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REVIEW PAPER

Habitat conservation research for amphibians: methodological improvements and thematic shifts

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Abstract Amphibian conservation is a central theme of biodiversity research, as demonstrated by the growing number of studies on this theme. I combined a review of the literature with a quantitative analysis of papers published from 1992 to 2013, to evaluate whether methodological and thematic shifts occurred during the last two decades, and to identify major lines along which amphibian biodiversity research may be developed and improved. Spatial autocorrelation and imperfect detection are major issues of the analysis of data from amphibian populations. During the last decade, technical developments allowed to take into account these statistical issues in a growing number of studies. Nevertheless, the use of these approaches may be more widespread, particularly for the analysis of spatially-autocorrelated data. It is widely recognized that amphibian decline is often determined by the joint effect of multiple processes. However, the majority of recent studies focused on one potential threat only, and research rarely integrated analyses on terrestrial and aquatic environments. Finally, tropical areas remain insufficiently represented in amphibian conservation studies, despite they harbour most of biodiversity and threatened species. A better incorporation of technical advancements, and an expansion of themes and geographical scope can improve our understanding of processes determining

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the amphibian biodiversity crisis, and to improve the linkages between conservation research and practical actions.

Keywords Habitat management · Global amphibian decline · Occupancy modelling · Spatial autocorrelation · Statistics · Tropical biodiversity

Introduction

Amphibians are an exemplary case of the global biodiversity crisis. The International Union for Nature Conservation (IUCN) has currently completed the assessment of 91 % of >7000 described amphibian species: 41.5 % of assessed amphibians are recognised as threatened by extinction, a figure higher than any other animal taxonomic group (Stuart et al. 2004; Chanson et al. 2008; Hoffmann et al. 2010; IUCN 2014). The amphibian

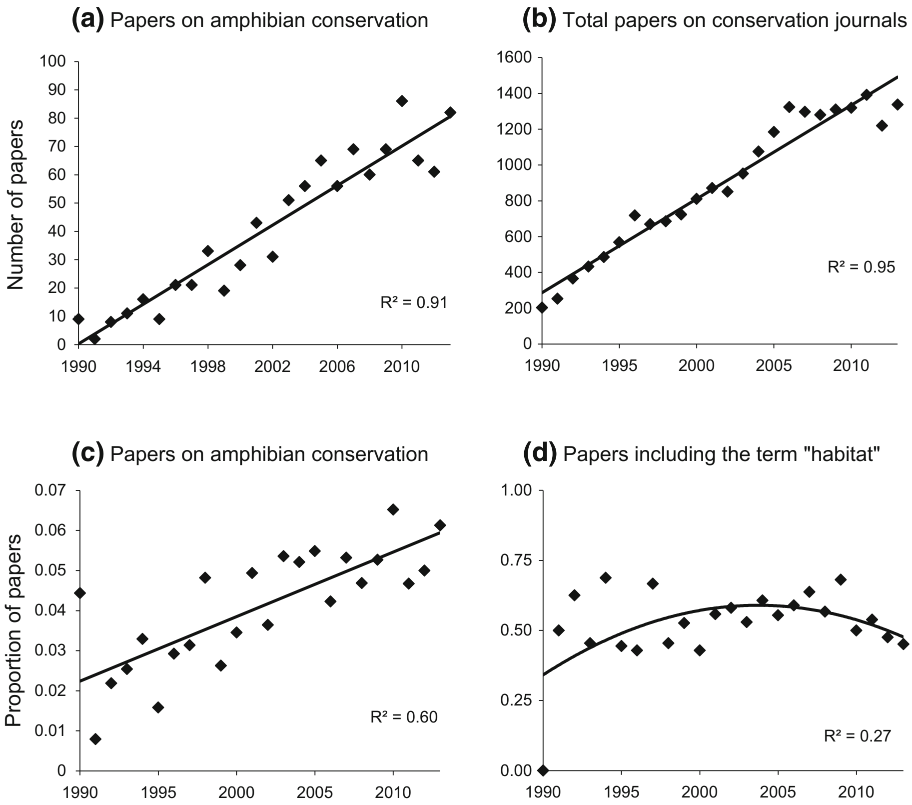

Fig. 1 Temporal variation of published papers in eight biodiversity conservation and applied ecology journals (Animal Conservation, Biodiversity and Conservation, Biological Conservation, Conservation Biology, Diversity and Distributions, Ecography, Ecological Applications, Journal of Applied Ecology). **a** Number of research papers or reviews including amphibian keywords; **b** total number of papers; **c** proportion of papers including amphibian keywords; **d** proportion of amphibian papers including the term "habitat"

biodiversity crisis has been recognised since the late 1980s (Barinaga 1990), and has stimulated a growing interest in ecologists and conservation scientists. More than two decades of research have documented worldwide patterns of decline and extinction (e.g. Pounds and Crump 1994; Houlahan et al. 2000; Lips et al. 2004, 2006; Botts et al. 2013), and have tried to identify the processes determining amphibian decline. It is now clear that the amphibian biodiversity crisis is not caused by one single agent, and multiple factors are currently recognised as major causes of amphibian conservation crisis. These include habitat loss and degradation, fragmentation of landscape and isolation, emerging infectious diseases, invasive alien species, climate change, pollution, UV-B radiation and human-caused mortality (Beebee and Griffiths 2005; Chanson et al. 2008). Some of these factors act in synergy, and their joint effect may have particularly severe consequences (Blaustein and Kiesecker 2002; Hof et al. 2012; Menéndez-Guerrero and Graham 2013). Nevertheless, habitat loss remains the major known threat for amphibians. Even if the impact of some processes (e.g. diseases, climate change) is probably underestimated because of limited data, habitat-related processes remain the threatening factors affecting the largest number of amphibian species. Actually, according to the global amphibian assessment, habitat loss or deterioration is a major threat for about 63 % of all amphibian species, while diseases impact about 10 % of amphibians (Chanson et al. 2008).

The amphibian biodiversity crisis has promoted studies on amphibian ecology and conservation. The growing number of studies on these themes during the last decades (Fig. 1a) now allows a better understanding of the processes underlying amphibian decline. In this essay, I combine a review of the literature with a quantitative analysis of published papers, to evaluate whether methodological or thematic shifts are occurring in studies focusing on habitat conservation for amphibians. Comparisons were performed for two key aspects: statistical approaches used, and themes considered. First, I evaluated to what extent recent developments in statistical techniques are routinely used by scholars, and whether there is a shift in the approach to data analysis. I focused on detection probability and spatial autocorrelation: these two topics have been the focus of major technical developments (reviewed below), and have been indicated as major issues in the analysis of relationships between amphibians and their habitat (e.g. MacKenzie et al. 2002; Miller et al. 2011; Ficetola et al. 2012a).

Second, I evaluated whether there is an increase in research focusing on three themes: interaction between breeding and terrestrial habitat, research in poorly studied tropical areas, and multiple potential threatening factors. Previous analyses identified these themes as areas were research efforts should be intensified to improve the conservation relevance of studies on amphibians (e.g. Blaustein and Kiesecker 2002; Cushman 2006; Schiesari et al. 2007; see below for a more complete review).

Quantitative analysis of the literature

I used the ISI Web of Science to quantitatively evaluate the patterns of publications on amphibian conservation. I searched for terms that refer to amphibians (*amphibian** or *frog** or *toad** or *newt** or *salamand** or *gymnophion** or *anura** or *caudat**) in the title, abstract or keywords of papers published in six major journals in the "*biodiversity conservation*" and "*ecology*" categories of the ISI Journal Citation Report (Animal Conservation, Biodiversity and Conservation, Biological Conservation, Conservation Biology, Diversity and Distributions, Ecography, Ecological Applications and Journal of Applied Ecology), considering "*articles*" and "*reviews*" only.

The search from 1990 to 2013 yielded 967 papers (Biological Conservation: 280 papers, Conservation Biology: 226; Biodiversity and Conservation: 117; Ecological Applications: 106; Ecography: 70; Animal Conservation: 66; Diversity and Distributions: 63, Journal of Applied Ecology: 39). There was an impressive and almost linear growth for the number of papers on amphibians in these journals during the last 20 years (Fig. 1a; Pearson's correlation: $r = 0.95$, $N = 24$, $P < 0.0001$). During the early 1990s, less than ten papers per year matched the search criteria, while $\sim$60 or more papers per year are currently published. This growth can be partially explained by the overall growth of conservation science, with more papers published each year in these journals, and with some journals that recently started publication (Fig. 1b). Nevertheless, there was also a proportional increase of amphibian papers. In the early 1990's, papers matching the amphibian keywords were about 3 % of all conservation papers, while they now are about 6 % ($r = 0.77$, $N = 24$, $P < 0.0001$; Fig. 1c). For comparison, amphibians represent 8.9 % of globally threatened species (IUCN 2014).

I then classified amphibian conservation papers considering habitat as those including the term "*habitat*" within title, abstract or keywords. On the basis of this search, about half of amphibian conservation papers considered habitat, and this proportion remained rather stable through time (Fig. 1d). The proportion of habitat papers showed a non-linear relationship with year [multiple regression also including a quadratic term: year: $F_{1,21} = 5.09$, $P = 0.035$; (year)^2: $F_{1,21} = 5.08$, $P = 0.035$; overall $R^2 = 0.27$; Fig. 1d], but the significance of the quadratic term mostly arose because the proportion of papers with the term "habitat" was zero in 1990 (Fig. 1d). It this outlier was removed, the trend and the quadratic term were not anymore significant [year: $F_{1,20} = 0.618$, $P = 044$; (year)^2:-$F_{1,20} = 0.617$, $P = 0.44$].

To ensure that these results are not biased by the search terms or by the limited set of journals, the analysis was repeated considering all the Web of Science Journals; the "amphibian conservation papers" where those containing the search terms *amphibian decline*∗ or *amphibian conservation*, and the "habitat papers" where those also containing the terms *habitat fragmentation* or *habitat loss* (i.e., the same search terms used by Ohmer and Bishop 2011). This second search yielded consistent results, with a strong increase of the number of amphibian conservation papers, but a non-linear pattern for habitat papers, with a possible decline in the last years (Fig. S1). Analyses covering the period 1990–2009 suggested that the research interest on amphibian habitat conservation remained rather stable during the last 20 years, but also observed that papers on habitat loss received less citation and/or were published in journals with lower impact factor, compared to the ones on chytridiomycosis and climate change (Ohmer and Bishop 2011). As research on chytridiomycosis and climate change is perceived as being more "innovative", it may have gained more visibility and interest (Ohmer and Bishop 2011). In the long term, this might determine a lower research effort on habitat loss, which nevertheless remains a major issue with high scientific uncertainty (Gardner et al. 2007).

Subsequently, to evaluate in detail trends in research, I closely examined and reviewed research papers published in three periods: 1992–1994; 2000–2002 and 2011–2013 (Table S1). I started from the full list of amphibian habitat papers retrieved from the journals belonging to the "*biodiversity conservation*" and "*ecology*" categories. This list (176 papers) was refined manually, by examination of all the abstracts and full texts of papers. I identified primary research papers that considered into analyses the relationships between environmental factors and parameters of amphibian populations or communities: distribution and abundance, community richness and structure, genetic diversity, dispersal or other fitness components. Comparisons of proportions among the three periods were performed using likelihood ratio tests.

Improvement of statistical approaches

Taking into account detection probability

All field biologists are aware that, during surveys performed in natural environments, detecting all the species and the individuals is impossible. In other words, detection probability of species and individuals is always <1. Detecting amphibians may be particularly difficult, as many species have cryptic colour, are nocturnal, live underground or in turbid water, are active during short periods of the year and under specific weather conditions (e.g. mostly in rainy periods) (Mazerolle et al. 2007). However, traditional analyses (e.g. generalized linear models, most ecological niche models…) are often performed under the implicit assumption that detection probability is one: incorrectly assuming perfect detection may bias the results and interpretation of analyses. Effects of non-detection on regression analyses include modification of regression coefficients and increase of their standard errors (Gu and Swihart 2004; Lahoz-Monfort et al. 2014).

Therefore, in the last years an increasing number of approaches have been developed to analyse species distribution data, taking into account imperfect detection. An exhaustive review of these methods is beyond the aim of this paper, and interested readers may refer to more extensive work (MacKenzie et al. 2006; Mazerolle et al. 2007; Gotelli and Colwell 2011). Imperfect detection and incompleteness of inventories may be taken into account using multiple approaches, which can be applied at both local and broad scales. For instance, imperfect detection is routinely integrated in the analysis of capture—mark—recapture data, allowing estimates of population size or trends, and of the environmental drivers of population declines or increases (Schmidt 2004; Schmidt et al. 2005). Furthermore, biologists performing biodiversity inventories are aware that detecting all the species within one area is challenging, and developed approaches such as accumulation curves, to estimate the completeness of their biodiversity estimates (Colwell and Coddington 1994; Gotelli and Colwell 2011). At the landscape scale, amphibian inventories such as calling surveys may not detect and misidentify species. Recognizing this limitation has fostered the development of methods taking into account imperfect detection in patch occupancy analyses (MacKenzie et al. 2002; Miller et al. 2011). Biodiversity knowledge is also incomplete at the broadest scale, and information on the quality of data can be integrated into marco-ecological models, for instance by considering measures of sampling effort or of accessibility (Phillips et al. 2009; Ficetola et al. 2013). Neglecting imperfect detection may have serious consequences for conservation: for instance, the decline of shrinking population may remain undetected (Schmidt 2004; MacKenzie 2005), and analyses may fail to identify the habitats favouring the presence of target species (Gómez-Rodríguez et al. 2012; Lahoz-Monfort et al. 2014). As a consequences, managers may miss populations requiring conservation, or may prioritize the preservation of the wrong environmental features (MacKenzie 2005).

How frequently is detection probability integrated in amphibian conservation studies? The analysis of imperfect detection is a recent field. For instance, the first methods taking into account imperfect detection in occupancy analyses have been published less than 20 years ago (Boulinier et al. 1998; Cam et al. 2000; Nichols et al. 2000; MacKenzie et al. 2002), therefore it is not surprising that none of the papers published in 1992–1994, and

10 % only of papers published in 2000–2002 considered the issues of imperfect detection (Fig. 2, Table S1). Approaches frequently used in this period included accumulation curves that, for instance, allow comparisons among sites with different sampling efforts (Andreone et al. 2000). Amphibian biologists are increasingly aware of the problem of imperfect detection and, as a consequence, the proportion of studies considering this issue significantly increased: 58 % of recent studies considered imperfect detection, with a clear increase across the three periods ($\chi^2_2 = 29.6$, $P < 0.001$) (Fig. 2, Table S1), indicating that the detection probability approach is becoming well integrated in the toolbox of amphibian conservation ecologists. It should be remarked that explicit modelling of detection probabilities is not always necessary, and should not be uniformly adopted by all the studies (see Banks-Leite et al. 2014; Guillera-Arroita et al. 2014 for discussions). For instance, variation in detection probability may be controlled through appropriate study design (Banks-Leite et al. 2014), even though effectively standardizing field methods is extremely difficult (Schmidt 2005). Furthermore, the relevance of detection probability issues also depends on research questions, and imperfect detection of individuals may be not a major issue for certain study typologies (e.g. some studies on movement or population genetics).

Nevertheless, there is still room of for a better integration of detection probability analyses in studies of amphibian habitats. Recent developments allow to integrate detection probability into models even if part of sites are surveyed only once (e.g. Gómez-Rodríguez et al. 2012). Furthermore, accessible software allows a straightforward implementation of computationally intensive techniques, such as Bayesian hierarchical models (Kéry et al. 2009; Kéry 2010; Ferreira and Beja 2013), that may run at a useful speed with the present-day computation power. In some cases taking explicitly into account detection probability may be complex, such as in community analyses, nevertheless approaches are emerging to combine detection probability of multiple species, and draw more accurate conclusions at

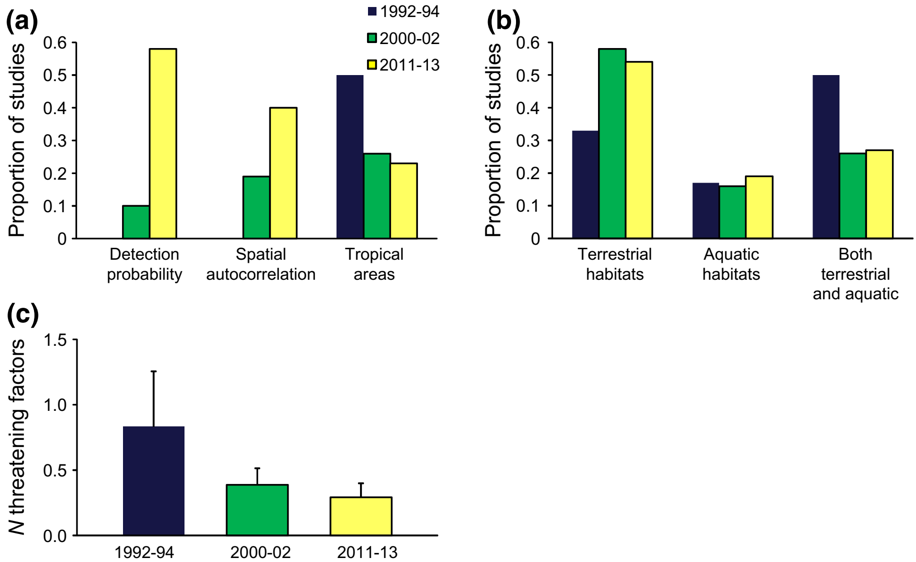

Fig. 2 Temporal variation for **a** proportion of studies considering detection probability, spatial autocorrelation, or tropical areas; **b** studies focusing on terrestrial and aquatic habitats; **c** number of threatening factors considered, beside habitat. In **c**, *error bars* are standard errors of the mean

the community level (Royle and Dorazio 2008; Ferreira and Beja 2013). Even in the most complex situations, or when performing complex analyses may appear not necessary, researchers should provide measures of the level of the effectiveness of their sampling strategy (Banks-Leite et al. 2014), which may help to identify potential limitations of analyses.

Spatial autocorrelation

Spatial autocorrelation (SAC) is pervasive in ecological data. Spatial autocorrelation arises when nearby localities have similar values for the measured parameters, such as abiotic features, habitat and species distribution data (Legendre 1993; Dormann et al. 2007; Ficetola et al. 2012a). SAC of biological data may be determined by two major pathways (Wagner and Fortin 2005). First, species are often related to environmental features (such as habitat, climate, resources, topography…) which in turn show SAC. In this case, SAC of distribution data is a consequence of the dependence of species from these exogenous variables. Second, species distribution data can be spatially autocorrelated because of endogenous biological processes such as aggregation, dispersal, competition or metapopulation processes. SAC has been considered for many years as a potential source of bias for ecological analyses (Legendre 1993; Dormann 2007), as it violates the assumptions of independence of classical statistical models such as regression and ANOVA (Lichstein et al. 2002; Wagner and Fortin 2005). Several analyses showed that not considering autocorrelation may be a major source of bias. Ignoring autocorrelation may lead to overestimating the significance of variables (spatial pseudoreplication) (Hurlbert 1984; Legendre 1993; Dormann 2007) and may bias regression coefficients, therefore leading to erroneous interpretation of data. For instance, Kühn (2007) analysed relationships between the species richness of plant communities and environmental features in Germany. Using traditional linear regression, he observed a positive relationship between community richness and altitude. However, the relationship between species richness and altitude become negative when SAC was integrated into the model, probably because in this area altitude increased from north to south, so that the pattern of latitudinal increase of biodiversity was confounded by an opposite pattern of altitudinal decrease (Kühn 2007). The increasing concern on the issues associated with spatial autocorrelation has led to multiple calls for the integration of SAC into models (Dormann 2007; Kühn 2007; Veloz 2009; Hawkins 2012), and to the development of techniques to take into account SAC, or to remove it from models (see Dormann et al. 2007; Beale et al. 2010 for description and evaluation of the performance of multiple approaches).

Spatial autocorrelation is pervasive in amphibian distribution data, as adjacent sites are often occupied by the same species. In amphibian distribution data, SAC may arise because of both extrinsic factors (autocorrelation of habitat) and endogenous processes determining clustering of populations, such as dispersal. For instance, an analysis on the fire salamander *Salamandra salamandra* showed that streams that are up to 2,000 m apart have very similar occupancy, because they share analogous habitat features. Even if the effect of habitat was partialled out, autocorrelation remained strong and significant at distances to 500 m, and this probably corresponds to the distance at which populations are connected through dispersal. In other worlds, streams that are less than 500 m apart show very similar occupancy, independently from habitat features (Ficetola et al. 2012a). Not considering SAC would lead to the confusion between the effect of habitat and dispersal, limiting understanding of the drivers of salamander distribution. If explicitly accounted for, autocorrelation may provide information on dispersal processes that are relevant to ensure population persistence.

Is spatial autocorrelation integrated in analyses of relationships between amphibians and habitat? Many researchers are aware of the issues of spatial autocorrelation, and used different approaches to take it into account (Table S1). First, they try to select study sites that are spatially independent, for instance by avoiding overlapping terrestrial buffers (Carr and Fahrig 2001; Ficetola et al. 2009; Eigenbrod et al. 2011). Nevertheless, simulations suggest that this approach is not a good option (Beale et al. 2010). Others have used approaches developed to take into account spatial autocorrelation. Such spatially-explicit techniques have been mostly developed during the last years, still several researchers already attempted to take into account SAC in the 2000–2002 period (Hazell et al. 2001; Scribner et al. 2001) (Table S1). Overall, none of the 1992–1994, and 19 % only of the 2000–2002 studies considered the SAC issue. This figure doubled during 2011–2013 (40 %), with a significant increase across the three periods ($\chi^2_2 = 8.1$, $P = 0.018$). Nevertheless, SAC gained popularity less quickly than detection probability between 2000–2002 and 2011–2013 (Fig. 2a).

The complexity of some of the statistical techniques for SAC analysis may be a major limitation to the diffusion of these approaches. Furthermore, SAC issues are not relevant to certain study typologies, such as those focusing on one site only, or those analysing temporal series, although other issues (e.g. temporal autocorrelation, non independence from nearby sites) must be taken into account. SAC analysis is particularly important in studies collecting spatially-replicated data, which currently constitute the majority of amphibian conservation papers, and is also relevant in analyses using presence-only or presence-background data (Veloz 2009). The recent availability of user friendly (e.g. Spatial Analysis in Macroecology; Rangel et al. 2010) and freeware software (e.g. packages spdep and nlme in R: http://www.r-project.org) for spatially explicit analyses should favour the diffusion of this approach, improving our understanding of the role of spatial processes on amphibian distribution.

Themes and geographic coverage

Not just ponds: integrate landscape and more

Amphibians are often described as "semi-aquatic", because many species require water for breeding, but not for post-breeding activities. The adults perform post-breeding migrations, and come back to the terrestrial habitats where they spend the rest of the year. In the scientific literature, there have been repeated calls for more attention toward landscape (Semlitsch and Bodie 2003; Cushman 2006; Schmidt 2008). First, even though juvenile survival and recruitment are certainly important (Hels and Nachman 2002), in many cases mortality during adult life stages has the strongest impact on population dynamics (Vonesh and De la Cruz 2002; Govindarajulu et al. 2005). For the species with terrestrial adults, alterations of upland habitats make the environment unsuitable, hampering species persistence. Furthermore, the landscape surrounding breeding wetlands is extremely important for dispersal. Habitat split and fragmentation impede dispersal, disrupting the dynamics of extinction/colonization associated with metapopulations (Ficetola and De Bernardi 2004; Willson and Hopkins 2013), cause genetic drift and loss of genetic diversity (Hitchings and Beebee 1997, 1998; Rowe et al. 1999; Ficetola et al. 2007; Johansson et al. 2007), and may ultimately result in loss of fitness (Hitchings and Beebee 1998; Rowe et al. 1999; Rowe and Beebee 2003; Ficetola et al. 2007; Johansson et al. 2007) and population extinctions (Saccheri et al. 1998; Ficetola and De Bernardi 2004; Becker et al. 2007; Willson and Hopkins 2013). Actually, the presence of terrestrial habitat nearby breeding wetlands has been proposed as a major parameter to assess threat status of species (Almeida-Gomes et al. 2014). In addition, the terrestrial and aquatic environments are not independent. Terrestrial ecosystems can provide a subsidy of energy to freshwaters (Pace et al. 2004; Jansson et al. 2007), and the alteration of terrestrial landscapes influences both chemical and physical features of freshwaters, with relevant effects on communities of aquatic and semiaquatic organisms (Dunham and Rieman 1999; Kiffney et al. 2003; Allan 2004). Therefore, the modification of terrestrial habitat can have indirect effect on aquatic life stages, mediated through the modification of waterbodies. Actually, in some cases landscape modifications may have an impact on aquatic community of amphibians, that is stronger than the effect of alteration of aquatic environments (Ficetola et al. 2011). Finally, many amphibian species are completely independent from water (Gomez-Mestre et al. 2012). Examples of fully terrestrial amphibians include some of the most species rich clades, such as the frogs belonging to the Terrarana clade (families Brachycephalidae, Ceuthomantidae, Craugastoridae, Eleutherodactylidae and Strabomantidae; >1,000 described species), or most of plethodontid salamanders.

Nevertheless, amphibian conservation actions often focus on ponds construction and restoration (Biebighauser 2004; Dolmen 2005; Hoffman et al. 2008; Pellitteri Rosa et al. 2008; Gamble and Mitsch 2009; Rannap et al. 2009; Silva et al. 2009). This may be explained by multiple factors, such as: (i) During breeding, amphibians may congregate in high numbers, being more easily detectable. (ii) Aquatic breeding is particularly prevalent in temperate regions (e.g. Europe and North America) (Gomez-Mestre et al. 2012), which still account for a large proportion of amphibian conservation studies and management actions (Fig. 2a). (iii) Breeding success is crucial (even though it is not enough) for population survival. (iv) Management of breeding sites, such as pond building or restoration, is more easily implemented than the management of larger terrestrial environments, and may provide quick and easily disseminated results (Silva et al. 2009).

Many studies called for the importance of jointly considering aquatic and terrestrial habitat. What is the emphasis currently given to these two environments? During 1992–1994, 33 % of studies considered issues of terrestrial environments only, 17 % focused on aquatic habitats and 50 % jointly considered aquatic and terrestrial features. In 2000–2002, 58 % of papers focused on terrestrial environments and landscape only, 16 % focused on wetlands only, and 26 % jointly considered terrestrial and aquatic features. During 2011–2013, 54 % considered terrestrial environments only, 19 % wetlands only, and 27 % considered both aquatic and terrestrial features. Overall, the number of papers jointly considering terrestrial and aquatic ecosystems did not show significant changes ($\chi^2_2 = 1.4$, $P = 0.50$) (Fig. 2). The high proportion of papers focusing on uplands environments probably arises because the development of geographic information systems and large databases (e.g. Sillero and Tarroso 2010; Ficetola et al. 2014; Sillero et al. 2014) now allows performing broad scale analyses, even continental or global (e.g. Embert et al. 2011; Hof et al. 2012; Sillero et al. 2012; Menéndez-Guerrero and Graham 2013; Ficetola et al. 2015). However, these studies are often based on data that are available for download rather than on explanatory variables that directly influence species. As capturing wetland features over broad scales is challenging, analyses are forced to focus on terrestrial habitats. Furthermore, broad scale studies, encompassing large geographical areas, may be particularly appealing for scientific journals, which tend to publish papers of general interests. However, the interplay between waterbodies and landscape modifications is crucial both in temperate and tropical areas (Almeida-Gomes et al. 2014; Lion et al. 2014), and local-scale studies are more likely to produce direct conservation indications. Actually, remote-sensing rarely allows obtaining the fine-scale information on the small breeding wetlands required by many amphibians, and this may limit the interest of broad scale analyses for practical conservation. Even though the great importance of terrestrial environments is well recognized by the present research, we need more analyses integrating the effects of modifications on multiple habitats, and fine-scale analyses, measuring micro-habitat in the field, remain unvaluable for the conservation actions.

Amphibian biodiversity and threats peak in the tropics

The tropics harbour the highest biodiversity, and this is particularly true for amphibians (Grenyer et al. 2006; Lamoreux et al. 2006). The tropics host not only the highest number of species, but also species with small geographic ranges (i.e. very high endemism), and the highest proportion of threatened species (Grenyer et al. 2006; Whitton et al. 2012). The higher species richness of the tropics, and the differences in land-use history compared to the temperate regions, may require different approaches to conservation. Furthermore, tropical amphibians often have different life history and ecology, compared to the temperate ones (e.g. Gomez-Mestre et al. 2012), thus conclusions of studies performed in temperate regions may be not generalizable to the tropics. However, ecological research suffers a strong geographical bias, with a concentration of studies in rich continents with limited biodiversity (Europe and North America), while less studies are performed in areas with high biodiversity but limited or more recent economic growth (Martin et al. 2012). Analogous geographical patterns are observed in the global distribution of amphibian taxonomists, which are mostly concentrated in Europe and the North America (Rodrigues et al. 2010).

Nevertheless, tropical biodiversity has always been the focus of some of the major studies on amphibian conservation. For instance, one of the most charismatic cases of amphibian decline was the extinction of the golden toad *Bufo periglenes* from apparently pristine forests of Costa Rica (Pounds and Crump 1994). Still, a geographical bias is present in amphibian conservation studies. For instance, out of the 85 studies analyzed here (Table S1), 26 % only was performed in Latin America, tropical Asia and Africa, despite these continents hosting most of amphibian biodiversity (Stuart et al. 2008). Studies on tropical amphibians have several unique features. First, due to the high species richness, analyses are often performed at the community level, and species richness/community structure are the variables of interest more frequently than the presence/absence of individual species or other, more complex parameters (Table S1). Furthermore, tropical studies most often focus on terrestrial environments, possibly because deforestation is a major threat in these areas (Hansen et al. 2013). Third, tropical studies rarely incorporate autocorrelation (9 % of studies, against 38 % for studies in non-tropical areas; $\chi^2_1 = 7.3$, $P = 0.007$). It should be remarked that issues such as spatial autocorrelation or imperfect detection are pervasive, and are also widespread in tropical environments (e.g. Mazerolle et al. 2007; Ernst and Rödel 2008). Not considering spatial pseudoreplication may lead to a biased perception of the effect of deforestation on biodiversity. For instance, lack of appropriate spatial replication may determine a >50 % probability of detecting significant impacts of deforestation, even if such effects actually do not exist (Ramage et al. 2013).

As the majority of threatened amphibians live in the tropics (Stuart et al. 2008), and given the repeated calls on the importance of studies on tropical amphibians for their conservation (Schiesari et al. 2007), we may ask whether the proportion of studies focusing on tropical amphibians is increasing. In the target journals, the proportion of studies in tropical areas published was 50 % during 1991–1994. 26 % during 2000-2002, and 23 % in 2011–2013, with a significant decline across the three periods ($\chi^2_2 = 8.1$, $P = 0.018$). As the Afrotropical, Neotropical and IndoMalayan regions altogether host nearly 90 % of globally threatened amphibians (Chanson et al. 2008), this pattern confirms the need of more studies on the biology and conservation of amphibians in these tropical areas (Schiesari et al. 2007; Ficetola et al. 2014). Remote sensing data and large online databases can certainly help performing broad scale analyses in remote or poorly studied areas (Ficetola et al. 2015), but field studies remain invaluable and urgently needed. Nevertheless, it should be remarked that amphibian research is quickly growing in several tropical countries (e.g. Brazil), and is frequently published in specialist or regional journals. Despite I selected representative journals of the Biodiversity and Conservation and Ecology categories, the papers analysed here may not represent a complete picture of the ongoing research on tropical amphibians.

Multiple causes of amphibian decline

There is a growing awareness that amphibian decline is a complex process involving multiple causes, and for the need of integrating multiple factors, such as from habitat modifications, diseases, invasive species and global changes (Blaustein and Kiesecker 2002; Hof et al. 2012; Menéndez-Guerrero and Graham 2013). Focusing on one driver only may provide incomplete pictures: the effect of the driver tested may be masked by the noise contributed by uncontrolled factors, and the processes at play may appear only when multiple factors are analysed (e.g. because of interactions among stressors) (Hilborn and Stearns 1982). In some cases, the same factor could have different impact on different populations of the same species, because of interactions (Blaustein and Kiesecker 2002). For instance, the American bullfrogs are introduced worldwide, and are often carrier of the pathogen *Batrachochytrium dendrobatidis* (Garner et al. 2006). Observing a negative relationship between bullfrogs and native amphibians may indicate a direct impact of the invasive bullfrogs, but may also be caused by a negative impact of *B. dendrobatidis* on populations. Only studies considering both factors can identify the process actually taking action, and propose the appropriate management strategies. In a different system, the impact of the invasive crayfish *Procambarus clarkii* on amphibian communities was so strong, that the distribution of all amphibians was mostly determined by crayfish abundance. In this area, relationships between amphibian communities and habitat were hardly detectable, because the impact of the invasive species overwhelmed the effect of habitat modifications (Ficetola et al. 2012b). All these observations stress the importance of considering multiple factors, jointly to habitat.

I therefore evaluated the number of threatening factors considered in the 85 papers analysing relationships between amphibians and environment. Beyond habitat, papers considered three major factors that may influence amphibians: diseases, invasive alien species and climate. In 1992–1994 67 % of papers considered additional threatening factors, while during both 2000–2002 and 2011–2012 only a few studies analysed multiple threats. Two studies only (Fellers and Drost 1993; Knapp and Matthews 2000) jointly considered habitat, invasive species and climate; one study jointly considered habitat, diseases and climate (Menéndez-Guerrero and Graham 2013), and 29 % only considered habitat and one additional factor. Actually, in the journal set analysed, the number of studies considering multiple threats decreased between the two periods, although not significantly so (67 % in 1992–1994, 35 % in 2000–2002, 27 % in 2011–2013; $\chi^2_2 = 3.7$, $P = 0.16$), with the number of additional threatening factors (beside habitat) considered in each study decreasing from 0.83 in 1992–1994, to 0.38 in 2001–2003, to 0.29 in 2011–2013 (ANOVA: $F_{2,82} = 2.7$, $P = 0.073$, Fig. 2c). Therefore, despite repeated calls on the complexity of drivers of amphibian decline (Blaustein and Kiesecker 2002; Beebee and Griffiths 2005), we are not moving toward a better integration of the multiple factors.

Conclusions

Conservation science is a crisis discipline, and practical actions must be among its main commitments (Soulé 1985). Assessing whether scientific papers are translated into conservation actions is a complex task. For instance, some studies revealing global trends of threat perhaps did not propose explicit management strategies, still are at the basis of the present-day conservation policies (Stuart et al. 2004). Conversely, research providing clear management recommendations may be never translated into practice. Amphibian conservation ecology is becoming a central theme of biodiversity studies. The increasing number of papers on this theme (Fig. 1) is only a facet of the interest toward these animals, that have been proposed as "canaries" of the overall deterioration of the condition of the planet (Norris 2007; but see also Kerby et al. 2010 for additional discussions). The growing interest toward these animals is reflected by increasing efforts for their conservation, and by a better awareness of the broad public. Amphibian conservation studies have achieved impressive scientific successes during the last 25 years, and we now better understand the multi-factorial processes underlying the amphibian biodiversity crisis. Most importantly, some of these scientific advances are being translated into conservation practice, with at least some successes (Griffiths and Pavajeau 2008; Pellitteri Rosa et al. 2008; Rannap et al. 2009). Nevertheless, there are several areas where we may improve our contribution to amphibian conservation.

Recent statistical developments can certainly help our analyses, by improving the rigour and reliability of results. During the years, we observed an impressive increase of the quality of analyses performed. During the early 1990s, many studies published in top conservation journals did not perform complex quantitative analyses, and often provided conservation indications on the basis of observations only (e.g. Corke 1992; Fellers and Drost 1993; Hedges 1993), while it is now impossible publishing without quantitative analyses, and complex statistical approaches are routinely used (Fig. 2a). Spatial autocorrelation and detection probability are two important aspects, still there are many developments also for other techniques, not considered here (e.g. new species distribution models, multi-scale analyses, new approaches for community analysis…). Improving the statistical aspect of our analyses is often challenging, but allows us to obtain results that would be impossible achieving with standard approaches (Hocking et al. 2013). A better integration between spatial autocorrelation and imperfect detection may be an important point. To date, very few studies jointly considered these two statistical issues, often without an explicit integration. For instance, current research sometime check whether detection probability is sufficiently high, and then apply spatial explicit approaches (Ficetola et al. 2012a), or try ensuring spatial independence of data, and then apply models considering imperfect detection (Eskew et al. 2012). It should be remarked that this review focused on a subset of top biodiversity journals, but the attention toward complex/novel analyses might be lower in regional/herpetological journals. A more explicit integration between autocorrelation and imperfect detection may improve analyses of data showing complex features, which certainly are very frequent, and is already feasible thanks to the advancements of hierarchical Bayesian models (Kéry 2010; Bled et al. 2011; Mattsson et al. 2013).

However, the technical advances should not limit the linkages between conservation research and practical actions. During the last 20 years, refined approaches have been implemented at all the levels of the research, from data collection to statistical analyses, but such refinements should not come at the cost of losing sight of the complexity of real issues. More than one decade ago, Blaustein and Kiesecker (2002) remarked that too many conservation studies consider one single stressor: as such studies may be simplistic, more multi-factorial analyses are required. Despite repeated calls, amphibian conservation studies are now even more focused on one theme only, and the interaction among multiple potential drivers of species diversity and distribution is not investigated often enough. Similarly, despite most of threatened amphibians live in the tropics, the proportional interest toward these areas remains too low, and their presence in top biodiversity journals is actually decreasing (Fig. 2a). Here I analysed a subset of biodiversity journals only, and more tropical studies are certainly present in regional or herpetological journals. However, as publishing in top journals often requires very large sample size and sophisticated statistics, researchers might be tented to analyse relatively simple and well studied systems, where target species are well known and field activities less cumbersome, and focus on specific, trendy themes that may get better citation rate (Ohmer and Bishop 2011). Conservation scientists and biodiversity journals should not sacrifice complexity on the altar of impact factor or technical novelty. Actually, appropriate technical approaches may be the key of unravelling complex multi-factorial relationships, and help to obtain robust inference also from data collected where field activities are more complex. Only the integration of multiple approaches (study of wetlands, terrestrial habitats, landscape, diseases, climate, invasive species and more), and a better geographic coverage, may allow us a more complete understanding of the amphibian biodiversity crisis, and to develop effective conservation actions.

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