

Conservation genetics in the European Union – Biases, gaps and future directions



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ABSTRACT

The importance of genetic diversity for the assessment and maintenance of biodiversity is widely recognised, although not yet explicitly incorporated into conservation decision making in many European Union Member States. A detailed assessment of 4311 genetic studies relevant for the conservation and management of European species revealed that research is extensive and, therefore, could be more effectively implemented in existing conservation programs. However, research was overly biased towards the study of species with an economic value or iconic status, with research on threatened species or species with undetermined conservation status being scarce. The largest volume of research focused on species identification and relationships, population subdivision and dispersal; with microsatellite and mtDNA sequences as the most widely used markers. These results emphasize the need for further collaboration between researchers and conservation stakeholders to devise genetics research programs that can provide effective solutions for species conservation in Europe.

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1. Introduction

Europe is characterised by a rich biodiversity due to the different terrestrial and marine habitats it contains, and the large number of endemic species found in particular in the Mediterranean region, a global biodiversity hotspot (Cuttelod et al., 2008; Myers et al., 2000). As in many other regions of the world, Europe is facing a biodiversity crisis due to the different anthropogenic pressures that landscapes have been (and are being) subjected to (de Heer et al., 2005; Dullinger et al., 2013; EEA, 2015); with many species and habitats threatened or at risk of extinction (EEA, 2010). The protection and maintenance of biodiversity in Europe has been a matter of concern, with initial European Union (EU) environmental legislation in place since the 1970s and the establishment of the Habitats Directive and Birds Directive since the early 1990s (European Commission, 1992). More recently, the EU Biodiversity Strategy to 2020 stands as an ambitious attempt to reverse biodiversity and ecosystem degradation trends (European Commission, 2011), with the aim of halting biodiversity loss in the current 28 EU Member States by 2020 and to protect biodiversity and ecosystems services by 2050 (European Commission, 2011).

Genetic diversity is crucial for the long-term survival of populations (and species) and their evolutionary potential (Frankel, 1974; Stockwell et al., 2003), and the application of genetics methods is now widely accepted in biodiversity assessments and conservation and management

programs (Soulé and Wilcox, 1980; Soulé, 1985). The United States and Canada have pioneered the explicit incorporation of genetic information into conservation decision making via the US Fish and Wildlife Service's Endangered Species Act and the Committee on the Status of Endangered Species in Canada's guidelines. Furthermore, environment agencies from these countries, such as the U.S. Geological Survey and Environment Canada, have set up dedicated conservation genetics laboratories and are at the forefront of the implementation of genetic and genomic techniques for wildlife management and environmental law enforcement (Haig et al., 2016). Such guidance and commitment to implement genetic techniques into wildlife management and conservation policy is still lacking elsewhere in the world, including Europe (Laikre, 2010; Laikre et al., 2010). The European Union Member States are currently addressing this with the EU Biodiversity Strategy to 2020 where genetics is explicitly mentioned in Action 9 and 10 of Target 3 (*Increase the contribution of agriculture and forestry to maintaining and enhancing biodiversity*), and Action 20 in Target 6 (*Help avert global biodiversity loss*). Some of these actions emphasize the importance of conserving genetic resources in an socio-economic context, similar to the Aichi target 13 in the Strategic Plan for Biodiversity 2011–2020 (United Nations Environmental Programme, 2010), and only Action 20 in Target 6 includes the protection of genetic resources in wild species due to their pivotal role in the protection of global biodiversity.

The low impact of genetic and evolutionary biology studies on EU conservation programs or policies (Laikre, 2010; Santamaría and Méndez, 2012) has partly been attributed to the poor accessibility of

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scientific studies to stakeholders (Fuller et al., 2014; Hoban and Vernesi, 2012) and a lack of communication and collaboration between scientists and conservation practitioners (Lacy, 1988; Smith et al., 2009). However, a number of EU-funded initiatives have attempted to increase collaboration between academics and conservation stakeholders. These have included EUFORGEN (European Forest Genetic Resources Programme, euforgen.org), PGR Secure (Plant Genetic Resources Secure, pgrsecure.org), and ConGRESS (Conservation Genetic Resources for Effective Species Survival; congressgenetics.eu).

The ConGRESS project, in particular, has served as a platform for increasing communication and knowledge transfer between conservation geneticists and conservation practitioners across Europe (Hoban et al., 2013a). A key finding of the ConGRESS project was that within the policy and management community there was very limited knowledge of published genetics studies on European threatened taxa, and an assumption that relevant studies were lacking (Hoban et al., 2013a). Here, we present the first comprehensive assessment of conservation-relevant genetic studies in European species. The main aims of this study were to provide absolute measures and temporal patterns of i) the volume of conservation genetics research available for European species; ii) biases and gaps of research towards certain taxonomic groups or species with a particular conservation status; iii) the topics that conservation genetics research has focused on; iv) the use of different genetic markers; and v) the journals where the majority of conservation genetics research has been published.

2. Methods

Analyses were restricted to studies published in peer-reviewed scientific journals that were indexed in publication databases. Conservation or management organisations' reports, the so-called 'grey literature' were not included in this study, although these can include relevant genetic information (Haddaway and Bayliss, 2015). The scope of the assessment included research mainly conducted in the current 28 EU Member States, from 1992 until 2014. The following information was gathered from each publication: journal and citation details, species studied, IUCN conservation status for the species under study, topic(s) of the study, and genetic marker(s) used. Publication details were gathered between 2011 and 2015 by searching the ISI Web of Knowledge, Google Scholar and Google using all possible combinations of the terms *conservation*, *management*, *genetics*, *biodiversity*, *Europe*, *European*, names of main taxonomic groups, and the names of 348 species considered of relevance in EU conservation and management programs, either for their conservation status, economic or recreational value, invasive nature, or their importance as wild relatives of crops (see Tables S1–S5). Gathering of publications was not limited to those including the 348 initially selected species; the final data set included studies for over 1500 species. The terms for 'topics of study', 'genetic markers' and species of concern were selected through discussions between scientists and conservation practitioners during meetings and workshops organised by the ConGRESS consortium.

A relational database to gather information from publications was developed and populated using FileMaker v. 10 (FileMaker Inc.). Over 10000 publications were initially evaluated. To proceed to full evaluation, they were required to comply with the two main criteria. The first criterion was that the publication included an empirical study using molecular genetic data. Reviews, theoretical papers, and population viability analyses were not included in this study; although they represent important contributions to conservation genetics, these were out of the scope of this study. The second criterion was that the study needed to include samples from wild populations collected in EU Member States, including the outermost regions of the Azores, Madeira, Canary Islands, and those considered as special Member State territories, e.g. Channel Islands, Faroe Islands, Gibraltar. A total of 4311 publications complied with the above criteria and were selected for further analyses. Studies were individually evaluated with details for all of the following variables recorded:

taxonomic information, IUCN conservation status, topic of study, genetic markers, and journal where the study was published. Multiple entries for each of the variables were recorded if applicable (i.e. a publication could cover several topics, use different genetic markers, and study more than one species). The conservation status of species was collated from the IUCN Red List of Threatened Species (<http://www.iucnredlist.org>). Data were exported to Excel v. 15.19 (Microsoft) and evaluated in terms of percentage of studies conducted for any particular variable of interest, as well as the number of studies per year for any given variable. To evaluate research effort within each taxonomic group, counts of species per taxonomic group were used to standardise the data. Counts for animal species were collated from all the available European Red List reports (<http://www.ec.europa.eu/nature/conservation/species/redlist/>) and Fauna Europaea's online resource (<http://www.faunaeur.org>). For vascular plants, a total number of 25000 species were assumed and the number of vascular plant species per order was collated from Flora Europaea (Halliday, 1983; Tutin et al., 1968, 1972, 1976, 1980; Tutin et al., 1964) following the Angiosperm Phylogeny Group (APG) III classification system (APG III, 2009).

Statistical analyses were conducted using the software XLSTAT v. 20016.04.32331 (Microsoft). Potential taxonomic bias in genetic research within taxonomic groups was evaluated by visualising the data in a scatterplot in which percentage of studies evaluated for an order was plotted against the percentage of species within that taxonomic order. Trends in the number of studies across years for all the studied variables were evaluated through time series analyses. Smoothing of the data was conducted using a model of moving average with equal weights. Mann-Kendall trend tests were used to identify statistically significant trends, and the Pettitt's test was used to evaluate homogeneity of the trend and identify the time of shift for increasing values in the distribution.

3. Results and discussion

3.1. Taxonomic bias in genetic research

Genetic research was found to be biased towards certain taxonomic groups. In absolute number of studies, the most studied taxonomic groups were mammals and vascular plants, with 25% and 24% of the studies, respectively. Following these were arthropods (14%), fish (11%), birds (10%), molluscs (5%), reptiles (4%) and amphibians (3%). Only 9% of the studies were conducted in the remaining other 11 taxonomic groups analysed (Table S2). For the eight most studied taxonomic groups (listed above) research significantly increased over the years (all Mann-Kendall tests $P < 0.0001$; Fig. 1a). Research on mammals and vascular plants have predominated since the early 1990s, with research on arthropods considerably increasing during the latter years analysed. The increase in number of studies was not homogeneous across time (all Pettitt's tests $P < 0.0001$), with 2002 identified as the shift year (i.e. the year for which the average of number of studies increased considerably) for all groups listed above except molluscs, for which 2001 was identified as the shift year. This notable increase in the number of studies during the early 2000s coincides with the time when genetic analyses became more applicable and cost-effective for a wide range of organisms (Frankham, 1995; Sunnucks, 2000).

Taxonomic bias in research has been previously reported in taxonomy (Gaston and May, 1992) and conservation biology (Clark and May, 2002); however, some of the patterns of taxonomic bias found in our analyses differed from previous reports. Taking into account the total number of species in each taxonomic group in Europe, genetic studies on birds and fish were not overrepresented; on the contrary, research on these two taxonomic groups was underrepresented. These results were unexpected considering that funding for conservation projects and research is predominantly on mammals and birds (Clark and May, 2002; Metrick and Weitzman, 1998), and specific conservation policies for the protection of birds such as the EU Birds Directive exist in Europe (European

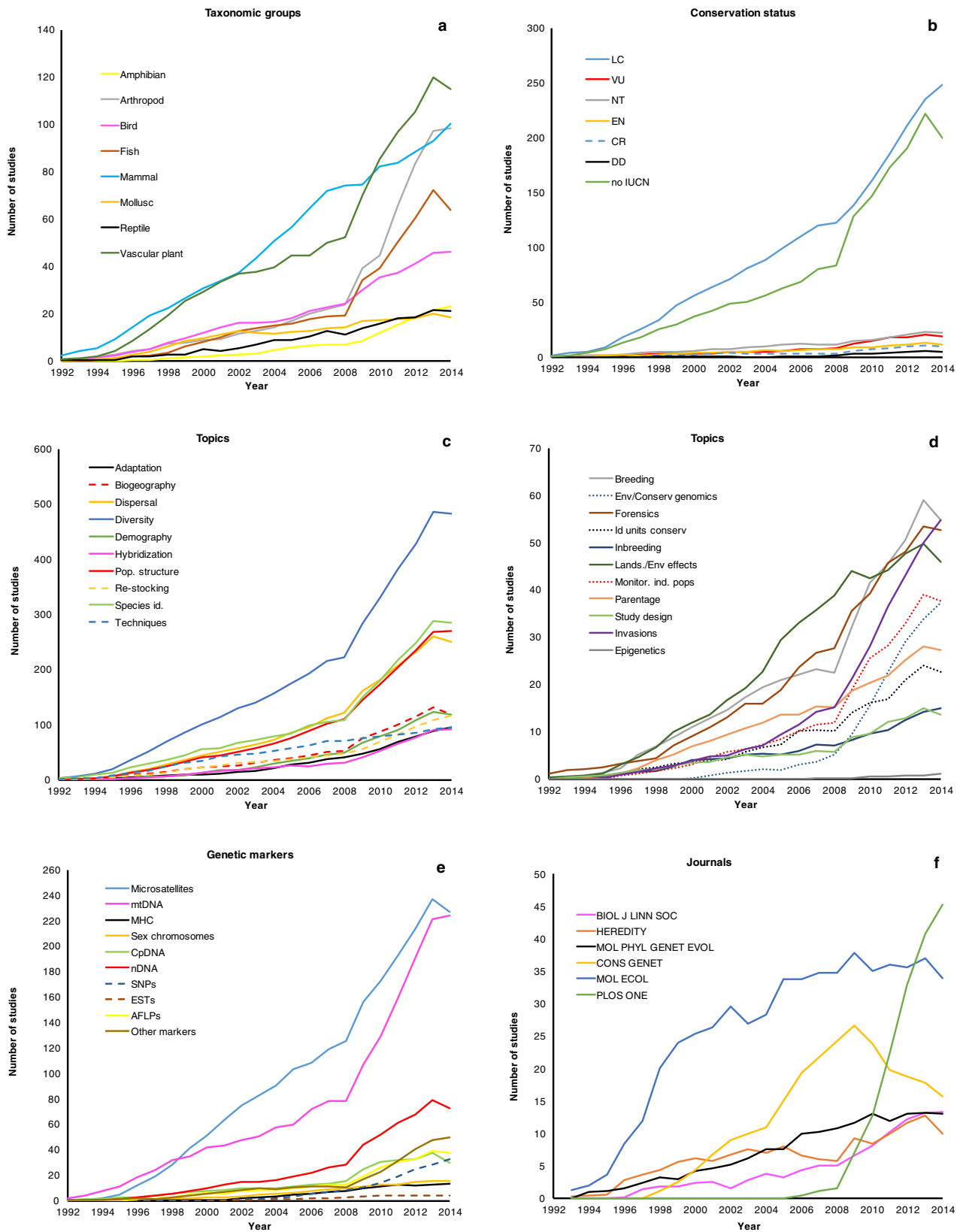


Fig. 1. Annual trends of variables assessed from 4311 publications useful for conservation and management programs of European species. In order, variables were: main taxonomic groups (a), IUCN conservation status (b), topics studied (c & d), genetic markers used (e), and journals (f). For all the time series a significant increase was confirmed by Mann-Kendall tests ($P < 0.0001$).

Commission, 2010). Similarly, the underrepresentation of research on fish was also unexpected, given serious threats to marine ecosystems and the fact that at least 80% of the commercially exploited marine species in the

EU are affected by overfishing (Nieto et al., 2015). Conversely, genetic studies on molluscs were overrepresented, while the percentage of genetic studies on amphibians and reptiles were more balanced, in contrast to

the previously reported underrepresentation of these two taxonomic groups in conservation research (Clark and May, 2002).

Research bias within taxonomic groups was also evident (Fig. 2a & b), with more studies on orders containing species with an economic or recreational value, and orders with iconic or emblematic species. The strongest bias was found towards the study of Bivalvia (bivalves) and Galliformes (gamebirds) and, to a lower extent, Testudines (turtles, tortoises, and terrapins), Salmoniformes (salmonids), Accipitriformes (most of the diurnal birds of prey), Carnivora (carnivores), and Ungulates. The most understudied orders were Gastropoda (snails and slugs) and 'Other vascular plants' (this category included 26 vascular plant orders for which <10 studies were recorded) and to a lesser extent Rodentia (rodents), Coleoptera (beetles), and 'Other fish' (this category included 14 fish orders for which <10 studies were recorded). Closer inspection of the densest region within the scatterplot revealed similar trends, with an overrepresentation of studies on economically important or iconic species (Fig. 2b). The most studied species within groups were: the red deer (*Cervus elaphus*) representing 8.38% of the mammal studies, the olive tree (*Olea europaea*) in vascular plants (4.08%), the honey bee (*Apis mellifera*) in arthropods (5.11%), the brown trout (*Salmo trutta*) in fish (18.13%), the capercaillie (*Tetrao urogallus*) in birds (4.95%), the Mediterranean mussel (*Mytilus galloprovincialis*) in molluscs (15.48%), the loggerhead turtle (*Caretta caretta*) in reptiles (11.05%), and the common frog (*Rana temporaria*) in amphibians (20%).

Taxonomic bias was also found to exist at the level of European conservation programs. Conservation stakeholders consulted during the CONGRESS trans-border workshops identified three main taxonomic groups of concern - large carnivores, birds, and vascular plants (in particular forest trees) - with most concern expressed for the following species: brown bear (*Ursus arctos*), wolf (*Canis lupus*) and monk seal (*Monachus monachus*) in carnivores, bearded vulture (*Gypaetus barbatus*) and capercaillie (*Tetrao urogallus*) in birds, and European yew (*Taxus baccata*) in vascular plants. While a significant number of genetic studies are available for wolf, brown bear and capercaillie (all listed with a conservation status of least concern), limited genetic research is available for monk seal, bearded vulture and European yew, despite the two former species

being listed as endangered and near threatened, respectively (BirdLife International, 2015; Temple and Terry, 2007).

Research bias towards orders containing species important for hunting, fisheries and forestry is expected due to the larger financial resources dedicated to applied research; however, the unbalance in research effort described here is alarming. A greater emphasis on, and increased funding for, research across all taxonomic orders is urgently needed if we are to achieve the EU targets for the protection and maintenance of biodiversity. Furthermore, a greater coordination between researchers and stakeholders is also required to effectively implement the results from genetic research already conducted into EU conservation programs and policy, including the extensive genetic research already available for many taxa.

3.2. Conservation status

More than half (61%) of the publications analysed included at least one species in IUCN Red Lists. Of those studies including IUCN listed species, 78% were on species classified as least concern (LC), 8% vulnerable (VU), 6% near threatened (NT), 4% endangered (EN), 3% critically endangered (CR) and 1% data deficient (DD). The bias of research towards the study of species categorised as LC is not characteristic of conservation genetics research alone but has also been reported in other conservation research areas or projects (Seddon et al., 2005; Sitas et al., 2009). However, it should be noted that most of the species (plants and animals) listed in European IUCN Red lists have been classified as LC. Studies on listed species were predominantly on mammals (c. 40%), followed by vascular plants (c. 17%), fish (c. 15%), and birds (c. 12%). The time series analyses revealed a broad increase in genetic research on species within all IUCN conservation categories (Mann-Kendall tests, $P < 0.0001$; Fig. 1b), with significant increases in studies in the years 2001 (VU, CR), 2002 (LC, NT, EN) and 2004 (DD); Pettitt's tests $P < 0.0001$. The increase in genetic research on species with an assessed conservation status is positive, but a concerted strategy to fill research gaps on species with a more threatened or undetermined conservation status is required.

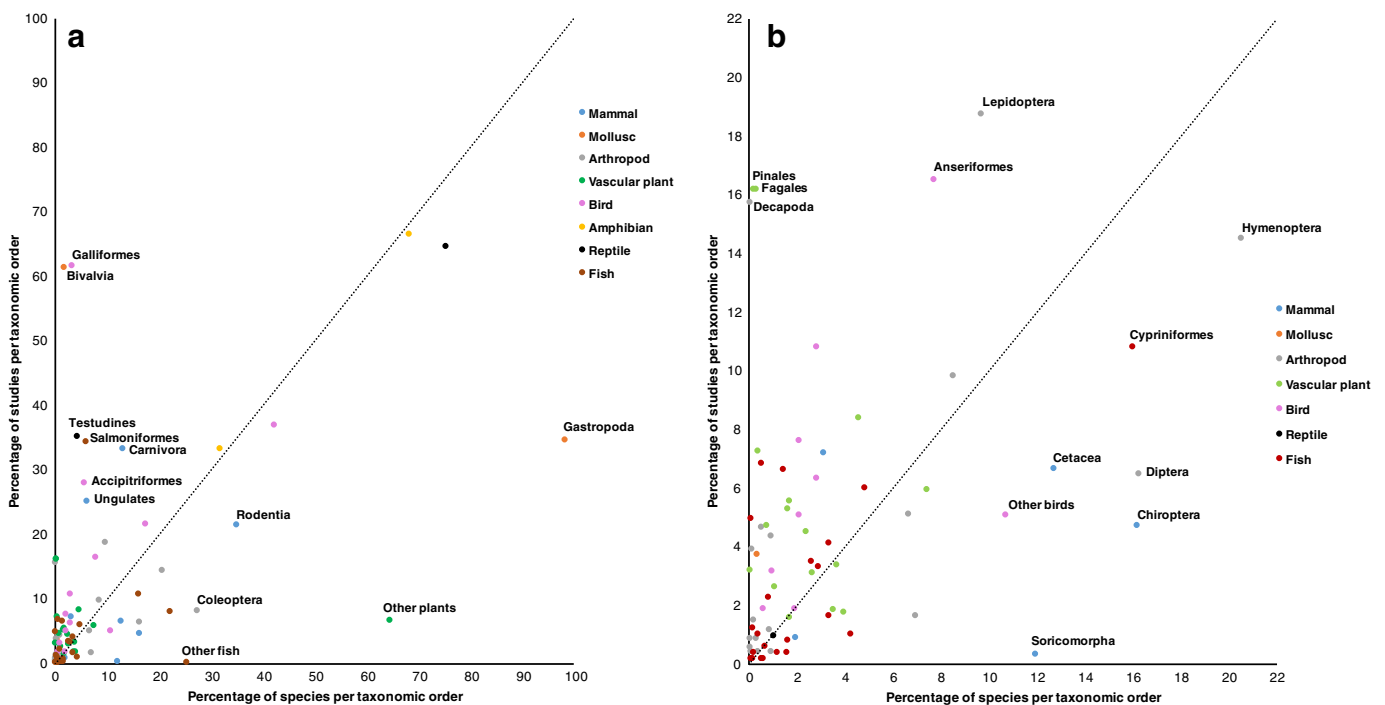


Fig. 2. Assessment of bias in genetic research within taxonomic groups. The diagonal dotted line indicates balanced research (i.e. percentage of genetic studies equals percentage of species within the taxonomic order). Dots further from and above the dotted line indicate overrepresented orders. Dots further from and below the dotted line indicate underrepresented orders. The area with the highest density of points is zoomed and represented in a separate graph (b). Taxonomic orders for which the largest biases were found have been labelled in the graph.

3.3. Study topics

The classification of studies by selected topics indicated that estimates of genetic diversity predominate, as over 95% of the studies included genetic diversity measures. Following this, the topics most studied were species (or haplotypes) identification and relationships (52.3%), dispersal (48.9%), population structure (47%), genetic techniques (25%), biogeography (23.7%), re-stocking and selective harvest (21%), and demography (20.4%). Research on all the selected topics was found to have significantly increased over the years (Mann-Kendall tests $P < 0.0001$, Fig. 1c & d), in particular since the year 2002, except for epigenetic studies for which a significant increase occurred in 2006 (Pettitt's tests $P < 0.0001$). Despite several reviews on the advent of genomics and its potential applications for conservation since the early 2000s, studies on adaptation or environmental/conservation genomics were less abundant than expected. This can be mainly attributed to the fact that genomics techniques, and the associated computational tools, are still not affordable and/or tailored to address conservation-related issues (Frankham, 2010; Luikart et al., 2003; Shafer et al., 2015). Other topics for which research was limited concerned issues important for the protection and day-to-day management of species and populations, such as inbreeding depression, the definition of conservation/management units, and wildlife forensics. In fact, the ranking of topics studied did not coincide with the use of genetics by European conservation practitioners consulted by ConGRESS. The conservation stakeholders consulted indicated that the use of genetics in their programs was mainly for identifying units for conservation, monitoring individuals and populations over time, species identification and taxonomy, and to a lesser extent to estimate population sizes, measure inbreeding, and obtain estimates of connectivity and hybridization (Hoban et al., 2013a; Hoban et al., 2013b). These findings highlighted the differences between conservation stakeholders priorities and conservation genetics research (Salafsky et al., 2002; Vernesi et al., 2008).

For an effective integration of genetic studies into conservation programs and policy in Europe, it is crucial to establish collaborative initiatives between scientists and stakeholders so research programs are better designed to provide relevant and feasible solutions to current conservation issues (Hoban et al., 2013a; Soulé and Wilcox, 1980). The IUCN has done remarkable work to establish collaborations between researchers and practitioners to implement genetics in their projects such as the identification of Key Biodiversity Areas (Brooks et al., 2015), and the conservation of many species through the actions of the IUCN Conservation Breeding Specialist Group. Similar efforts are needed in other areas within the conservation biology community, in addition to a more effective communication of genetic research outcomes beyond the scientific circles (Bickford et al., 2012; Wilson et al., 2016). There is a perception that conservation genetics is the weaker branch of conservation biology because academic scientists do not always appear to have a strong interest in the direct application of their studies to conservation programs (Soulé and Wilcox, 1980). This perception might be partly explained by the pressure on academics to win large grants and deliver high impact publications, both of which normally require large datasets obtained using state of the art techniques (Shafer et al., 2015; Vernesi et al., 2008). Research at this level contrasts with the more modest datasets and methods required for practical conservation projects. If we are to make conservation genetics research pivotal to achieving conservation targets, the disconnect between the drivers of academic research and conservation targets needs to be acknowledged and addressed within academic environments and by funding agencies.

3.4. Genetic markers

Microsatellites were the genetic marker most widely used in the publications analysed (49% of the studies), followed by mtDNA sequences (39.4%), and nuclear sequences (12.6%). The use of all types of genetic markers increased over the years (Mann-Kendall tests

$P < 0.0001$; Fig. 1e), with a predominance in the use of microsatellite and mtDNA sequences prevailing to the present day. An increase in the use of all markers was detected in 2002, except for chloroplast DNA sequences for which the increase was detected in 2003 (Pettitt's tests $P < 0.0001$). The wider use and applicability of microsatellite markers confirmed that these are still the preferred marker for conservation genetic studies (DeSalle and Amato, 2004; Frankham, 2003; Goldstein and Schötterer, 1999; Hedrick, 2001; Jarne and Lagoda, 1996). Despite the typical requirement to develop species-specific microsatellite markers, their high polymorphism, amenity to multiplex high-throughput analyses, and the large number of free statistical software packages available still makes microsatellites a cost effective and versatile marker to assess multiple topics relevant to conservation and management programs (DeSalle and Amato, 2004; Goldstein and Schötterer, 1999; Jarne and Lagoda, 1996; Sunnucks, 2000). The analyses of mtDNA sequences for identifying species and understanding their relationships, in particular since its re-branding as DNA barcoding (Hebert et al., 2003), has overcome some of the problems associated with traditional taxonomy (e.g. cryptic species) that could have slowed down species protection (Bickford et al., 2007; Standley, 1992). The application of DNA sequences in general has recently increased due to their usefulness for monitoring biodiversity (Hajibabaei et al., 2007), to identify the presence of invasive (or alien) species (Darling and Blum, 2007), to determine the diet of protected species (Valentini et al., 2009), and for wildlife forensics (Alacs et al., 2010).

Recent technological innovations in genetic techniques such as the genotyping of a large number of Single Nucleotide Polymorphisms (SNPs) were predicted to supersede the use of more traditional genetic markers such as microsatellites, due to the higher abundance in the genome and the simpler mutation models of SNPs (Morin et al., 2004). However, the application of SNPs was found to be limited (3.71% of the studies). The slower uptake of SNP genotyping can be partly explained by the higher economic cost and time needed to develop and analyse SNPs markers in non-model organisms (Helyar et al., 2011), as well as to scientific inertia. Similar reasons explain the less widespread use of other markers suitable for studies on adaptation such as the Major Histocompatibility Complex (MHC) despite their importance for determining the genetic potential of wild animal populations to combat future disease outbreaks, in particular in the context of climate change and the associated emergence or re-emergence of disease in wildlife (Altizer et al., 2003).

Closer examination of the use of genetic markers in the most studied taxonomic groups (Fig. 3) showed that microsatellites have been predominantly used in mammals (29.1% of studies) and vascular plants (23.7%); followed by studies on fish (13.1%), birds (11.5%) and arthropods (10.5%). mtDNA sequences were also predominantly used in mammals (30%), followed by studies on arthropods (22.2%), fish (12.7%), and birds (12%). For other genetic markers, the patterns were as follows: nuclear sequences were predominantly used in studies on vascular plants (37.3%) and arthropods (20.8%); cpDNA sequences were mainly used in vascular plants (93%), but also in different animal taxonomic groups for diet studies; AFLPs in vascular plants (77.8%); SNPs in vascular plants (27.4%) and mammals (26.2%); sex chromosome DNA sequences in mammals (70.6%) and birds (21.7%); MHC sequences in mammals (52.9%) and birds (26.9%); ESTs in vascular plants (61.3%) and fish (16.1%). 'Other markers' which included allozymes, RAPDs, ISSRs and genomic approaches have been mainly used in vascular plants (39.2%).

3.5. Journals

A total of 82 out of 511 scientific journals contributed to ≥ 10 of the studies evaluated (Table S5), indicating a widespread interest in the publication of genetic studies by many journals. The journal for which the highest number of studies was recorded was *Molecular Ecology*, with 13% of the studies; followed by *Conservation Genetics* (5.8%), *PLoS*

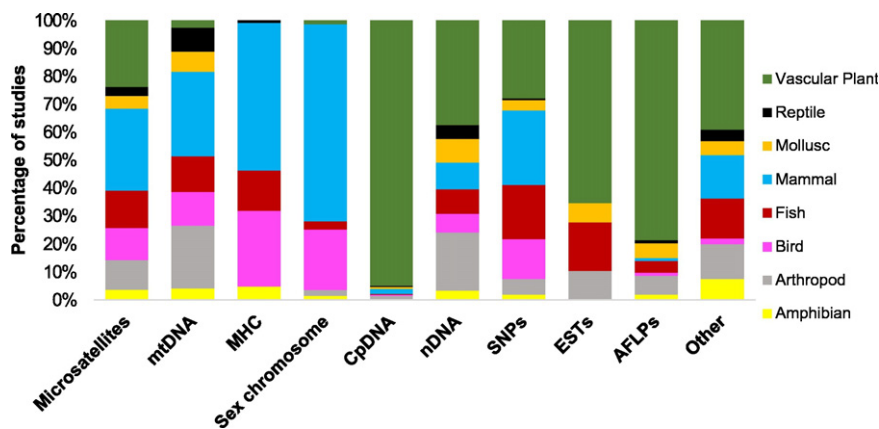


Fig. 3. Use of different genetic markers across the most studied taxonomic orders. Note: cpDNA used in animal groups is from diet studies.

One (4.04%), *Molecular Phylogenetics and Evolution* (3.57%), *Heredity* (3.27%) and *Biological Journal of the Linnean Society* (2.34%). Time series analyses for these top six journals indicated that the number of genetic studies in these journals has increased over the years (Mann-Kendall tests $P < 0.0001$; Fig. 1f), with number of studies significantly increasing in 2001 for *Heredity*, 2003 for *Biological Journal of the Linnean Society*, *Conservation Genetics*, and *Molecular Phylogenetics and Evolution*, and 2004 for *Molecular Ecology* (Pettitt's tests $P < 0.0001$). For *PLoS One* the first year for which studies were assessed was 2007 following the initiation of this open-source journal in 2006. The annual trends of genetic studies in these six journals revealed some interesting publication dynamics. Although publications in *Molecular Ecology* have predominated since 1993, this journal has recently been superseded in publications by *PLoS One*. *Conservation Genetics*, although having a significant impact on the number of genetic studies published since its origins in 1999, has undertaken a noticeable decrease in publications since the year 2009, possibly due to the publication of genetic studies in other conservation relevant journals.

4. Conclusions

The achievement of the EU Biodiversity Strategy to 2020's targets is vital if we are to protect Europe's biodiversity as well as to guarantee Europe's economy and the well-being of its society. Conservation genetics research can provide important insights for the protection and management of European species; however, the impact of genetic research on EU conservation programs and policies is still low despite the availability of genetic research for many taxa. An increased synergy between conservation geneticists and conservation practitioners, and greater recognition for the achievement of conservation targets within academic environments would help to increase the impact of genetic research on conservation programs.

Taxonomic bias in conservation genetics research demonstrates the need for greater funding and research effort on the study of species with a more threatened status and species without an obvious economic value. From an academic point of view, conservation geneticists should aim to target their research on those topics most relevant to particular conservation and management issues. Furthermore, due to the unrealised potential of genomics in conservation, further technological and analytical development of genomics tools is required to make them cost effective and applicable to a wide range of conservation studies.

Conservation genetics was devised as a discipline to provide solutions that would help to maintain genetic diversity and avoid or decrease species extinction risks; a stronger commitment is needed to increase the number of research projects that achieve this goal. Furthermore, an explicit incorporation of genetics into conservation decision making and environmental law enforcement in the EU Member States

is crucial to increase the impact of conservation genetics research for the protection of Europe's biodiversity.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.biocon.2017.01.020>.

Author contributions

Sílvia Pérez-Espona developed and populated the database, conducted all statistical analyses and wrote the manuscript. The ConGRESS consortium actively participated in the selection of variables to be included in the database, with special mention to Richard Nichols and Mike Bruford.

Competing financial interests

The authors declared no competing interests.

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