Painting maps with bats: species distribution modelling in bat research and conservation

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Abstract

Species distribution models (SDMs) offer an effective tool for identifying species conservation requirements and forecasting how global environmental changes will affect species diversity and distribution. This approach is particularly relevant for bats because their nocturnal behaviour hinders detectability and identification in flight. Despite their important contribution to global biodiversity and wide geographical ranges, bats have been under-represented in early SDM studies, and only in the last few years has this approach become more widely used in bat research. We carried out a meta-analysis of the published literature to review the history of the use of SDMs in bat research and their application in conservation, climate change assessments and genetic studies. We focus on the geographical coverage, theme and modelling algorithm of published studies, and compare studies that are uniquely dedicated to bats to multi-taxa studies that include bats. We provide recommendations for good modelling practices through considering spatial scale and spatial biases, selecting ecologically relevant variables, following rigorous modelling protocols, and recognising the limitations of extrapolation across temporal scales. We suggest future developments that will further favour the use of SDMs to study bat ecology and biogeography, as well as inform conservation management. We conclude that despite an increase in bat SDM studies, their scope and application can be further enhanced through incorporating dispersal, landscape connectivity and biotic interactions between bats, their prey and their pathogens.

Background and objectives

The past two decades have seen an impressive increase in the application of species distribution models (SDMs) in the scientific literature (Franklin 2009), accompanied by an ever wider range of ecological applications (Elith and Leathwick 2009; Scoble and Lowe 2010). The number of published SDM studies grew exponentially from only 30 papers summarised by Franklin (1995) in one of the first comprehensive reviews of SDMs' state of the art, to a total of 478 listed by Elith and Leathwick (2009) less than 15 years later.

Despite their high taxonomic diversity and wide geographical distributions, bats have been under–represented in early SDM studies. Scheel et al. (1996) published what can be considered one of the first studies dealing with predictions of bat distributions, both for the present and under climate change scenarios. Although this study did not use species distribution modelling techniques (at that time very few algorithms had been developed), it used statistical methods to predict the future location of suitable habitats for bats and estimated the spatial patterns of future bat diversity in Texas. Jaberg and Guisan (2001) were the first to apply SDMs to study the spatial distribution of bats. Since then, the number of publications using SDMs to investigate the ecology and biogeography of bats slowly increased to an average of around 13 papers per year in the last five years. A variety of bat SDM studies have been published from different geographic areas, dealing with an increasingly broader spectrum of ecological themes and using various statistical tools.

We review the use of SDMs in bat research and conservation because this approach is particularly suitable for bats due to their unique biology, and because of the potential of bat SDMs to inform our understanding of wider societal challenges from biodiversity conservation to human health and food security. SDMs offer a powerful tool to plan and implement appropriate management and protection to address the global decline of many bat populations as a result of human pressures (Mickleburgh et al. 2002). Bats are elusive, nocturnal mammals that are difficult to observe and identify. Some species are hard to capture because they either fly high above the canopy, are highly manoeuvrable, and therefore able to evade nets, or roost in inaccessible sites, such as trees scattered in large forest patches, making direct observation problematic. Although the nowadays widespread use of acoustic monitoring (bat detectors) has greatly increased the chances of recording bats, some species cannot be easily detected because of low intensity, high frequencies emitted or highly directional echolocations calls (e.g. Waters and Jones 1995), while others are difficult to differentiate based on their echolocation calls (e.g. Russo and Jones 2002; Walters et al. 2012; Russo and Voigt 2016). The application of molecular techniques has revealed the presence of many cryptic species within the order (e.g. Myer and von Helverson 2001; Clare 2011), calling into question known species' geographical ranges assigned based on morphology alone. For such species, genetically confirmed occurrence records are often scarce. Moreover, distribution data from systematic surveys are available only for a few study regions. As a result datasets of bat species occurrence are commonly small and / or do not cover the full bat community. For the same reason, it is often not trivial to distinguish genuine absence from false absence due to incomplete sampling, rarity or surveying difficulties. Presence-only modelling methods may overcome such problems because they can provide robust predictions based on limited occurrence datasets and do not rely on absence data for model calculations. Therefore, SDMs present an important tool to tackle questions on bat distribution, biogeography, past and future responses to environmental changes and conservation biology.

Our main objectives in reviewing the use of SDMs in bat research and conservation are to:

1) give an account of prevailing trends in the scientific literature on SDMs and bats;

2) summarise the main applications of SDMs to bat conservation and management;

3) review common problems and assumptions affecting SDMs in bat studies and offer good practice guidance for modelling that can also be applied to other taxa;

4) suggest directions to improve predictions and increase the scopes of the application of SDMs to bats, and how bat SDMs can inform wider societal challenges.

Trends in the scientific literature

We performed a meta-analysis on published studies, using ‘Web of Science’ and ‘Google Scholar’ to search for SDM studies including bats among the target species, without constraining the publication date. We used the following keywords, alongside the terms “bats” or “mammals”: “ecological niche modelling”, “ecological niche models”, “species distribution models”, “habitat suitability modelling”, and “habitat suitability models”. We inspected the first 20 pages of the listed search results. Studies were excluded if they: 1) were not published in peer-review journals with an assigned impact factor or 2) did not provide an unambiguous definition of the analysed species in the main text or in the Supplementary Materials. We collected a total of 89 papers (listed in Supplementary Materials). The following information was extracted from each paper: “year of publication”, “geographic area”, “theme”, “modelling algorithm” and “bat versus multi–taxa” (i.e. bat-specific studies versus studies including bats among other taxa). The latter comparison aims to explore the extent to which bats are seen as a priority subject for SDM studies deserving a separate analysis, and whether bat-specific studies differ in scope or focus on different research questions than multi-taxa studies. The literature covers a time span ranging from 2001 to January 2016, and includes at least one paper per year except for 2003. The number of published papers significantly increased through time (GLM [family=”poisson”]: $R^2 = 0.88$, $P < 0.05$), though the quadratic term of this relationship was not significant (Fig. 1).

The studies were predominantly carried out in Europe (> 40%), followed by Africa (13.5%) and South America (10.1%), while Oceania was the least represented geographic area. A small proportion of the papers covered multiple geographic areas: North–Central America (2.2%), Europe–Asia (1.1%) and Central–South America (1.1%). Only 4.5% of the papers applied SDMs to study bats on a worldwide scale (Fig. 2).

The selected studies focused on six main themes, the most common of which (29.2%) was biodiversity conservation (i.e. effect of climate change or forest management on distribution, conservation planning, etc.), closely followed by biogeography (for example, mapping richness/diversity patterns, quantifying niche overlap; 27%) and phylogeography (phylogenetic analyses coupled with a reconstruction of paleo-distributions; 14.6%). Other themes covered were methods (15.7%), species–habitat relationships (11.2%) and epidemiology (2.2%). Conservation represents the most recurring theme in European studies (34.2%), whereas phylogeography is the most frequent theme in Africa (41.7%) and biogeography in South America (66.7%; Fig. 2).

Nine statistical algorithms emerged from our literature search as the most commonly used in bat SDM studies. To those, we added two other categories to cover papers that used an ensemble of different algorithms, which either included or did not include the maximum entropy algorithm Maxent (Phillips et al. 2006). More than 55% of the analysed studies used Maxent as a single algorithm to model the distribution of bats. Among the papers using an ensemble of algorithms, those including Maxent were more frequent (10.1%) than those excluding Maxent from the ensemble approach (4.5%). When taken together, studies using an ensemble modelling approach formed the second most frequent category, followed by those using the Genetic Algorithm for Rule-set Prediction (GARP, Stockwell and Noble 1992). Studies carried out on European species applied seven of the 11 algorithms, while only three algorithms were applied in African and South American studies. Maxent was used in almost half of the studies carried out in each of these geographic areas (Fig. 2). Examining the use of the different algorithms through time, we found that Maxent was the only algorithm to show a significant (R^2=0.98, $P<0.01$) linear increase in its application in bat SDM studies over time, with also a weak, though significant ($P<0.05$), exponentially–shaped decrease in 2015 (Fig. 3a). All other algorithms were irregularly adopted over the last 15 years, without a significant temporal trend (Fig. 3a). The popularity of Maxent across studies and taxa is attributed to its good performance and high predictive accuracy relative to other methods (e.g. Elith et al. 2006), in particular when sample sizes are small (Hernandez et al. 2006; Wisz et al. 2008), but also to the accessibility and ease of use of the software (Merow et al. 2013).

Overall, almost two thirds of the analysed scientific literature focused exclusively on bat species. The proportion of bat–only papers was not equally distributed among the different geographic areas, decreasing from 84.2% in Europe to 44.4% in South America. Noticeably, the number of papers exclusively focused on bats showed a significant linear increase (R^2=0.86, $P<0.001$) in the past 15 years (Fig. 3b), while the number of studies that also included other taxa peaked between 2007 and 2009 and subsequently declined (R^2=0.50, $P<0.05$; Fig. 3b).

The degree of statistical association among the parameters “bat versus multi–taxa”, “modelling algorithm” and “theme” was assessed by checking the residuals of chi–squared tests (Yates 1934), whereby residuals >2 or <–2 indicate significant positive or negative associations, respectively (Agresti 2007), and through Cramér’s V (Cramér 1946). We found a strong, significant association between “bat versus multi–taxa” and “modelling algorithm” (χ^2=43.193, $P<0.01$, V=0.697), with a significant overrepresentation of GARP and ensemble algorithms (excluding Maxent) in studies modelling the distribution of not only bat species (multi-taxa). In addition, a significant, though less strong, association was found between "bat versus multi–taxa" and "theme" (χ^2=17.142, P<0.01, V=0.439). We also found a trend, albeit not significant, of over-representation of the biogeography theme in bat-only studies. Finally, we identified a strong association between "modelling algorithm" and "theme" (χ^2=71.388, P<0.01, V=0.896), with several significant overrepresentations. Ecological Niche Factor Analysis (ENFA, Hirzel et al. 2002) was overrepresented in studies of species–habitat relationships, while ensemble algorithms (including Maxent), General Additive Models (GAM, Hastie and Tibshirani 1990) and Multivariate Adaptive Regression Splines (MARS, Friedman 1991) in method papers.

Applications in bat research and conservation

When the limitations and caveats of SDMs are appropriately considered, they can be a relevant tool for bat conservation, contributing to the development of management guidelines (e.g., Sattler et al. 2007), helping forecast threats (e.g., Hughes et al. 2012) or providing new insights on population structure and history (e.g., Kuo et al. 2014). The primary aim of some of the first applications of SDMs in bat conservation was to design surveys or provide a preliminary assessment of bat distributions (Jaberg and Guisan 2001). However the field rapidly evolved to include a wider array of applications, from deriving spatial predictions of threats to bat populations (e.g., Roscioni et al. 2014) to the design of acoustic monitoring networks (Amorim et al. 2014). SDMs and niche analysis have been used to detect variables influencing habitat selection patterns at two scales in a bat and a longhorn beetle (Russo et al. 2015), both threatened, highlighting that despite their considerable sympatry, those species exhibit fine-grained differences in habitat selection implying different management strategies. One of the most common applications of SDMs is forecasting bat distributions under climate change scenarios to better understand future threats to bat populations and to provide base-line data for decision makers and conservation managers (e.g., Scheel et al. 1996; Rebelo et al. 2010; Aguiar et al. 2016). More recently, the field of SDMs expanded to integrate other types of information, like morphological, demographic and genetic data. In particular, the integration of genetic data with SDMs has offered insights into the evolutionary history of bat populations (e.g., Flanders et al. 2011) and tools to identify the location of isolated bat populations of conservation concern (Razgour et al. 2014). It is expected that the usefulness of SDMs for bat conservation will increase with further development and integration of multi-disciplinary approaches in spatial ecology.

Assumptions, problems and good practice in developing SDMs for bats

The usefulness of SDMs depends on their appropriate use. The modelling protocol should consider the specific ecological and biogeographical situation, the study aim (explanation of environmental correlates of species distribution versus prediction through extrapolating geographical distributions across space or timeframes) and the constraints associated with the available data (Araújo and Peterson 2012). Elith and Leathwick (2009) recommend that good modelling practices should be based on gathering relevant, accurate and comprehensive species data, a complete set of relevant predictor environmental variables, and robust modelling procedures that includes model evaluation, assessing performance relative to test data and model improvement in light of the modelling process. Here we discuss these different aspects in more details in relation to the application of SDMs to bat research and conservation.

Fundamental versus realised distributions

It is assumed that presence-only modelling estimates the species' fundamental distribution, i.e. in the absence of biotic or historical constrains (Brotons et al. 2004). Bats are a relatively vagile group of organisms with relatively high dispersal abilities, and therefore it is frequently assumed that there is little difference between the fundamental and realised distribution (the truly occupied area) of a species (e.g., Rebelo et al. 2010). However this may not be the case for less vagile bat species with limited long distance dispersal abilities, and therefore caution should be taken when modelling the distribution of these species.

Considering spatial scale and spatial biases

Although SDMs can be generated for all organisms for which presence records are known, model accuracy will vary depending on the ranging behaviour and environmental tolerance of the species. It is generally easier to model the potential distribution of ecologically specialised species with smaller geographical ranges that are limited by their environmental tolerance (Hernandez et al. 2006). However, for all species, the ability of the model to demonstrate clear associations with environmental variables depends on selecting the appropriate spatial and environmental extent and on the completeness of the distributional dataset (Araújo and Peterson 2012; Russo et al. 2015). Determining the appropriate study area for model calibration is particularly important for predictive SDMs, especially when models are extrapolated to other geographic locations or timeframes (Anderson 2012). Presence records should offer a good coverage of the range of the species to encompass the full spectrum of conditions within the species' environmental tolerance (Anderson 2013). Because political units (states, administrative counties) often do not equate to biological borders or species' environmental limits, setting the study extent based on geopolitical borders that only correspond to a part of the species' range can result in incorrect identification of species response to environmental variables (Guisan and Thuiller 2005; Meirmans 2015). It is important to ask ourselves whether it is reasonable to model the distribution of highly vagile and wide ranging bat species within geopolitical borders. Is the spatial extent of the study area broad enough to cover the environmental conditions limiting the distribution of the species or are we simply over-fitting a model to our dataset of presence records instead of the species' environmental niche? Yet, at the range margins of species' distributions it may be reasonable to model regional distributions with partial-niches (the environmental conditions limiting the distribution of the species in the specific area rather than across its entire range) using finely-tuned environmental variables. Under these circumstances, regional models are more sensitive than continental models to the suboptimal or extreme ecological conditions at the range margins, and therefore can better represent the environmental niche of peripheral populations (Vale et al. 2014).

A fundamental assumption of SDMs is that presence records are the product of a systematic and random sampling design encompassing the entire study area. Yet spatial bias towards more accessible or better surveyed areas is common in distribution datasets both of rare or elusive species and of under-reported common or widespread species (Kramer-Schadt et al. 2013). Such spatial bias is often found in museum and natural history collections (Araújo and Guisan 2006), but is especially pronounced in global on-line databases, like GBIF (www.gbif.org), due to difference in funding and data sharing between countries (Beck et al. 2014). Spatial bias is particularly problematic when it results in over-representation of a set of environmental conditions that are prevalent in intensively surveyed areas (environmental bias) because SDMs will base their predictions on differences in the environment sampling efforts instead of the species' requirements (Anderson 2012; Kramer-Schadt et al. 2013).

Spatial autocorrelation (SAC), the geographic clumping of presence records, can result from the response of individuals to the distribution of environmental conditions (Elith and Leathwick 2009). SAC may also be a feature of central place foragers, like cave-dwelling bats, where occurrences are more restricted to the areas around the roost (Rainho and Palmeirim 2011). However, when SAC is an artefact of spatial bias in sampling efforts, it should be tested and corrected for. Methods to address spatial bias include the removal of locations falling within a certain radius, for example corresponding to the species' maximum home range (Kramer-Schadt et al. 2013), or – when sample sizes are too small – the introductions of a bias grid to account for uneven sampling (Elith et al. 2011). Alternative approaches focus on generating background data (pseudo-absences in presence-only modelling) with the same spatial bias. If the distribution of sampling efforts is unknown, it can be estimated through collating presence records of taxonomically related species sampled using the same techniques as the focal species (target group sampling, Phillips et al. 2009). This approach was used by Bellamy and Altringham (2015) to correct for sampling bias in bat roost records from a biodiversity data centre in the UK. However, it should be used with caution when modelling the distribution of bats in areas with less comprehensive survey efforts and when relying primarily on field data because of differences in bat detectability, capture rates and in the reporting of common species.

An additional problem arising from the use of museum data and on-line databases relates to inadequate taxonomic knowledge and variable quality of species identification (Anderson 2012). This is particularly the case for the order Chiroptera, where cryptic species complexes are frequent and new species are still being discovered, especially, but not exclusively, in the tropics (Fenton and Simmons 2014). While some bat SDM studies circumvent this problem by modelling the distributions of species complexes (e.g. Herkt et al. 2016), increasingly, SDM studies of bats belonging to cryptic species complexes are relying on molecular tools to confirm species identification (e.g. Rutishauser et al. 2012; Santos et al. 2014; Razgour et al. 2015).

Selecting ecologically relevant environmental variables

Knowledge of the species' ecology, population dynamics and sensitivity to disturbance is paramount for building meaningful SDMs (Araújo and Guisan 2006). Predictor environmental variables included in the model should be preselected to offer good representation of ecophysiological processes (Austin and Van Niel 2011). Using distal, rather than functionally-relevant predictors can lead to errors when extrapolating across space and time (Elith and Leathwick 2009). Hence it is important to select environmental variables that are likely to limit the geographical distribution of the studied bat species physiologically, ecologically or behaviourally, and explain the modelled response curves in light of the species' biology. Studies should also account for collinearity (linear relationship) between predictor variables, a common pattern in frequently used climatic datasets, like the BioClim variables downloaded from WorldClim (www.worldclim.org). Non-independence in predictor variables affects parameter estimation, leading to incorrect identification of relevant predictors and serious errors when extrapolating to different geographic regions or climatic conditions (Dormann et al. 2013).

Following robust modelling procedures

Over the past few years bat SDM studies have begun to explore more carefully the effect of parameter settings on model predictions and performance, moving away from reliance on default values and from treating the modelling process as a black box. Although Maxent offers flexibility in the selection of background samples, features, regularization (controlling for model overfitting), output format and evaluation methods, using the default settings without clear justification is still a common practice in the modelling literature (Merow et al. 2013). Inappropriate complexity and over-parameterisation affect model performance and reduce the ability of the model to infer habitat quality and relative variable importance, as well as its transferability to other timeframes (Warren and Seifert 2011). Hence models should be tuned according to the study species and goal, in the case of Maxent, through selecting feature types and adjusting regularization settings (Elith et al. 2011). Merow et al. (2013) provide detailed recommendations for robust Maxent modelling procedures. We advocate that researchers and conservation practitioners modelling the distribution of bats follow these recommendations and critically evaluate how different settings affect model predictions.

Evaluating model performance

Evaluation is an integral component of any modelling process. In the case of SDMs, model evaluation is essential for determining whether the model adequately describes the requirements of the species without overfitting the predictions to biases in the presence data (Anderson 2012). Judging whether the output maps are a good approximation of the biological reality is particularly challenging when they were generated by models that are based on spatially-biased location data and built using complex functional relationships (Yackulic et al. 2013). While variable selection can be confirmed through evaluating the ability of the model to fit the training data, using models to predict species distributions within and across geographical areas and timeframes requires an evaluation of model generality and transferability using independent datasets or data resampling (Araújo and Guisan 2006; Elith and Leathwick 2009).

A commonly used measure of SDM predictive accuracy is the area under the receiver-operator curve (AUC), which, in the context of presence-only modelling, refers to the model's ability to distinguish between presence locations and randomly selected background points (Merow et al. 2013). AUC has been criticised for being sensitive to spatial biases in the data (Beck et al. 2014), for not considering over-fitting and consequently supporting over complex models (Radosavljevic and Anderson 2014), for its dependency on the ratio of prevalence to background points, for using background data as true absences in presence-only modelling (Lobo et al. 2008), and for being based on trivial distinctions (Yackulic et al. 2013). Most importantly, it cannot be used to compare models that were built for different landscapes, species and background samples, and when using different test data (Merow et al. 2013). Although currently there is no clear alternative to AUC as a measure of the performance of presence-only SDMs, null models can be used to test whether the model AUC value is significantly different from expected AUC values generated from random location data (Raes and ter Steege 2007). In addition, Warren and Seifert (2011) advocate the use of information criterion approaches (e.g. Akaike Information Criterion) for model and parameter selection in place of AUC, although these approaches provide no measure of performance but just a comparison of the most informative and parsimonious model.

Predictive modelling across temporal scales

SDMs are increasingly applied to predict the effects of future climate change on bat distributions and diversity (forecasting; e.g. Rebelo et al. 2010; Lundy et al. 2010; Hughes et al. 2012; Lee et al. 2012; Razgour 2015) or to reconstruct the evolutionary history of species in phylogeographic studies (hindcasting or paleo-SDMs; e.g. Flanders et al. 2011; Rebelo et al. 2012; Razgour et al. 2013; Kuo et al. 2014; Alberdi et al. 2015; Razgour et al. 2015). Extrapolation across timeframes or to novel environments can be problematic due to changes in biotic interactions and in how environmental variables affect distribution, and due to the novel combination of climatic conditions. Moreover, extrapolation requires an understanding of how genetic variability, phenotypic plasticity and dispersal affect species responses to changing conditions (Elith and Leathwick 2009). It is important to remember that predictive SDMs only identify potential distribution areas under future or past climatic scenarios based on the inferred relationship between species present distribution and climatic variables (Araújo and Peterson 2012). As such they rely on the assumption that the fundamental niche of the species remains conserved over time (niche conservatism; Wiens and Graham 2005). Although it should not be taken as given that species' current climatic niche reflects future climatic tolerances (Guisan and Thuiller 2005), studies testing this assumption in bats have found evidence for past niche conservatism, at least in terms of tolerance to colder climatic conditions (Rebelo et al. 2012; Razgour et al. 2013). Projections into future climatic scenarios also assume that current distribution data reflects the fundamental niche of the species, which may not be true for all species. It has been shown that disregarding range contractions suffered by giraffes during the 20th century resulted in severe underestimations when modelling their future range suitability (Martínez-Freiría et al. 2016). This is likely to be the case for many species that are sensitive to human activities (land use change, hunting, etc.).

It is questionable whether SDMs based solely on climatic variables are sufficient for quantifying the effects of future climate change on species distributions (Araújo and Luoto 2007). The distribution of many bat species is not limited by climate alone and is profoundly influenced by their strict reliance on specific habitat types for roosting and foraging. Obvious examples are the strong reliance of woodland bats on forests for foraging and roosting (e.g. Russo et al. 2004, Lacki et al. 2007) and bats from arid or semiarid regions on water bodies and their associated vegetation (Korine and Pinshow 2004; Korine et al. 2016). Stanton et al. (2012) show that including non-climatic variables (e.g. land cover) that are important predictors of species distribution, improves model performance and predictive ability. This holds true even in the absence of corresponding future projections for these variables.

However they warn against including static environmental variables, like altitude and latitude, which only indirectly affect species distribution but are highly correlated with climatic variables, because the relationship between the static variable and the dynamic climatic variables will change (Stanton et al. 2012). Despite their recognised overestimations, climatic variables are informative for understanding broad-scale patterns of range suitability changes because species are likely to only occur in suitable habitats within the modelled climatic envelope (Pearson and Dawson 2003). A number of future land cover scenarios have been published, but there is still some controversy over predictions in areas that are highly modified by humans because of the difficulties associated with anticipating changes in markets, technologies, societal preferences or biophysical forces (Lawler et al. 2014).

Future directions and wider applications

Although significant progress has been achieved in the application of SDMs to study bat distributions and characterise environmental niches, there is still scope for future developments that will further increase the relevance of SDMs to bat research and conservation, and the contribution of bat SDMs to addressing wider societal challenges. We highlight some new and emerging trends and suggest some future avenues of research and modelling methods development.

Improving future predictions

To date, most SDM studies predicting the effects of climate change on the distribution of bat species contributed mainly to understanding the future distribution of suitable climatic conditions rather than the future distribution of the bats themselves. Thus far, the effect of projected future land cover changes has rarely been included in bat SDMs (with the exception of: Hughes et al. 2012; Di Febbraro et al. 2015; Struebig et al. 2015). A handful of studies commented that availability of suitable foraging and roosting habitats, dispersal or biotic interactions are likely to limits future range suitability (Hof et al. 2012; Razgour et al. 2013; Razgour et al. 2015), but most of these parameters are yet to be directly incorporated into the modelling process. Moreover, none of the studies have considered the possibility that populations may be able to persist in areas predicted to experience climatic conditions outside the species' current environmental niche through genetic adaptations or their available phenotypic plasticity (Hoffmann and Sgro 2011). For SDMs to be informative about the future distribution of bats, output maps of climatic suitability will require spatially-explicit post-processing to approximate the areas that the species can occupy given the constraints of dispersal and population establishment requirements (Anderson 2013).

Despite the importance of understanding dispersal limitations for predicting species ability to occupy areas projected to be suitable under future climate change (Travis et al. 2013), SDM studies commonly fail to consider dispersal, assuming instead that species are capable of reaching all suitable geographical areas (Bateman et al. 2013). This assumption is likely to be unrealistic for the majority of species, including less vagile bat species. Better realism can be achieved through the use of 'hybrid models' that incorporate dispersal and demographic mechanisms into SDMs. However these models rely on detailed movement and life history parameters that are unavailable for the majority of species (Thuiller et al. 2013). Obtaining the fine-scale data needed to parameterise these complex models will require long-term ringing and genetic studies of target bat species. An alternative, simpler approach is to incorporate basic elements of dispersal limitations by applying the likely maximum dispersal distances to buffer SDM projections (Bateman et al. 2013). For example, Barbet-Massin et al. (2012) used information from the literature on mean and standard deviations of natal dispersal estimates for European breeding birds to adjust future SDM suitability values to reflect the constraints of dispersal. Molecular data can be used to estimate post-glacial range expansion rates (e.g. through model-based inference using the Approximate Bayesian Computation framework [Beaumont 2010]), as a proxy for species migration rates, to parameterise future dispersal distances from current known range.

Model evaluation can be improved through validation with datasets collected at different timeframes. Validation of SDMs is particularly problematic when projecting species distributions to future timeframes due to the absence of independent test datasets. The partitioning of present datasets through cross-validation or bootstrapping is problematic because of spatial and temporal autocorrelations in the calibration and validation datasets. A promising approach to validating the predictions of future models is the use of recorded distributional shifts over the past few decades as independent test datasets (Araújo et al. 2005). Lundy et al. (2010) validated the predictions of future bat SDMs by using historical occurrence records (1940–2006) to build the model and known new records (post 2006) to test the predictive ability of the future models. This approach can become highly relevant over the next few decades for bat species in countries or regions where comprehensive long-term monitoring programmes have already been established (e.g. Barlow et al. 2015). However caution must be taken when comparing occurrence data from past and current distributions because changing patterns of recorder effort may distort real trends or range shifts. To account for variation in the sampling effort across space and time, studies should only consider in the analysis areas that were sampled in all time periods. Range changes in subsequent time periods can then be assessed in relation to these areas only (Casey et al. 2015).

Incorporating landscape connectivity

Landscape connectivity can inform studies of species distributions, population demography, genetic variability and population viability across heterogeneous landscapes (Vasudev et al.

2015). Within the context of predictive SDMs, the ability of individuals or populations to move across the landscape and reach climatically suitable areas may be limited by biogeographical barriers that impede landscape connectivity. Landscape genetics, the study of the effects of environmental heterogeneity on the spatial distribution of genetic variation (Manel et al. 2003), can help advance SDMs through incorporating the effect of landscape connectivity on species ability to track changes to their environmental niche (Scoble & Lowe 2010). The integration of landscape genetics approaches into SDMs has been mainly limited to the use of SDMs to characterise landscape resistance to movement as a function of habitat suitability (e.g. Wang et al. 2008; Razgour et al. 2014). More recently, studies have begun applying this approach in a predictive manner to assess how species will shift their ranges to track suitable climatic conditions and identify important future movement pathways/routes (Lawler et al. 2013; Razgour 2015, for bats). Other studies used SDMs to look at the effect of development (wind farms) on landscape connectivity for bats (Roscioni et al. 2014), or included landscape connectivity measures when assessing suitable areas for a forest bat in a fragmented landscape (Teixeira et al. 2014). Bat SDM studies can lead the way in developing novel approaches to integrate the effect of landscape connectivity into distribution modelling.

Increasing the scope of bat SDMs

The scope of bat SDM studies can be increased to address different levels of organisation, from diversity below the species level to interactions between species and between trophic levels, and to incorporate into the modelling process the temporal scale of the dataset. On the one hand, bat SDMs should better reflect the high cryptic diversity in the order and the strong signature of population structure within species, which may correspond to differences in local environmental adaptations and niche requirements. Molecular data can provide vital information on geographic population structuring and date the split between groups. This information can be subsequently used to define separate modelling units, particularly for widespread species, that better reflect differential population responses to environmental variables (Gotelli and Stanton-Geddes 2015). For example, Alberdi et al. (2015) identified contrasting responses to past climatic changes across the Palearctic in genetically separated eastern versus western populations of the alpine long-eared bat, indicating that the response of this bat to future climate change will be best studied at the population, rather than whole species, level. On the other hand, there is a need to better integrate biotic interactions, in the form of interspecific competition and predator-prey (or herbivore-plant) interactions, into the modelling process (Thuiller et al. 2013). While several multi-species studies looked at patterns of bat species richness or differential responses to environmental variables and future climate change (e.g. Bilgin et al. 2012; Hughes et al. 2012; Bellamy et al. 2013; Amorim et al. 2014; Herkt et al. 2016), interactions between species have been largely neglected. Exceptions are Santos et al. (2014), who showed how interspecific interactions potentially shaped the distributions of cryptic species pairs in the Iberian Peninsula, and Russo et al. (2014) that looked at how bat species on a resource limited island minimise competition through niche displacement. However, improvements in modelling are needed before species interactions can be explicitly considered in SDMs (Hellmann et al. 2012).

Bats are the reservoirs of several zoonotic diseases, including rabies, Ebola and SARS (Calisher et al. 2006). Through improving our understanding of the bat host distribution, SDMs can help explore key epidemiologic questions and predict patterns of disease spread. Bats are also important pollinators and seed dispersers of several agricultural crops, play important roles in forest regeneration and are the main nocturnal predators of arthropods, including several important agricultural pests (Boyles et al. 2011; Kunz et al. 2011). As such, a better understanding of factors that affect bat distribution and future changes to bat distribution in response to global climate change can highlight challenges to food security due to changes in the ecosystem services provided by bats.

Concluding remarks

Despite an increase in bat SDM studies in the past decade, a large proportion of studies still focus on geographical areas that hold lower levels of bat diversity but have better availability of occurrence data (Europe). The use of presence-only modelling is pervasive in bat studies because of difficulties associated with obtaining reliable absence data. A new approach suggested by Newson et al. (2015) harnesses the power of citizen science to generate comprehensive bat activity datasets that can form the basis of presence-absence and abundance-based distribution models. However this approach may be more difficult to implement over larger spatial scales. Although bat SDM studies cover a variety of topics, most focus on conservation and biogeography, while the application of SDMs to epidemiological studies is still limited despite their potential to inform wider societal challenges. An important future development that will increase the scope of bat SDMs and their relevance to wider conservation and society challenges is the integration of biotic interactions between competing bat species, bats and their prey, and bat hosts and their pathogens. Recent studies have begun applying genetic data to inform models and to assess the effect of landscape connectivity and evolutionary history, but studies have yet to include physiological and demographic data to gain a better understanding of bat species responses to climate change. In the forthcoming years SDMs are set to become an essential tool for bat conservation, for epidemiology modelling and for understanding changes to the ecosystem services provided by bats, thus contributing to tackling current and future societal challenges.

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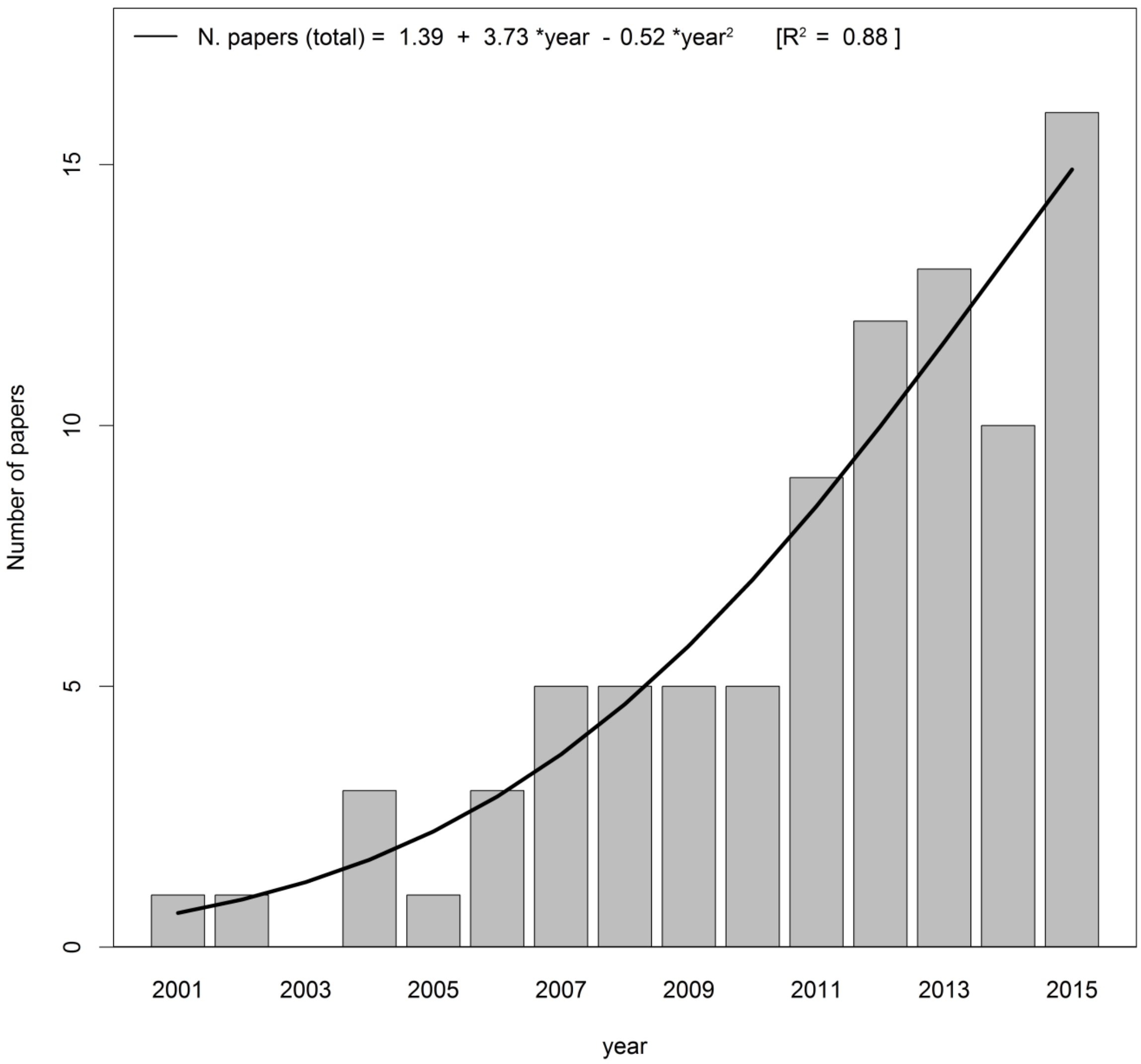
Figure Captions

Figure 1 – Number of published SDM studies per year including bats as the target organisms. The solid line depicts the relationship between the number of papers and time.

Figure 2 – Relative proportions of the four parameters examined in the literature search: “year of publication”, “geographic area”, “theme”, “bat versus multi–taxa” and “modelling algorithm” (left). Map with the number of papers per geographic area. Papers covering multiple geographic areas were counted for each area (upper right). Relative proportions of “theme”, “bat versus multi–taxa” and “modelling algorithm” for the three most represented geographic areas (lower right).

Figure 3 – Number of published papers per year grouped by “modelling algorithm” (A) and “bat versus multi–taxa” (B). In panel A, solid line represents the statistical relationship between the number of papers using Maxent and time. In panel B, dashed and dotted lines depict the statistical relationship between time and the number of papers focused on either bat species or multiple-taxa, respectively.

Figure 1


N. papers (total) = 1.39 + 3.73 *year - 0.52 *year²   [R² = 0.88]
Number of papers
0
5
10
15
2001
2003
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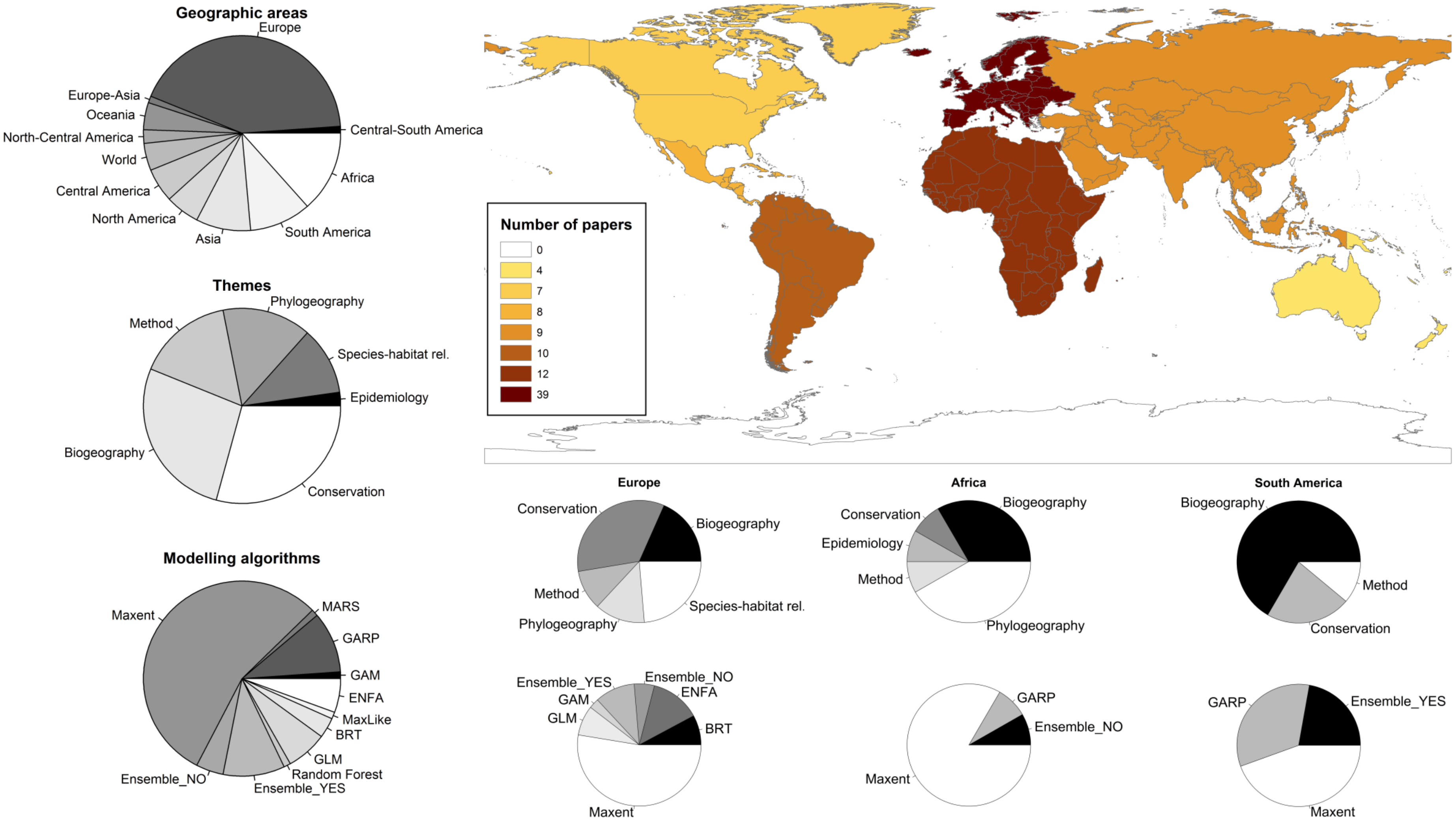
2011
2013
2015
year

Figure 2


Geographic areas
Europe
Europe-Asia
Oceania
North-Central America
World
Central America
North America
Asia
South America
Africa
Central-South America
Themes
Phylogeography
Method
Species-habitat rel.
Epidemiology
Biogeography
Conservation
Modelling algorithms
Maxent
MARS
GARP
GAM
ENFA
MaxLike
BRT
GLM
Random Forest
Ensemble_YES
Ensemble_NO
Number of papers
0
4
7
8
9
10
12
39
Europe
Conservation
Biogeography
Method
Species-habitat rel.
Phylogeography
Africa
Conservation
Biogeography
Epidemiology
Method
Phylogeography
South America
Biogeography
Method
Conservation
Ensemble_YES
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GAM
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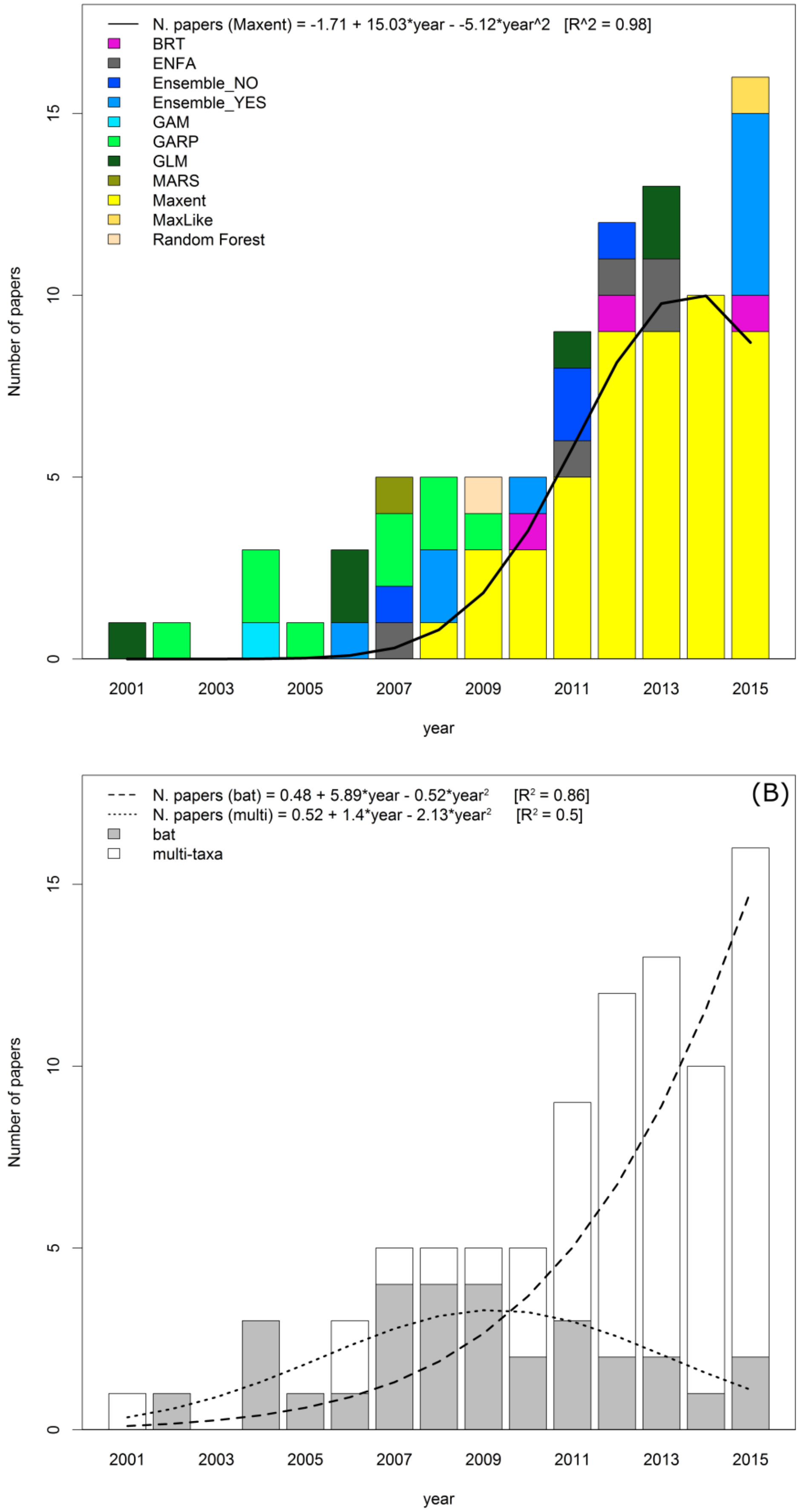
N. papers (Maxent) = -1.71 + 15.03*year - -5.12*year^2 [R^2 = 0.98]
BRT
ENFA
Ensemble_NO
Ensemble_YES
GAM
GARP
GLM
MARS
Maxent
MaxLike
Random Forest
Number of papers
0
5
10
15
2001
2003
2005
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2009
2011
2013
2015
year
(B)
N. papers (bat) = 0.48 + 5.89*year - 0.52*year²   [R² = 0.86]
N. papers (multi) = 0.52 + 1.4*year - 2.13*year²   [R² = 0.5]
bat
multi-taxa
Number of papers
0
5
10
15
2001
2003
2005
2007
2009
2011
2013
2015
year

Figure 3