reeds (e.g. floodplains and marshes) [76]. The same sites were reported in the articles extracted in this systematic review, in particular swamps, medium-large ponds and rice fields (Table 2).

High densities of *An. hyrcanus* s.l. were reported in the Camargue (France), where rice fields are predominant and considered to be the main breeding sites for this species [33, 34, 68, 70, 77, 78]. In particular, Tran et al. [77] reported that large populations of *An. hyrcanus* s.l. were frequently associated with rice-growing areas. However, in the same study, the authors also indicated that "larvae were also reported in other biotopes, such as reed beds and marshes with *Scirpus* […] this result is of great

importance in explaining the presence of this species in the area even when rice paddies are dry (end of summer and autumn)". In agreement with this evidence, *An. hyrcanus* s.l. larvae reported in countries of central and southeastern Europe were found mainly in large water collections, such as pools, fishponds and swamps [37, 79–82].

Resting/overwintering behavior

Anopheles hyrcanus s.l. adults are exophilic, with outdoor resting sites during the day. Gadzhieva [75] made detailed observations on the resting behavior of this mosquito, noting that females remained in indoor sites (houses and cowsheds) only for the day following the blood meal, while males and females at different physiological stages rested longer outdoors among the vegetation. In particular, the resting behavior of *An. hyrcanus* s.l. was

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Fig. 5 Occurrence map of *Anopheles labranchiae* in Europe at different geographical levels (see legend at upper-left of figure) according to retrieved literature (January 2000–September 2021)

influenced by environmental humidity; consequently, it is a species for which the proximity of the breeding sites is linked to the hygrophilous vegetation.

Diapausing females were observed to mainly exploit natural shelters, including clefts in the ground, grasses and reed bushes, while indoor-resting specimens were rarely observed [83].

Feeding behavior

Anopheles hyrcanus s.l. has historically been described as strictly mammalophilic, with a high degree of anthropophily. This behavior is confirmed by several recent studies that performed human landing catches and used animal baited traps [33, 68, 70, 71]. In particular, Ponçon et al. [33] reported that "*Anopheles hyrcanus* presented a huge anthropophily with spectacular aggressiveness on humans: during this study, scientists underwent massive attacks from females of this species". Moreover, Aldemir

et al. [71] reported that this mosquito exhibited similar anthropophilic biting patterns both indoors and outdoors. Recent information also indicates that this species can be collected by traps baited with birds, although the numbers are very low compared to the number of mosquitoes caught in other traps baited with other animals, such as horses [68, 70] (Table 3).

Vector competence

In terms of its role as a vector, some species of the *An. hyrcanus* group are considered vectors of malaria parasites. In a number of studies, the authors assumed *An. hyrcanus* s.l. to be involved in malaria transmission, specifically in northern Afghanistan and in the Camargue region of France [19, 33, 84, 85]. In the countries of Central Asia, *An. hyrcanus* s.l. was considered to be a secondary malaria vector. Regarding vector competence, *An. hyrcanus* s.l. can easily be infected with *P. vivax*, while there is no evidence that it can transmit

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P. falciparum [83]. The only recent, but questionable information for Europe is from a study carried out in Austria, in which a pool of *An. hyrcanus* s.l. was found to be molecularly positive for *Plasmodium* sp. [86]. In conclusion, the potential role of this species in malaria transmission can be considered to be high (Tables 4, 5). As such, this species should be the focus of study in the contexts of high mosquito densities (e.g. at the end of summer) when, in association with its high anthropophily, it may potentially be involved in local transmission events.

Anopheles labranchiae Falleroni, 1926
Occurrence

The extracted articles identified the typical distribution of *An. labranchiae* in Europe to be the Mediterranean and the warmest areas of Europe [4, 87] (Table 1; Fig. 5). Its present distribution is similar to that reported in the past, with this species still common in central Italy [31–35]. In addition, two studies [88, 89] reported its presence also in Sardinia, but with a more limited occurrence than in the past. In Corsica, a single survey conducted in 2008 [87] indicated that *An. labranchiae* maintains its former abundance. In addition to these findings, Boccolini et al. reported the presence of *An. labranchiae* in southern Italy and in new, hilly areas northeastward, indicating a potential expansion of the species area to new ecological settings [90, 91]. *Anopheles labranchiae* was found for the first time in Romania [92] as larvae in a natural pond. The molecular analysis of collected specimens showed a similarity of 96% to specimens from Italy, suggesting that this species was imported from that country, taking into consideration that many inhabitants of the area worked in Italy and came back to Romania during the summer.

Breeding sites

The biology of *An. labranchiae* has been described in several old and often not easily accessible scientific articles,

Fig. 6 Occurrence map of *Anopheles maculipennis* s.s. in Europe at different geographical levels (see legend at upper-left of figure) according to retrieved literature (January 2000–September 2021)

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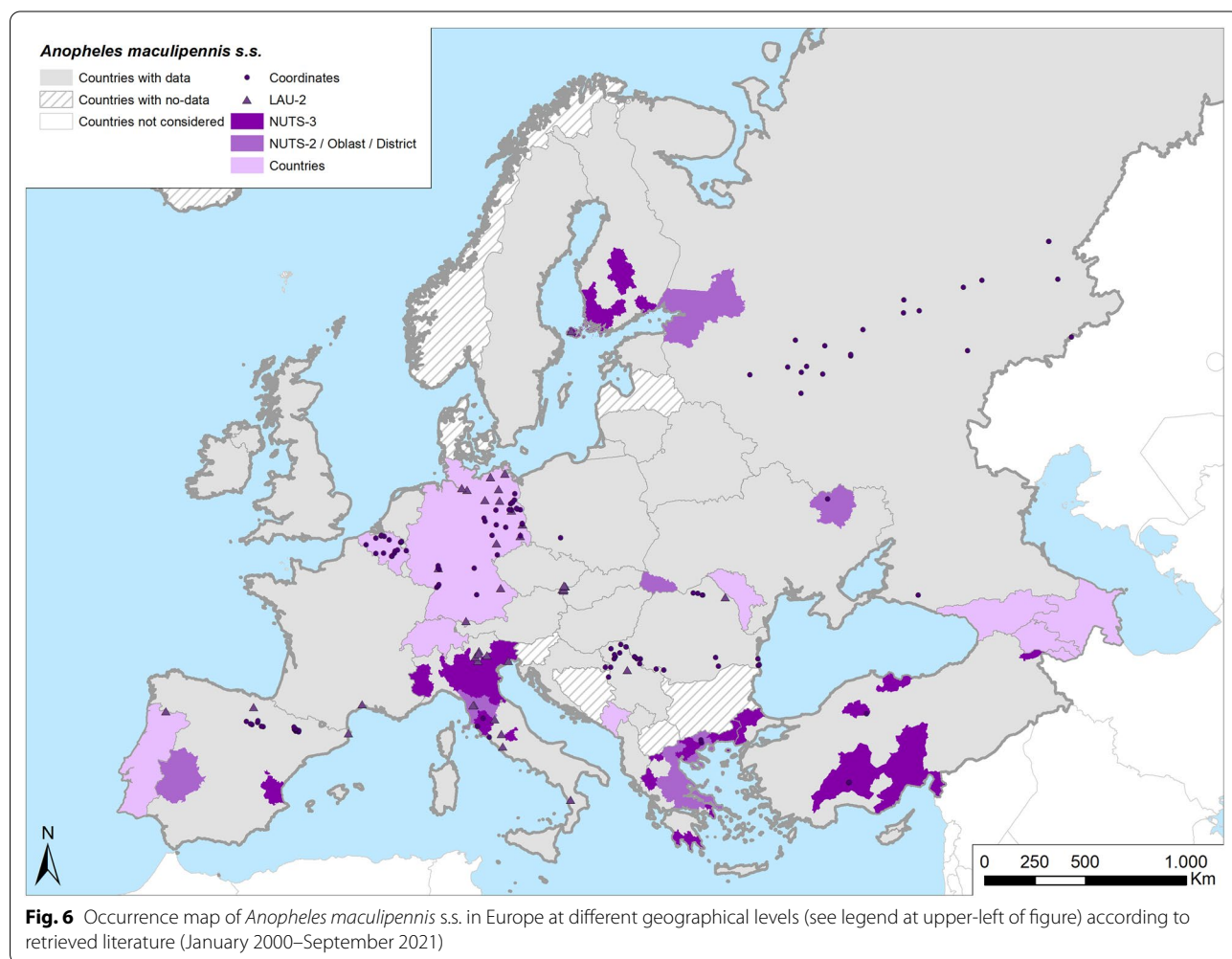
with the typical larval habitats reported to be stagnant and slow-moving freshwater sites, in particular rice fields. Larvae were described as able to develop in every type of larval habitat, with a preference for those exposed to sunlight, but they were considered unable to tolerate high levels of organic or mineral pollution. In recent years, little research has been carried out on the characteristics of larval sites of this species. In the literature retrieved for this systematic review, most of the studies were carried out in central Italy, where the most described breeding sites were rice fields (Table 2), indicating that the occurrence of *An. labranchiae* in Italy is closely correlated to the presence of rice fields, with high abundance in the coastal areas, where higher temperatures contribute to their development [93, 94].

Resting/overwintering behavior

Anopheles labranchiae is described in the retrieved literature as hibernating at the adult stage in both complete and incomplete hibernation states. Occasional winter blood-feeding is also described. Reproductive activity starts again when temperatures reach 16 °C [87]. No more information is available from the recent literature for this species.

Feeding behavior

Females of this species are considered as one of the most aggressive human biter *Anopheles*, with mainly exophagic behavior, although attempts to enter the dwellings to bite the hosts have been described [4]. However, the retrieved data indicate that the feeding behavior of *An. labranchiae* is predominantly opportunistic, with biting of both humans and animals. In studies from Italy and Corsica, mosquito females were collected during human landing catches around sunset, but they were also found resting in animal shelters. Analysis of the blood meals of sampled specimens revealed feedings on multiple animals, with the choice of host dependent on its availability [87, 93, 94] (Table 3).

Vector competence

In the past, *An. labranchiae* was considered to be the main malaria vector in the Mediterranean region, especially in malaria endemic areas during the first half of twentieth century, with studies showing naturally infected mosquitoes with high sporozoite indices. However, experimental assays of infection on *An. labranchiae* populations from central Italy and Corsica showed a very low susceptibility to tropical *P. falciparum* (laboratory strain NF54) [86, 89]. On the contrary, the competence of this species for natural strains of *P. vivax* seems possible. In fact, *An. labranchiae* has been implicated in autochthonous cases of malaria by *P.*

vivax that have occurred both in Corsica and Italy [95–97], indicating that this species can still be considered a potential threat of malaria transmission in Europe (Tables 4, 5).

Anopheles maculipennis s.s. Meigen, 1818

Occurrence

Anopheles maculipennis s.s. is probably the most widespread *Anopheles* species in Europe (Table 1; Fig. 6), even following the definition of *An. beklemishevi* Stegnii and Kabanova, 1976 as a new sibling species that replaced *An. maculipennis* s.s. in the northernmost areas of Europe [98]. In the most recent papers, *An. maculipennis* s.s. is confirmed as occurring all over Europe, with additional findings in north Italy [29, 32, 99] and Finland [100–102]. In particular, this species has been recorded in southeastern Europe [88, 103–106].
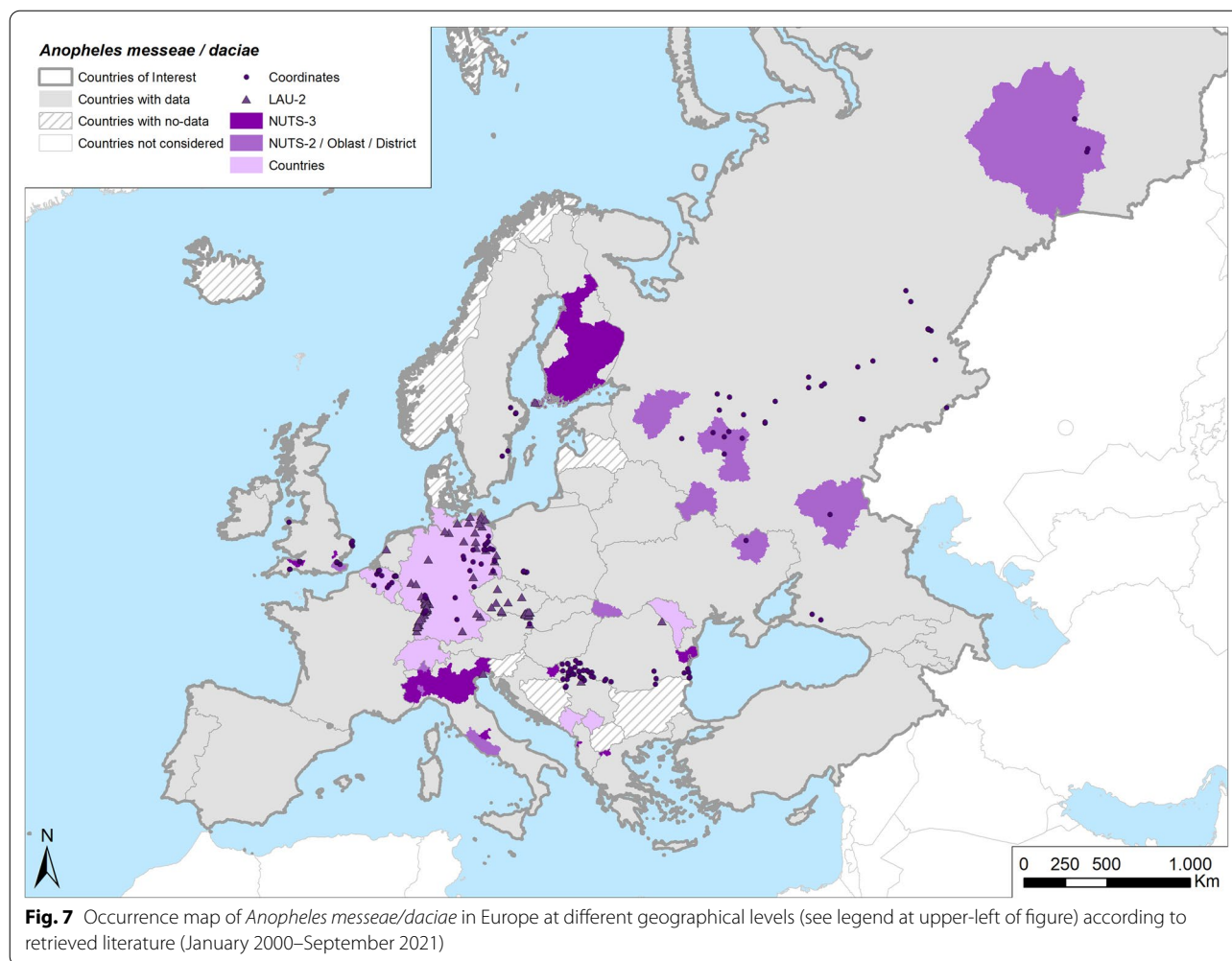
Breeding sites

Anopheles maculipennis s.s. can be found in different environments, ranging from coastal regions to inland areas. Larvae have been found both in clean waters and those moderately charged with organic matter, but there is as yet no evidence of its ability to exploit brackish water. The usual *An. maculipennis* s.s. breeding sites present vegetation or algae [104]. This species has a higher tolerance for moving water than other species of the *An. maculipennis* complex, with some data from recent studies reported in the retrieved literature confirming this tolerance (Table 2): larvae were frequently collected from streams, irrigation channels, river margins and, occasionally, in artificial lakes [50, 81, 107, 108]. As reported in the past, *An. maculipennis* s.s. was found at high altitudes and in hilly forested areas [109], reaching an altitude over 1500 m a.s.l. (Anatolia, Turkey [106]).

Resting-overwintering behavior

Anopheles maculipennis s.s. is known to be endophilic, resting in stables and dwellings. In recent literature, this species was reported to have been collected in large numbers in animal shelters, in particular those with pigs or sheep present [93, 110]. Diapause was described in older studies on this species, and no recent data are available. However, feeding activity and oviposition are described to be still possible during the winter, but stopped at lower temperatures [10].

Feeding behavior

Anopheles maculipennis s.s. is considered to be strongly zoophilic and, therefore, to play a secondary role in malaria transmission. However, in specific contexts (i.e. at high densities or where alternative hosts to humans

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Fig. 7 Occurrence map of *Anopheles messeae/daciae* in Europe at different geographical levels (see legend at upper-left of figure) according to retrieved literature (January 2000–September 2021)

are limited), the species has been found to show a certain degree of anthropophily [110]. Recent studies confirmed that animal blood meals are much more frequent, although some mosquitoes with human blood meals have been also found [93, 107, 111] (Table 3). Moreover, the authors of a paper reporting human landing catches carried out in Italy stated that "*An. maculipennis* s.s., although considered mainly zoophilic, also results as being very aggressive on humans during the night catches, both in presence or absence of animals" [93].

Vector competence

Among potential malaria vectors found in Europe, *An. maculipennis* s.s. is considered to be the mosquito with the lowest vectorial role in malaria transmission. Although no updated studies clarifying the real vector competence of this species for *P. vivax* or *P. falciparum*, in light of the recent information on its feeding behavior,

An. maculipennis s.s. might be considered a potential malaria vector in some eastern and south-eastern European countries [112, 113] (Table 4). The occurrence of malaria in some areas where this species was abundant has been considered to be an evidence of its involvement in the maintenance of malaria transmission. The ability of *An. maculipennis* s.s to colonize different environments from sea level up to high altitudes, combined with its tolerance for cold temperatures, might balance its uncertain ability to support *Plasmodium* infection in some contexts [114]. Therefore, we suggest that this species be considered to be moderately worthy of attention in terms of potential involvement of malaria transmission events, at least in anthropized areas and areas with high mosquito densities (Table 5).

Anopheles messeae/daciae

The species status of *An. messeae* has been debated for several years. Some authors suggest that it be split into

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two separated taxonomic units: *An. messeae* Falleroni, 1926 and *An. daciae* Linton, Nicolescu & Harbach, 2004 [17]. However, the hierarchical position of these taxa remains controversial. The existence of *An. daciae* as a distinct species was originally based on polymorphic sites at the ITS2 of the ribosomal DNA of *An. messeae* from Romania [17]. However, other authors consider this polymorphism to be an indicator of different forms/ecotypes that are consistent with the different geographical origins of the tested populations [32, 88, 115–117]. On the other hand, other authors have analyzed genomic differences and chromosomal inversions, especially on the *X*-chromosome, between *An. messeae* s.s. and *An. daciae* and argue that there is significant evidence for the diversification of the two lineages to be considered as distinct species [18, 118].

Following the definition of *An. daciae* as a new species, many studies (*n* = 26) assessed its occurrence in a number of countries, resulting in an increased number of studies focusing on *An. messeae* or *An. daciae*. However, the resulting literature was mainly based on the description of the molecular identification of *An. daciae*, with little additional information, and usually limited to reporting the location where the specimens were collected. Few articles reported ecological and biological differentiation between *An. messeae* and *An. daciae*, such as reproductive isolation, feeding behavior, vector competence, morphology, etc.

Occurrence

Anopheles messeae/daciae is one of the most widespread species of the *Anopheles maculipennis* complex in Europe (Table 1; Fig. 7). Its distribution ranges from Germany to Russia and to most parts of the Asian continent; it has not been reported in the Iberian Peninsula and France and is sporadically reported in southern Europe, with few records from Italy [29, 31, 32, 88, 99] and only one from Greece [103].

Anopheles daciae as a distinct species was identified first in Romania, then described using a molecular approach in Germany [41–44, 119–122], England and Wales [56, 123], the Czech Republic and Slovakia [39], Serbia [108] and more recently in Poland [124], Finland [101], Sweden [116] and Russia [18]. It has also been found in Italy and Belgium, with the provisional definition of *Anopheles daciae species inquirenda* [32, 117].

Breeding sites

Larvae of *An. messeae/daciae* have been found in many types of habitats, but most often in natural, forested areas with abundant vegetation, such as floating weeds or algae [89]. It seems to be a typical freshwater mosquito, preferring clean, oxygen-rich water with

a relatively low content of dissolved ions [18, 81, 108, 113, 120]. There have been no reports of the presence of larvae in brackish sites, confirming the negative association with a certain degree of salinity (Table 2). Larvae have been found in ponds, swamps and small lakes [35, 43]; likewise, no collections in rice fields were recorded. Novikov and Vaulin [98] found *An. messeae/daciae* often associated with other species, attributing this observation to its wide ecological plasticity.

Few articles have reported distinct data for *An. messeae* or *An. daciae* in terms of breeding sites [18, 43, 108, 118, 121]. Both species were found mainly in the zone of temperate deciduous and mixed forests, with *An. messeae* negatively correlated with agricultural areas and *An. daciae* negatively correlated with pastures [43, 121]. Naumenko et al. [18] described *An. messeae* breeding sites to be associated with oxygen-rich (1.8–4.0 mg/l) waters, while *An. daciae* was found in atypical breeding sites, in waters with low oxygen content (0.8 mg/l).
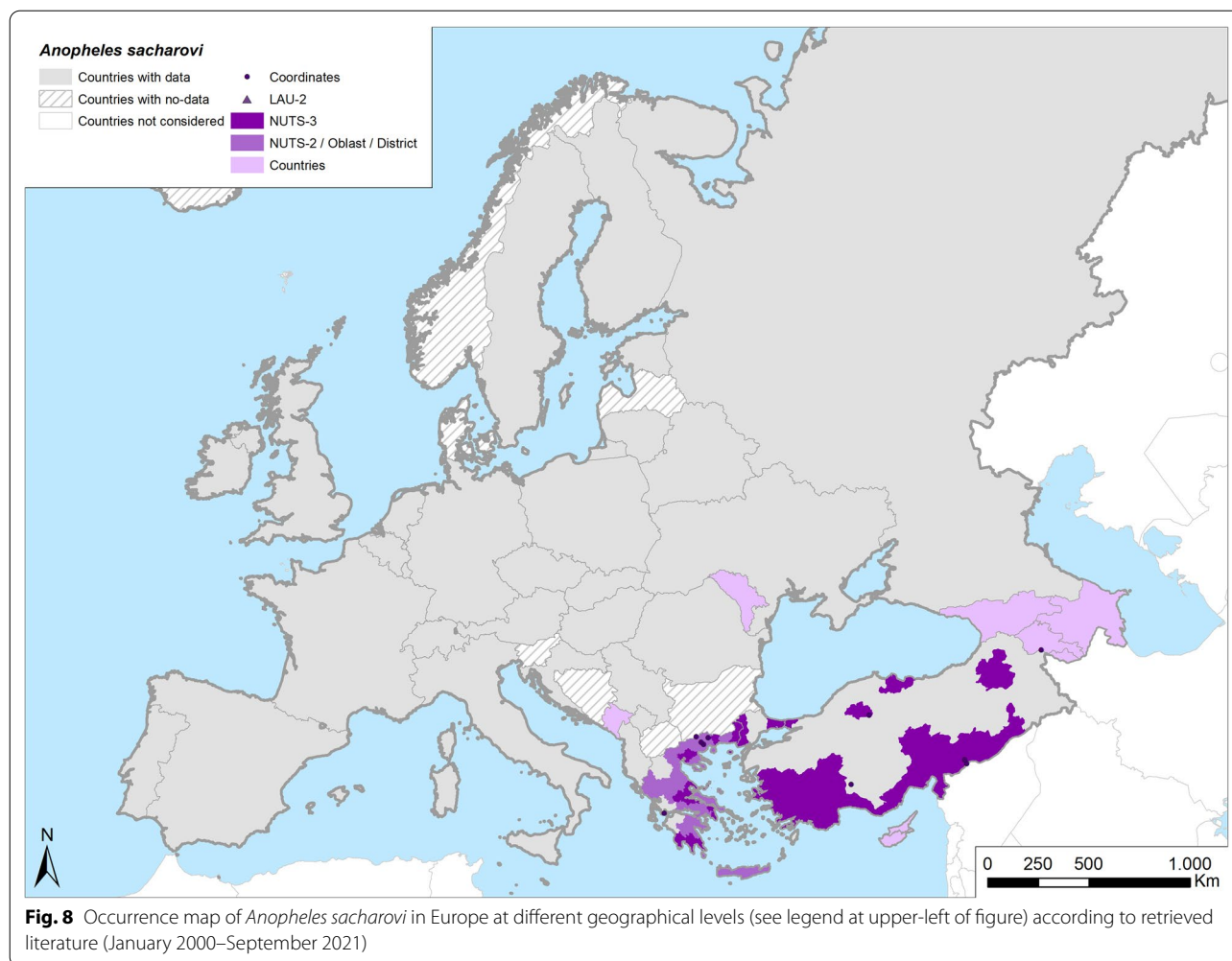
Resting/overwintering behavior

Adults of *Anopheles messeae/daciae* have been found resting outdoors and to be particularly abundant in animal stocks, which is in agreement with the strong relationship between the high abundance of this species in rural/natural habitats and the presence of animal shelters in these areas [108, 113, 125]. Females were also collected in human dwellings, but in low numbers [125, 126], indicating that this species might also be present in anthropized contexts.

New information on *An. messeae/daciae* diapause was not retrieved. Based on previous descriptions, during the winter this species enters into full hibernation at the adult stage without any feeding activity, resting in enclosed shelters or buildings [4].

Feeding behavior

This species was described in the past as a strongly zoophilic feeder. The authors of one article stated that *An. messeae/daciae* does not feed on humans and, therefore, considered it to be a malaria vector of negligible importance [35]. Several recent studies have indicated that this species is an opportunistic feeder (Table 3). *Anopheles messeae/daciae* was captured in animal housing that sheltered different animal hosts, such as cows, horses, sheep and goats, but the results of this study did not unequivocally demonstrate whether this was a consequence of sampling bias or host choice [108]. Similarly, other studies reported that the blood meal analysis demonstrated feeding events on several host species, such as birds, deers, humans, horses and goats, with no particular

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Fig. 8 Occurrence map of *Anopheles sacharovi* in Europe at different geographical levels (see legend at upper-left of figure) according to retrieved literature (January 2000–September 2021)

preference [54, 56, 111, 125]. In other articles the identification of *An. messeae/daciae* blood meals indicated cattle and dog as major hosts [58, 127]. It was also recorded that females of this species are also attracted by humans [126], and this host-seeking behavior was also confirmed in a study using human landing catches [53].

Considering *An. messeae* and *An. daciae* to be separate species, limited and inconclusive evidence can be obtained in the retrieved literature on their respective feeding pattern. According to Danabalan et al. [56], *An. daciae* may feed on animals and humans, whereas *An. messeae* s.s. appears to be strictly zoophilic. However, these observations were based on a single study that collected only a few samples and performed in a small area. Other authors speculated that *An. daciae* is more anthropophilic than *An. messeae* because it was found more frequently in larval habitats located close to human dwellings [118]. On the other hand, in a study carried out in two German zoological gardens to determine the feeding pattern of different mosquito species, *An. daciae*

blood-fed only on wild mammals, with no human blood detected, while *An. messeae* blood-fed on both birds and mammals, humans included [111].

Vector competence

Available information indicates that the role of *An. messeae/daciae* as a malaria vector remains controversial. It seems refractory to tropical *P. falciparum* strains (even if a successful infection with a strain from the Central African Republic was obtained [64]), but it is considered to be a potential vector of *P. vivax* in northwestern Europe [10, 64]. In addition, based on old published articles, it is considered a potentially important vector in eastern Europe and western Asia [4]. Linton et al. [123] attempted to link the distribution of malaria cases in eastern Europe to the occurrence of the two tentative taxa of *An. messeae/ daciae*. According to these authors, the different distribution of malaria cases might be an indication of the vector competence of both *An. messeae* and *An. daciae*, considering them as separate species with a different ecology

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and geographic distribution. The authors suggested that malaria cases that occurred in the past in Eurasia reflected the widespread distribution of *An. daciae* in this area and, consequently, they asserted that this taxon can be a better vector of *P. vivax* than *An. messeae* [39, 121]. Considering the lack of agreement on the existence of these two taxa, as well as the lack of recent information on vector competence for *Plasmodium* species of different populations of *An. messeae/daciae*, it is still difficult to assess its potential role in malaria transmission in Europe, but it should be cautiously considered as moderate (Tables 4, 5).

Anopheles sacharovi Favre, 1903
Occurrence
Of all the *Anopheles* species recorded in Europe, *An. sacharovi* has the most southern distribution (Table 1; Fig. 8) and is considered to be the most threatening malaria vector across southeastern Europe and the Middle East. Despite anti-vector campaigns implemented across the eastern part of Europe, this species remains abundant. As in the past, this species is currently frequently detected in Greece and Turkey. Conversely, *An. sacharovi* seems to have disappeared from islands of Corsica and Sardinia, and only two doubtful findings have been reported in mainland Italy [29, 128].

Breeding sites
Larvae of *An. sacharovi* can develop in different water collections, usually those containing freshwater but also in brackish-salt water collections with a salinity of up to 20%, and it can tolerate a wide range of temperatures up to 38–40 °C [107, 129, 130]. *Anopheles sacharovi* is generally found in any kind of habitat containing horizontal vegetation, such as swamps, marshes, river margins, streams, pools and ditches. The retrieved literature
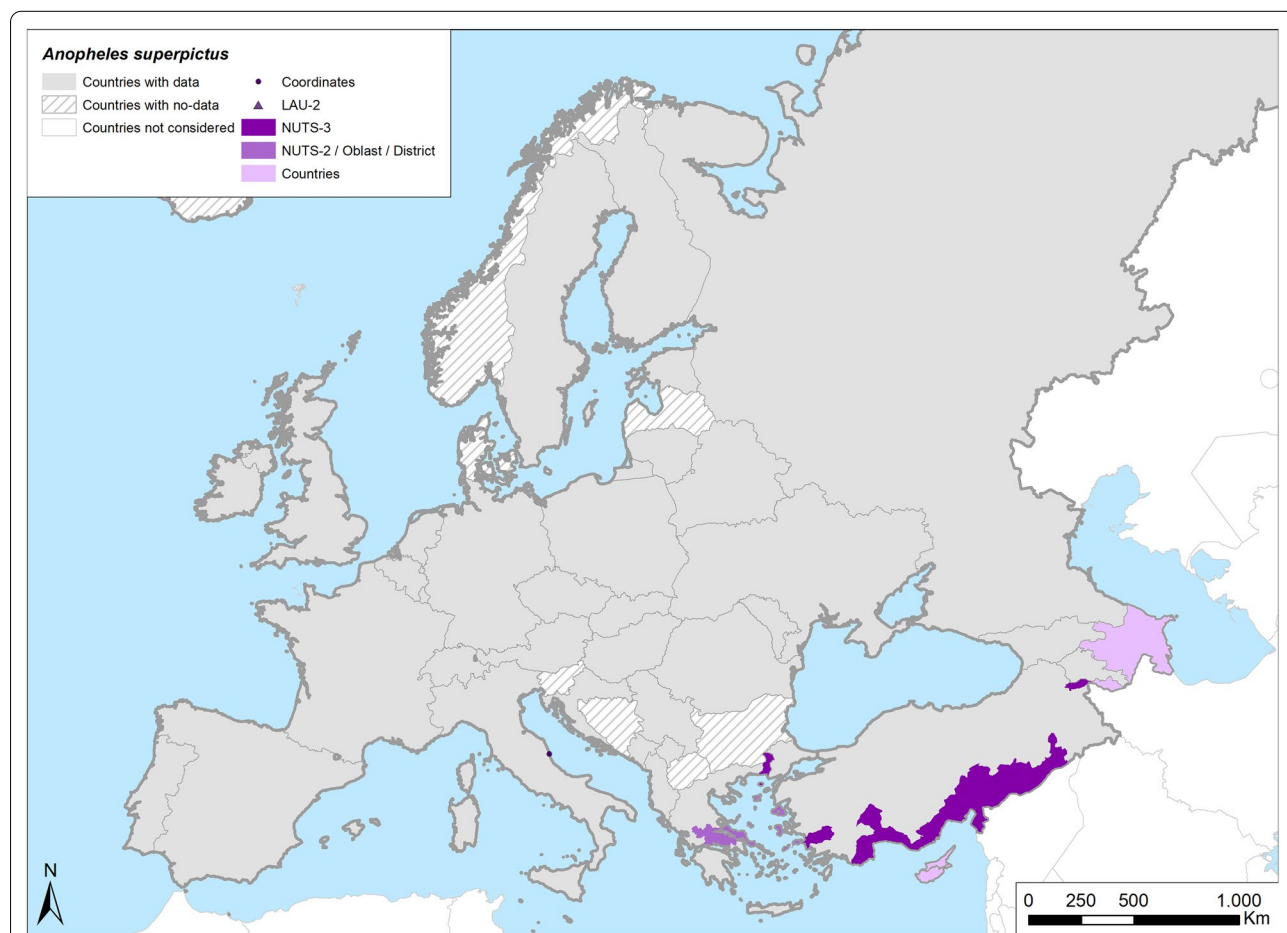

Fig. 9 Occurrence map of *Anopheles superpictus* in Europe at different geographical levels (see legend at upper-left of figure) according to retrieved literature (January 2000–September 2021)

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Fig. 10 Occurrence map of *Anopheles plumbeus* in Europe at different geographical levels (see legend at upper-left of figure) according to retrieved literature (January 2000–September 2021)
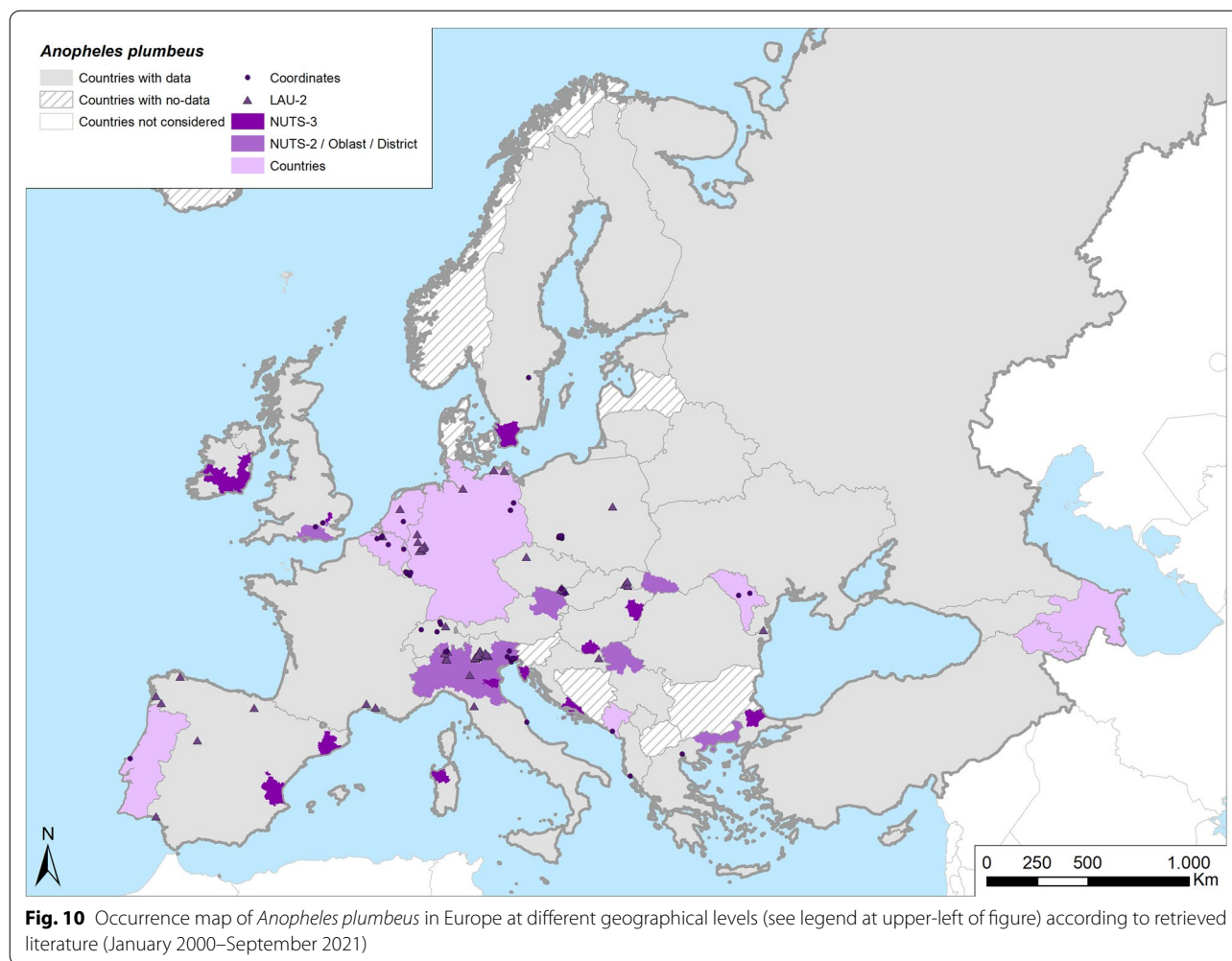
confirmed the occurrence of larvae mainly in natural and large water collections, but also in irrigation channels, with all water collections characterized by abundant vegetation. However, compared to the past records, *An. sacharovi* currently seems to be less frequently detected in rice fields, probably due to the introduction of pesticide treatments (Table 2).

Resting/overwintering behavior

In terms of adult feeding behavior, *An. sacharovi* has been principally described as endophagic. It tends to rest in all types of dwellings, including both animal shelters and houses [131, 132]. Adult hibernation is incomplete, with periodic feeding events during the winter. This behavior is probably due to the distribution of this species in areas with rather mild winter temperatures. However, oviposition during hibernation was not mentioned in any study included in this systematic review.

Feeding behavior

Among the *Anopheles* species described in this review, *An. sacharovi* was considered to be the most anthropophilic, as confirmed in the recent literature, although several papers reported a certain degree of opportunistic feeding behavior. Generally, mosquitoes that were found in animal shelters had had a blood meal on the species stabled in the shelter [110, 112], but exophagic activity was also observed. Kampen et al. [107] reported that 23 out of 24 resting *An. sacharovi* females collected in sheds had blood-fed on an animal (mainly goat), with only one female having had a blood meal on a human. Similarly, Tavşanoğlu and Çağlar [133] stated that *An. sacharovi* fed preferably on animals rather than humans even if mosquitoes were collected in houses. However, the results of these studies were affected by the proximity of the houses and animal sheds, both usually being open during the summer, thereby allowing free movement of blood-fed females searching for a suitable resting place (Table 3).

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Table 1 References reporting the occurrence of potential malaria vectors in European countries

Country	Potential malaria vectors in European countries[a]									
	atr	hyr s.l.	lab	mac s.s.	mes/dac	plu	sac	sup	mac s.l.	References
Albania					ML	MF			MF	[88, 170]
Armenia				ML			ML		MF	[28, 88, 112, 139, 150, 171]
Austria		MF				MF			MF	[74, 86, 172–176]
Azerbaijan		MF					ML	MF	MF	[88, 139, 177]
Belarus									MF	[178]
Belgium				ML	ML	MF			MF	[117, 143–145, 179–186]
Croatia		MF				MF			MF	[146, 187–193]
Cyprus							MF	MF		[141, 142]
Czech Republic		MF		ML	ML	MF			MF	[37–39, 79, 80, 155, 194–203]
Estonia				ML			ML			[204]
Finland				ML	ML				MF	[100–102]
France	ML	ML	ML	ML		MF			MF	[20, 30, 33, 34, 68–70, 77, 78, 87, 88, 203, 205–207]
Georgia										[139]
Germany	ML			ML	ML	MF			MF	[41–44, 111, 119–122, 151, 152, 159, 163, 208–219]
Greece		ML		ML	ML	MF	ML	MF	MF	[103, 104, 107, 110, 130, 135, 136, 203, 220–231]
Hungary		MF							MF	[82, 170, 232–234]
Ireland						MF			MF	[235]
Italy	ML	MF	ML	ML	ML	MF	MF		MF	[28–32, 52, 60, 88–91, 93, 94, 97, 99, 128, 138, 236–250]
Kosovo					ML				MF	[251]
Lithuania									MF	[252]
Luxembourg						MF			MF	[253]
Moldova	ML	MF		ML	ML	MF	ML		MF	[81, 254, 255]
Montenegro				ML	ML	MF	MF		MF	[170, 256]
The Netherlands	ML			ML		MF			MF	[35, 45, 88, 128, 154, 257, 258]
Poland				ML	ML	MF			MF	[124, 259–263]
Portugal	ML			ML		MF			MF	[25–27, 30, 46, 57, 264–271]
Romania	ML	MF	ML	ML	ML	MF			MF	[17, 30, 92, 272–274]
Russia		MF		ML	ML				MF	[18, 28, 75, 98, 115, 118, 125, 275–283]
Serbia	ML	MF		ML	ML	MF			MF	[108, 113, 284–287]
Slovakia	ML	MF		ML		MF			MF	[39, 40, 288–293]
Spain	ML	MF		ML		MF			MF	[30, 36, 47–51, 59, 61, 149, 165, 294–306]
Sweden						MF			MF	[116, 128, 307–310]
Switzerland				ML	ML	MF			MF	[148, 158, 245, 311–315]
Turkey		ML		ML		MF	ML	MF	MF	[20, 28, 71–73, 88, 105, 106, 109, 131–133, 140, 316–327]
Ukraine	MF			MF	MF				MF	[328, 329]
UK	ML			ML		MF			MF	[53–56, 58, 123, 126, 127, 147, 330–336]

MF, morphological identification; ML, molecular identification

[a] *atr, Anopheles atroparvus; hyr* s.l., *Anopheles hyrcanus* sensu lato; *lab, Anopheles labranchiae; mac* s.s., *Anopheles maculipennis* sensu stricto; *mes/dac, Anopheles messeae/daciae; plu, Anopheles plumbeus; sac, Anopheles sacharovi; sup, Anopheles superpictus; mac* s.l., *Anopheles. maculipennis* sensu lato

Vector competence

The role of *An. sacharovi* as a primary malaria vector is partially due to its wide distribution and densities, in addition to its high ecological plasticity at both the adult and larval stages. In southeastern Europe and the Middle East, most malaria cases were reported to be caused by *P. vivax*, with one of the primary vectors being *An. sacharovi* [134]. In support of this finding, the authors of some studies reported autochthonous malaria cases that occurred in Greece in 1994–1995 and 2009–2010, although the country was declared to be free of malaria in 1974. Following these events, the entomological investigations indicated *An. sacharovi* as the predominant mosquito (up to 80%) in those areas [107, 135, 136], despite *Plasmodium* never

Table 2 Breeding sites of potential malaria vector species

Mosquito species	Total number of reported breeding sites	Lagoons, brackish waters	Marshes, swamps, ponds, overflow rivers	Puddles, pools, pits	Irrigation channels	Rice fields	Artificial containers
An. atroparvus	32	6 (18.7)	6 (18.7)	4 (12.5)	7 (21.9)	8 (25.0)	1 (3.1)
An. hyrcanus s.l	17		12 (70.6)			5 (29.4)	
An. labranchiae	12	1 (8.3)	2 (16.7)	2 (16.7)	4 (33.3)	3 (25.0)	
An. maculipennis s.s.	31		11 (35.5)	6 (19.3)	9 (29.0)	4 (12.9)	1 (3.3)
An. messeae/daciae	24		12 (50.0)	4 (16.7)	5 (20.8)	2 (8.3)	1 (4.2)
An. plumbeus	23		1 (4.3)	7 (30.4)			15 (65.2)
An. sacharovi	19	2 (10.5)	8 (42.1)	1 (5.3)	6 (31.6)	2 (10.5)	
An. superpictus	4		2 (50.0)		2 (50.0)		

Data presented in table are the number (and percentage) of types of reported breeding sites as reported in the retrieved literature (January 2000–September 2021)

being detected in field mosquitoes. However, this species was demonstrated to be experimentally competent not only for *P. vivax* [137] but also for tropical strains of *P. falciparum* [64], indicating its major importance as a malaria vector in Europe (Tables 4, 5).

Anopheles superpictus Grassi, 1899
Occurrence
There are suggestions in the extracted literature that *An. superpictus* be considered a species complex [4]. Its wide distribution, ranging from the Mediterranean region to Southeast Asia, is probably the consequence of the distribution of different species partially overlapping in different geographic areas. However, no recent studies are available to confirm this hypothesis. Information on the biology of *An. superpictus* described in older publications refers to studies conducted outside of Europe [4]. All *An. superpictus* findings in the recent literature came from southeastern Europe, except for one study in Italy [138] where a few specimens were found on several occasions between 2011 and 2014 (Table 1; Fig. 9).

Breeding sites
Typically, the breeding sites of *An. superpictus* are temporary pools formed by fluctuations in the water level of rivers or streams caused by rain activity. Such sites are typically described as pools of clean water with gravelly riverbeds exposed to sunlight [4]. Several studies reported the presence of *An. superpictus* in man-made habitats, such as irrigation channels, rice fields, ditches and artificial pools [139]. Other larval samplings, such as those described by Yavaşoglu et al. [55, 140], were ponds, streams and swamps, while Violaris et al. [141] collected larvae from streams, slow-running waters, sunny seepages and irrigation systems. The ability of this species to tolerate a certain degree of salinity or pollutants

is unclear. Among the literature examined in this review, only one publication reported larvae of *An. superpictus* in breeding sites with low salinity and a chloride concentration ranging between 30 and 96 mg/l [107] (Table 2).

Resting/overwintering behavior
No information is available in the literature on the overwintering behavior of *An. superpictus.* The only records retrieved report data on resting females, which were often caught in animal stables and houses in rural areas [72, 107, 140, 142].

Feeding behavior
Data on the feeding behavior of *An. superpictus* are also not exhaustive, and no other recent information was found. This mosquito species is mostly considered to be zoophilic and exophagic, despite questionable data were reported in literature. According to some authors, humans are a secondary host and attacked only in the absence of farm animals, while other authors suggest that *An. superpictus* can bite both humans and animals without preference, especially in periods of high densities, such as in late summer [4, 10] (Table 3).

Vector competence
The role of *An. superpictus* as a vector of *Plasmodium* is unclear. Older studies reported the susceptibility to *P. vivax* [137] and the association between high mosquito densities and malaria outbreaks [10]. Only one recent paper confirmed these findings, with the authors stating "*An. superpictus* occurred in Savur (Turkey) where there was an important malaria focus" [140]; however, the information might simply be a consequence of a spurious association (Table 4). At most, the available evidence

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Table 3 Feeding behavior of potential malaria vector species

Species	Total number of reports	Human	Equid	Cattle	Small ruminants (sheep, goat)	Pig	Dog	Rabbit	Chicken	Birds other than chicken	Other mammals
An. atroparvus	26	3 (11.5)	4 (15.4)	4 (15.4)	2 (7.7)		3 (11.5)	3 (11.5)	2 (7.7)	3 (11.5)	2 (7.7)
An. hyrcanus s.l.	12	8 (67)	2 (17)							2 (17)	
An. labranchiae	11	4 (36.4)	2 (18.2)	3 (27.2)		2 (18.2)					
An. maculipennis s.s.	14	3 (21.4)	2 (14.3)	2 (14.3)	3 (21.4)	1 (7.1)			1 (7.1)	1 (7.1)	1 (7.1)
An. messeae/daciae	37	11 (29.7)	4 (10.8)	9 (24.3)	4 (10.8)		4 (10.8)		2 (5.4)	1 (2.7)	2 (5.4)
An. plumbeus	13	8 (61.5)			1 (7.7)				1 (7.7)	2 (15.4)	1 (7.7)
An. sacharovi	2			1 (50.0)	1 (50.0)						
An. superpictus	0										

Data presented in table are the number (and percentage) of reports of host species as reported in the retrieved literature (January 2000–September 2021)

Table 4 Competence of potential malaria vector species to *Plasmodium* species and their involvement in local transmission events according to the available literature

Species	*Plasmodium* species (tropical strains)	Competence tested	Post-eradication autochtonous cases (Europe, Middle East)	References
An. atroparvus	*P. falciparum*	No		[62–65, 337]
	P. vivax	Yes		[64]
	P. malariae	Yes		[64]
	P. ovale	No	Suspected	[64, 67]
An. hyrcanus s.l.	*P. falciparum*	No		[83]
	P. vivax	Yes	Suspected	[19, 83]
	P. malariae	Unknown		
	P. ovale	Unknown		
An. labranchiae	*P. falciparum*	Low		[62, 63, 87, 90, 97]
	P. vivax	Yes	Yes	[95–97]
	P. malariae	Unknown		
	P. ovale	Unknown		
An. maculipennis s.s.	*P. falciparum*	Unknown		
	P. vivax	Suspected	Suspected	[112–114]
	P. malariae	Unknown		
	P. ovale	Unknown		
An. messeae/daciae	*P. falciparum*	No		[10, 39, 64, 121]
	P. vivax	Low	Suspected	[10, 64, 123]
	P. malariae	Unknown		
	P. ovale	Unknown		
An. plumbeus	*P. falciparum*	Yes	Suspected	[155, 158, 159]
	P. vivax	Yes	Yes	[157, 158]
	P. malariae	Unknown		
	P. ovale	Unknown		
An. sacharovi	*P. falciparum*	Suspected		[64]
	P. vivax	Yes	Yes	[64, 107, 134–137]
	P. malariae	Unknown		
	P. ovale	Unknown		
An. superpictus	*P. falciparum*	Unknown		
	P. vivax	Yes	Suspected	[10, 137, 140]
	P. malariae	Unknown		
	P. ovale	Unknown		

Table 5 Relative importance of potential malaria vector species based on current information, in particular *Plasmodium* competence and anthropophily

Species	Known competence	Anthropophily	Importance as potential malaria vector
An. atroparvus	*P. vivax, P. malariae* (*P. ovale*)	Low	Low
An. hyrcanus s.l.	*P. vivax*	High	High
An. labranchiae	*P. vivax*, (*P. falciparum*)	Opportunistic	High
An. maculipennis s.s.	(*P. vivax*)	Low	Moderate
An. messeae/daciae	(*P. vivax*)	Low	Moderate
An. plumbeus	*P. falciparum, P. vivax*	High	High
An. sacharovi	*P. vivax*, (*P. falciparum*)	Opportunistic	High
An. superpictus	*P. vivax*	Low	Low

For *Plasmodium* species presented in parenthesis the competence is uncertain

indicates that this species might have a secondary role in the maintenance of malaria infection in areas where it reaches significant densities, such as in some areas of southeastern Europe (Table 5).

Anopheles plumbeus Stephens, 1828
Occurrence
Anopheles plumbeus is one of the most diffused species among those targeted in this review. It is widespread throughout Europe up to the Caucasus and Asia, from colder to warmer climates (Table 1; Fig. 10).

Breeding sites
This species is known to be associated to a sylvatic environment, especially forested areas, breeding in water-filled tree holes, wood stocks and ground holes characterized by high concentrations of organic substances and oxygen deficiency. More recently, a shift of habitats has been observed for this species, from forested to anthropic ones, such as parks and cemeteries, where larvae have been found developing in holes in beeches and poplars [40, 50, 143]. In the last decade, another habitat adaptation was observed for this species: *An. plumbeus* was found to exploit artificial containers with stagnant water that had a composition similar to that of water in tree holes due to organic contamination. In fact, almost all of the recent papers retrieved for this review reported larval samplings of *An. plumbeus* in artificial containers. Larvae were found in tires, manure collection tanks and any other kind of man-made artificial container, including *Aedes* monitoring ovitraps [143–151].
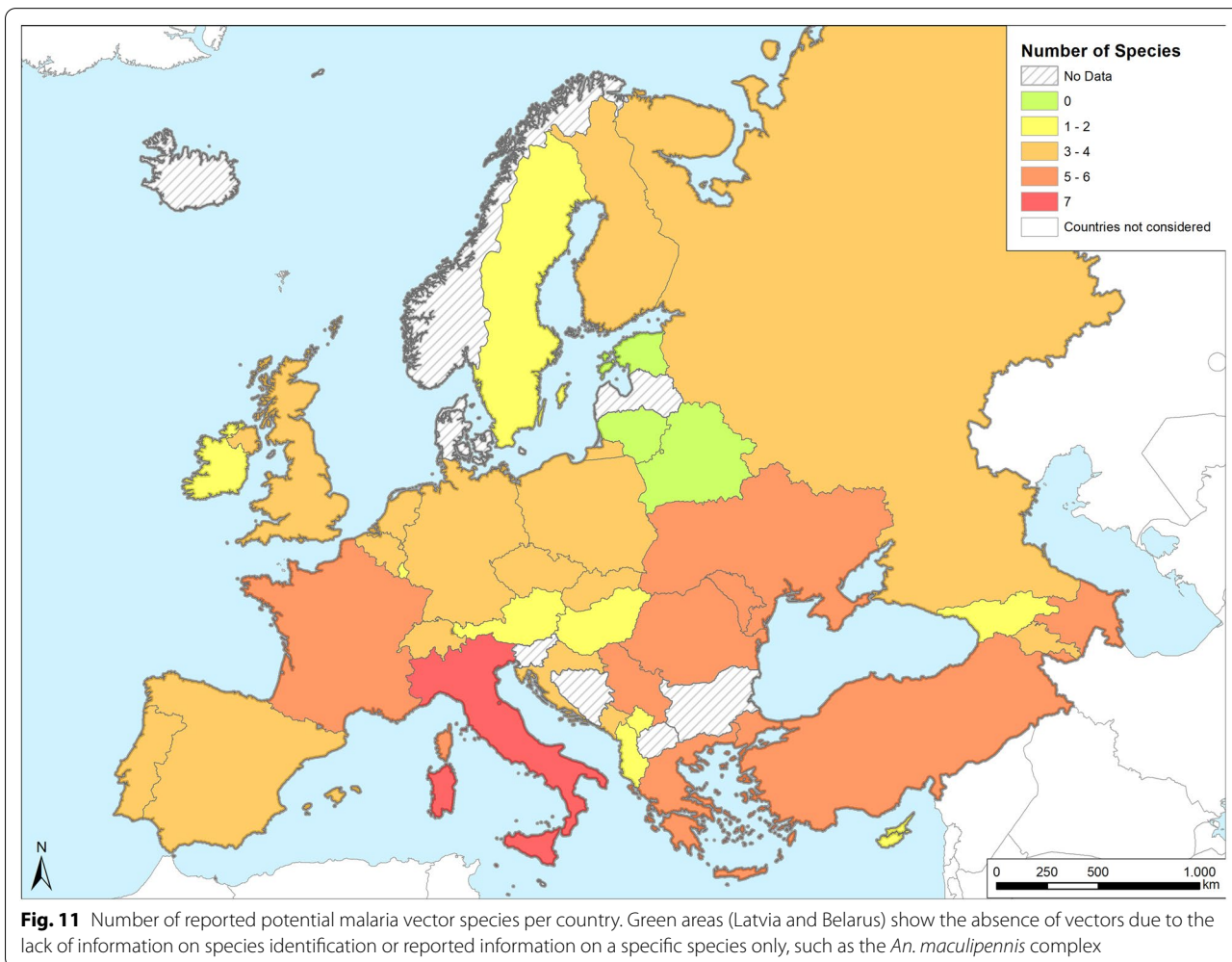
Fig. 11 Number of reported potential malaria vector species per country. Green areas (Latvia and Belarus) show the absence of vectors due to the lack of information on species identification or reported information on a specific species only, such as the *An. maculipennis* complex

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In these artificial containers, mosquitoes not only found appropriate alternative breeding sites but also a lot of space for mass development [143, 152]. This shift in habitats has allowed the colonization of new areas and the increase in local densities (Table 2).

Resting/overwintering behavior

No data are currently available on the resting and diapausing activity of this mosquito. The only record found reported *An. plumbeus* larvae in England during all months of the year, while adults were found from late April to early October [126]. This finding leads to the hypothesis that this species is adapted to pass cold months as larvae, which will be a unique example among the species here described.

Feeding behavior

In the past, *An. plumbeus* was described to have a feeding activity at any time of the day, even in daylight, biting humans with persistence and aggressiveness both in urban and forested areas [153]. This behavior has been confirmed in recent studies, in which *An. plumbeus* was reported to bite during the daytime, in particular during the early and late hours of the day [53, 80]. In addition, it was particularly aggressive in attacking humans when mass development occurred, causing a serious nuisance [152, 154]. *Anopheles plumbeus* can also feed on other hosts, such as horses, wild animals and, more rarely, birds [68, 79, 111, 155] (Table 3).

Vector competence

Some laboratory studies reported that *An. plumbeus* is able to produce sporozoites of tropical strains of *P. falciparum* [156], as well as of *P. vivax* [157]. More recently, the vector competence of *An. plumbeus* for these two *Plasmodim* species was confirmed [158]. Also, a retrospective study speculated about its possible involvement in two cases of autochthonous *P. falciparum* malaria that occurred in Germany [159] (Table 4). In conclusion, despite *An. plumbeus* never being included as a potential malaria vector in past reviews, it is a species that may play a primary role in malaria transmission (Table 5), in particular in light of its anthropophily and the ability to exploit artificial containers as larval sites, allowing closer contact of this mosquito with humans.

Conclusions

This systematic review provides an updated overview of the occurrence, ecology and vector competence of *Anopheles* mosquito species recorded in Europe that are historically associated with malaria transmission and/or currently potentially involved in autochthonous cases.

This information will be useful for identifying the most important species in the current European epidemiological scenario.

The retrieved literature indicates a limited research interest in the targeted mosquito taxa, probably due to the very low number of malaria cases that occur in Europe. This lack of interest is supported by the main subject of the articles retrieved, with most dealing with the determination of the culicid fauna in a specific area or the vector surveillance of pathogens other than *Plasmodium*, such as viruses or filarial nematodes. However, a reasonable number of recent publications specifically addressed *Anopheles* and, in particular, attempted to clarify the presence of some species, such as *An. messeae/daciae* or *An. hyrcanus/pseudopictus*. In this regard, the development and implementation of molecular techniques for species identification have made a significant and noteworthy contribution, and is a factor that was not stressed in studies published before 2000.

All of the *Anopheles* species targeted in this systematic review are considered to be potential vectors of malaria (*An. atroparvus*, *An. sacharovi*, *An. labranchiae*, *An. messeae/daciae*, *An. maculipennis* s.s., *An. superpictus*, *An. hyrcanus* s.l. and *An. plumbeus*) and are still present in European countries. In some areas of Europe they are also abundant in terms of species diversity, particularly in southern Europe (Fig. 11).

A north-to-south gradient of the presence of the targeted *Anopheles* mosquitoes is quite evident, indicating that, as expected, the majority of potential malaria vectors is mostly linked to the warm Mediterranean climate. Among all of the countries investigated, Italy is the only one in which more than six potential malaria vectors are found. This is not particularly surprising, considering the great diversity in habitats available in Italy, which is already exploited by one of the largest Culicidae fauna of the European continent (currently 64 species described [160], with several invasive species now established in the country [161]).

Despite this abundance, at the ecological level a reduction in their original habitats has been observed, as compared to the past (in particular for *An. sacharovi*). This reduction is mostly due to human interventions that modified the original larval habitats (wetlands in particular, which are currently mainly preserved nature areas of interest), and to the increasing usage of insecticides. Several *Anopheles* species (e.g. *An. atroparvus*, *An. labranchiae* and *An. maculipennis* s.s.) now exploit alternative larval habitats linked to some agricultural practices (e.g. rice cultivation and the use of extensive irrigation networks) that have increased in recent years, thereby allowing for the presence of mosquito populations also

in anthropized areas. In particular, anthropic habitats are now exploited by new potential malaria vectors, as shown by the presence of *An. plumbeus*, which is now able to exploit urban environments using small water containers rich in organic matter as habitats. This indicates that some potential malaria vectors possess a non-negligible ecological plasticity.

Recent literature shows that most records of field collections involving potential malaria vectors are derived from arbovirus surveillance programs in which the CDC light trap was used as a standard method. Targeted *Anopheles* species, when specifically sampled, are mostly collected manually as resting adults, indicating a substantial lack of standardization in the monitoring of the *Anopheles* target species. In fact, among the trapping methods available in literature, only a few studies involving European potential malaria vectors compared the traps used [59, 78, 162, 163]. This lack of knowledge stresses the need to develop appropriate sampling strategies for these species in order to evaluate their distribution and abundance and, therefore, the appropriate surveillance programs in case of need.

A major limitation in the evaluation of epidemiological risks of local malaria transmission in Europe is the paucity of information on the competence of potential malaria vectors for tropical *Plasmodium* species. In fact, those studies demonstrating the capacity of the *Anopheles* species targeted in this review to transmit the different parasites can be considered to be outdated and fragmentary (Table 4).

One of the reasons for this lack of information is the difficulty to develop species-specific insectary breeding protocols, as those adopted for tropical malaria vectors are unfortunately inadequate. This is a limiting factor in obtaining the appropriate numbers of adult mosquitoes needed for competence testing, thus imposing the requirement that field-collected larvae be used as biological material, which in turn necessitates sorting and proper identification before testing. The only potential malaria vectors for which recent standardized procedures are available are *An. atroparvus* [164, 165], *An. labranchiae* [166], *An. superpictus* [166, 167] and *An. scaharovi* [166, 168], indicating that more efforts are needed to optimize rearing procedures for all potential malaria vectors.

Moreover, no information is available on the vector competence of any of the *Anopheles* species targeted in this review for *P. knowlesi*. Despite the rarity of imported human cases in Europe for this zoonotic *Plasmodium* and the uncertainty surrounding its capacity to produce significant gametocyte concentrations in humans [169], the increasing epidemiological evidence for the circulation of *P. knowlesi* in humans suggests that the possibility of potential malaria vectors locally transmitting this parasite needs to be taken into account.

Based on this review, the list of potential malaria vector species should be redefined in their relative importance (Table 5). Compared to previous literature [4], recent scientific evidence supports the addition of three new potential vectors in Europe: *An. maculipennis* s.s., *An. hyrcanus* s.l. and *An. plumbeus*. Even if the information on vectorial capacity of each species is subjected to local geographic/ecological differences, based on the available information we could consider *An. hyrcanus* s.l., *An. labranchiae*, *An. plumbeus* and *An. sacharovi* to be vectors of major importance, and *An. messeae/daciae* and *An. maculipennis* s.s. to be vector species of moderate importance, despite their large diffusion. In contrast, *An. atroparvus* and *An. superpictus* should be considered vectors of lower importance, especially given their low anthropophily. This revised classification may help define the current risk of re-introduction and emergence of autochthonous cases of malaria in different European countries, but also highlights the gaps still present in the knowledge of these vectorial systems, not only in terms of vector competence but also in the definition of appropriate sampling approaches. Further research on these potential malaria vectors is needed given recent climate, environmental and socio-economic changes that compel the adaptation of surveillance systems with the appropriate tools and knowledge for each species.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13071-022-05204-y.

Additional file 1. List of articles matching the eligibility criteria and assessed in this review (bibliographical details, list of potential vector species occurrence, monitoring/field activity, year of monitoring activity, identification method(s), sampling technique(s) and geographical details of sampling sites. When the presence of *Anopheles* species was not assigned to a specific site, all the sites monitored during that study were considered to be negative and marked as NA. *Abbreviation*: DD, Decimal degree; *NA*, not available.

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Availability of data and materials

All data generated and analyzed in this review are included in this article, along with its additional files.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

Author details

[1]Istituto Zooprofilattico Sperimentale delle Venezie, Viale dell'Università 10, 35020 Legnaro, Italy. [2]Dipartimento di Sanità Pubblica e Malattie Infettive, Università di Roma "Sapienza", P.le Aldo Moro 5, 00185 Roma, Italy.

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