Using species co-occurrence networks to assess the impacts of climate change

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Viable populations of species occur in a given place if three conditions are met: the environment at the place is suitable; the species is able to colonize it; co-occurrence is possible despite or because of interactions with other species. Studies investigating the effects of climate change on species have mainly focused on measuring changes in climate suitability. Complex interactions among species have rarely been explored in such studies. We extend network theory to the analysis of complex patterns of co-occurrence among species. The framework is used to explore the robustness of networks under climate change. With our data, we show that networks describing the geographic pattern of co-occurrence among species display properties shared by other complex networks, namely that most species are poorly connected to other species in the network and only a few are highly connected. In our example, species more exposed to climate change tended to be poorly connected to other species within the network, while species more connected tended to be less exposed. Such high connectance would make the co-occurrence networks more robust to climate change. The proposed framework illustrates how network analysis could be used, together with co-occurrence data, to help addressing the potential consequences of species interactions in studies of climate change and biodiversity. However, more research is needed to test for links between co-occurrence and network interactions.

Assessments of the effects of climate change on the distributions of species have typically been conducted using bioclimatic modelling approaches that ignore local population processes (but see Keith et al. 2008, Anderson et al. 2009) and biotic interactions (but see Araújo and Luoto 2007). By ignoring biotic interactions, an implicit assumption is that responses of species to climate changes are 'individualistic' (Pearson and Dawson 2003). However, interspecific interactions may structure biotic communities even at coarser spatial scales (Heikkinen et al. 2007, Gotelli et al. 2010). Thus, the 'individualistic response' assumption is problematic because it fails to account for interdependencies between species, whereby the removal of species or changes in the density of individual species within ecosystems can have cascading effects giving raise, for example, to secondary extinctions (for reviews see Ebenman and Jonsson 2005, Tylianakis et al. 2008). The individualistic response approach may also fail by ignoring known properties of interaction networks, such as increased resilience of assemblages with increasing connectance (Dunne et al. 2002b, Eklof and Ebenman 2006), and the

long-term co-occurrence of species enhanced by asymmetrical interactions (Bascompte et al. 2006).

The question then is: how can ecological interactions be accounted for in predictions of the effects of climate change on species distributions? One possible approach is to perform controlled experiments, whereby the anticipated changes in climate are simulated and the responses of species under different treatments are recorded. The results of two recent studies using this approach reinforce the notion that ecological interactions do affect species responses to climate change and can even overturn pure climatic effects (Suttle et al. 2007, Harmon et al. 2009). The problem is that while bioclimatic models often lack explicit parameterization of biotic interactions (but see Araújo and Luoto 2007, Heikkinen et al. 2007, Meier et al. 2010), experimental approaches are generally not feasible. Here, we explore an alternative approach using matrices of species spatial co-occurrences (the fundamental unit of analysis in community ecology and biogeography, Gotelli 2000), derived from overlapping geographic distributions to infer the consequences of climate change on assemblages

of interacting species across large areas. The approach does not seek to incorporate biotic interactions in the modelling process. Instead, it seeks to generate inferences about the strength of potential interactions based on patterns of co-occurrence among species and assess the degree to which they are likely to constrain assessments of the species sensitivity to climate change.

One major difficulty that our approach begins to address is that data to characterize interactions among species in diverse communities are generally lacking and are unlikely to become available in the near future. In order to address this shortfall, we use an approach based on network analysis to make inferences about potential broad-scale interactions between species based on the analysis of patterns of geographic overlap in the distributions of species. The reconstructed relationships are then used to estimate broad network properties, such as their overall robustness or resistance to species loss, as well as properties of the networked species, such as the species contributions to network robustness or the species sensitivity to the loss of links in the network (see for alternative implementations of coexistence networks in biogeography and community ecology: Dos Santos et al. 2008, Blick and Burns 2009, Azaele et al. 2010, Bell et al. 2010). The relationship between measured network properties and projected species distributional changes is then explored. The approach is implemented with data on the distributions of reptile, amphibian, mammal, and bird species across most of western Europe. These data are used for illustration of the framework and its methods, rather than for testing inferences about biotic interactions from patterns of co-occurrence; future testing of the framework should seek to use networks with tested functional properties.

Individualistic behaviour and ecological networks

There is a general consensus among bioclimatic modellers that species respond to climate changes individualistically (Pearson and Dawson 2003). Reliance on this idea has received support from analyses of the fossil record (reviewed by Graham and Grimm 1990, Stewart 2009), particularly from analysis of pollen cores showing that even when species composition remains stable over time, abundances of individual species change and non-analogue communities may emerge (Williams et al. 2001, Simakova 2006). Analysis of fossil mammal faunas for the Late Pleistocene and late Holocene provide further evidence that climate change forces individual species distributions to shift in different directions, and at different rates, thus giving rise to assemblages with no modern analogues (Graham et al. 1996). The ability of species to persist in non-analogue communities is interpreted as providing evidence that species respond individualistically to climate changes and are able to survive in very different assemblages, playing down the role of biotic interactions. However, the appearance of non-analogue sets of coexisting species does not imply that biotic interactions are unimportant to shaping the composition of assemblages over time. What the evidence seems to suggest is that strong symmetrical interdependencies, which would cause species to depend on

one another to respond to environmental pressures, are not prevalent. In fact, asymmetry seems to characterize most interactions between pairs of species. Only competition $(-/-)$ and mutualism $(+/+)$ are symmetrical. Other types of interactions, such as amensalism $(-1/0)$, commensalism $(+1/0)$, predation and parasitism $(+1/-1)$ are asymmetrical. In cases of tight co-evolution between pairs of species, strong asymmetrical interdependencies may exist such that, for example, one animal species A might depend strongly on a given plant species B, whereas the plant B might depend weakly on animal A (Bascompte et al. 2006). When this happens, A needs to track the distribution of B, under climate change forcing, even if B does not depend strongly on A (see also Salomon et al. 2010). Arguably, in most cases – particularly in areas exposed to cyclic environmental changes, such as high-latitude regions – it is unlikely that species would maintain such strong and rigid interdependencies. Firstly, processes of co-evolutionary convergence require time (Thomson 2005), and time implies long-term climatic stability which has been absent from high latitudes due to the cyclical glaciations (Frakes 1979). Secondly, even if evolutionary convergence had been possible, such species would have had a higher likelihood of extinction and probably been removed from the system by natural selection. Under such circumstances, a more likely scenario might be that most species would have been able to shift from one resource to another if conditions forced them to do so. One example was described for Adélie penguins in the Antarctica, where the species was able to switch in <200 yr from a diet mainly composed of fish to one predominantly based on krill (Emslie and Patterson 2007).

The consequence of a predominance of asymmetrical interactions is that some species are relatively more important in maintaining the overall structure of the network than others. Analysis of complex networks of interactions have indeed shown that few nodes (e.g. species) may act as hubs of the networks, gluing them together, whereas the majority of the nodes display weak links with the other constituting nodes (e.g. see for reviews Proulx et al. 2005, Bascompte 2007). This property of networks has often been described by a power law function $p(k) \propto k^{-y}$, where $p(k)$ is the probability of a node having k links and y is the exponent. When plotted in a log–log plot, this relationship is given by a straight line of slope $-y$ for the entire range of k values. Not all networks display a frequency distribution of the number of links per node (i.e. k or the degree distribution) that fits a power law, but it is generally the case that many species have a limited number of interactions (low degree), whereas few have more interactions (high degree) than expected by chance.

In the context of the above discussion one can predict that if most assemblages include species with asymmetrical and/or weak links with other species, then there is little reason to expect that the networks of interacting species would respond to climate change as a cohort. In other words, the fact that species often respond to climate changes independently of other species does not imply a reduced role for biotic interactions; it could simply mean that because species predominantly have non-obligate links with other species, assemblages are unlikely to behave as discrete entities (as one might interpret from the work of Clements 1916). However, the finding that most networks display

shared non-random properties prevents the opposing interpretation; that is, that species responses to climate change are driven by species individual requirements or dispersal alone. The truth might lie between these two extremes. Thus, rather than opposing the view of individualistic vs assemblage responses to climate change, a more fruitful discussion is one based on measurements of the relative importance of interdependencies in different assemblages. Such dependencies can be explored using network analysis.

The critical question then is how to measure such interdependencies. Several studies have measured interactions between pairs of species with well-known ecologies (Nilsson 1988, Johnson and Steiner 1997), while others have measured interactions among species in simple communities (Colwell 1973). Only recently have researchers started measuring pairwise interactions for relatively larger groups of species (Camacho et al. 2002, Dunne et al. 2002a, Milo et al. 2002, Bascompte et al. 2003, Garlaschelli et al. 2003), but usually with a focus on a particular type of biotic interaction (e.g. predation, dispersal, pollination). Naturally, the sheer number and complexity of direct and indirect interactions linking species within ecosystems is so great that their complete documentation is beyond reach. Making progress in understanding the role of complex interactions as drivers of species distributional dynamics, and their responses to climate change, requires the investigation of alternative approaches, such as the one we explore in this contribution.

Methods

The proposed framework involves 1) building spatial co-occurrence networks from a species co-occurrence matrix; 2) making inferences about network robustness; 3) modelling the exposure of individual species to climate change; and 4) investigating the relationship between measurements of network robustness and species exposure to climate change. An application of the proposed framework is provided using geographical distributions comprising all terrestrial vertebrates of Europe. The data are used for illustration of the framework, rather than testing it.

Building spatial networks of co-occurrence

Spatial networks of co-occurrence were built in 4 steps. In short, the procedure consists in measuring the number of sites where species co-occur (step 1), generating the co-occurrence network based on the measured distributional overlap between species distributions (step 2), pruning the network from spurious links using a null model of expected distributional overlap between pairs of species (step 3), and use a known standard (the percolation threshold) for analyzing and comparing network properties (step 4). A synthetic description of this procedure is provided in Table 1, where assumptions and shortcomings of each one of the steps are summarized.

Step 1 – a pairwise Bray–Curtis distance matrix was constructed to measure the degree of geographical co-occurrence in the distributions of pairs of species (Bray and Curtis 1957), but any distance metric could be used. Distances ranged from 0 to 100, with 100 representing completely non-overlapping distributions and 0 representing completely overlapping ones.

Step 2 – a spatial network of co-occurrence with species treated as nodes was built with software programmed by AR. Each link joining pairs of species was labelled with the Bray–Curtis distance among them.

Step 3 – several connections between species may be due to chance alone (Connor and Simberloff 1979). In order to remove these links from the network a null model was generated. The general principle is that overlaps that are equal or lower from that expected by chance should be discarded. Rather than generating the null model from a randomized experiment (Blick and Burns 2009, Kones et al. 2009), we addressed the problem analytically. Consider a given geographical space occupied by randomly located non-overlapping individuals, regardless of whether they pertain to the same species or not. Suppose we represent this environment by a two dimensional regular lattice of size $A = N \times M$. Then the probability P_a of finding an individual of species a in any randomly chosen site can be calculated as $P_a = N_a/A$, where N_a is the number of sites occupied by species a. In this same context one can calculate the probability of finding individuals of species a and b simultaneously,

$$P_{a\&b} = P_a P_b$$

Table 1. Stepwise approach for building networks of interactions using large scale species distributions. A discussion of the major assumptions and caveats with each step in the framework is provided.

Step	Approach	Assumptions	Caveats
1	Build pair wise geographical dissimilarity matrix	The degree of spatial overlap in species distributions indicates degree to which species can potentially interact.	Species may overlap but do not interact either directly or indirectly.
2	Construct unweighted or weighted network of interactions in geographical space	If assumption 1 is correct, then distances can be converted in network interactions.	The same as in 1.
3	Remove interactions that are not more likely than expected by chance	Pairwise interactions not greater than expected by chance are not ecologically meaningful.	Interactions may be no greater than expected by chance and still be meaningful.
4	Prune network of interactions by identifying the percolation point	At large geographical scales all species interact directly or indirectly with one another, thus forming a connected network.	Procedure with untested properties in ecological systems. Needs empirical validation.

of finding just one species,

$$P_{a \, OR \, b} = P_a(1 - P_b) + (1 - P_a)P_b = P_a + P_b - 2P_aP_b$$

and of finding neither species a or b in a randomly chosen site

$$P_{\sim a \, \& \, \sim b} + (1 - P_b)(1 - P_a) = 1 - P_a - P_b + P_aP_b$$

Then it follows that

$$P_{a\&b} + P_{a \, OR \, b} + P_{\sim a \, \& \, \sim b} = 1$$

Consider now a multinomial random variable $X(a,b)$ with three possible states $S = \{$(i) site contains both species a and b, (ii) site contains one of the species a or b, (iii) site contains neither of the species, neither a nor b$\}$. So it is expected to find in average $<i> = AP_{a\&b}$ sites in state (i), $<ii> = AP_{a \, OR \, b}$ sites in state (ii) and $<iii> = AP_{\sim a \, \& \, \sim b}$ sites in state (iii); with a variance of $Var(i) = A \, P_{a\&b} \, (1 - P_{a\&b})$, $Var(ii) = AP_{a \, OR \, b} \, (1 - P_{a \, OR \, b})$ and $Var(iii) = AP_{\sim a \, \& \, \sim b} \, (1 - P_{\sim a \, \& \, \sim b})$ respectively.

In order to identify links between species that are different from that expected by chance, we retain links between pairs of species whose number of co-ocurrences is either above $<i> + 2(Var(i))^{1/2}$ (attractive overlap) or below $<i> - 2(Var(i))^{1/2}$ (repulsive overlap).

Step 4 – once the network has been pruned from non-significant links, further removal of links is done after identification of the network's percolation threshold. The percolation threshold is a mathematical term related to percolation theory, which is the formation of long-range connectivity in random systems (Stauffer and Aharony 1992). The percolation threshold is the critical value of the occupation probability, or more generally a critical surface for a group of parameters, such that infinite connectivity (percolation) first occurs. As such, it is a particularly useful point at which to examine networks as it represents the minimal set of links underlying network connectivity and provides a standard for comparing networks of different size and type. Below this threshold, a network is thought to lose its integrity and collapse into small clusters. In our application, co-occurrence among species in the network was expected for connections representing Bray–Curtis distance just below the percolation threshold (Rozenfeld et al. 2008), standing for geographical overlapping above a minimal cut-off. The precise location of this threshold is made with a standard methodology adapted for finite systems (Stauffer and Aharony 1992), i.e. by calculating the average size $<S>^*$ of the clusters excluding the largest one:

$$\langle S \rangle^* = \frac{1}{N} \sum_{s < S_{max}} s^2 n_s \qquad (1)$$

as a function of the last distance value removed and identifying the critical distance with the one at which $<S>^*$ has a maximum. N is the total number of nodes not included in the largest cluster and n_s is the number of clusters containing s nodes.

Making inferences about ecological network robustness

Starting with the working premise that co-occurrence networks provide a surrogate for potential interactions among species (but see summary of caveats in Table 1), three measures of robustness can be investigated (Table 2): species contributions to network robustness; species sensitivity to the loss of network nodes (i.e. species); and overall network robustness or network resistance to species loss.

Species contributions to network robustness

The species contributions to network robustness are often examined as a function of species degree k_i; that is, the number of species a given species interacts with. The assumption is that the greater the degree of a species, the greater its contribution to network robustness. In addition to k_i, we also calculate a weighted measure of interaction intensity (Barrat et al. 2004), known as species strength (Bascompte et al. 2006). Species strength s_i is a quantitative extension of species degree, and can be defined as the sum of dependences d_{ij} (or co-occurrence, see below) between pairs of species i and j

$$s_i = \sum_{j=1}^{N} a_{ij} d_{ij} \qquad (2)$$

where a_{ij} determines whether species i and j are connected ($a_{ij} = 1$) or not ($a_{ij} = 0$). The loss of a species linked with several highly dependent species is considered to affect network robustness more than a species with fewer links

Table 2. Measured network properties and their ecological interpretations.

Indicator	Measure	Definition
Pairwise sensitivity to species loss	Symmetry	The degree to which the dependence of species A on species B is equal to the dependence of species B on the species A.
Network robustness to species loss	Degree distribution	The frequency distribution of the individual species degree for the entire network.
	Strength distribution	The frequency distribution of the individual species strength (in) for the entire network.
Species contribution to network robustness	Species degree	The number of links that connect the focal species to the other species. Assumes symmetrical interactions.
	Species strength (in)	A quantitative extension of species degree accounting for asymmetrical interactions. It provides a weighted sum of the proportion of the geographical distribution of $B_{1..n}$ that overlaps with species A.
Species sensitivity to network loss	Species strength (out)	A quantitative extension of species degree but accounts for asymmetrical interactions. It provides a weighted sum of the proportion of the geographical distribution of A that overlaps with $B_{1..n}$.

with less dependent species. In practice, measures of strength and degree tend to be correlated (Barrat et al. 2004, Bascompte et al. 2006), but degree assumes dependencies between species to be symmetrical whereas the measure of strength incorporates the more realistic idea of asymmetry between species dependences.

The critical issue for measuring strength is to quantify the level of dependence between pairs of species (d_{ij}). In networks of co-occurrence, species strength may be calculated by first quantifying the proportion of the geographical distribution of species A that overlaps with species B and vice versa. The underlying ideas are that 1) the proportion of the geographical distribution of A that overlaps with B provides a surrogate of interaction intensity of species A with B; and 2) this proportion is asymmetrical, such that, for example, the geographical distribution of A may overlap with B to a greater extent than B overlaps with A (Fig. 1). Quantitatively, the degree of overlapping between A and B is defined as $O(A,B) = (a \cap b)/a$ as the proportion of a (A's area) that overlaps b (B's area). The degree of symmetry of the link is then calculated as

$$Sim(A, B) = \frac{|O(A, B) - O(B, A)|}{Max[O(A, B); O(B, A)]} \quad (3)$$

where Sim(A,B) can get values in the interval [0,1]. In one extreme of the interval (Sim = 0), the link is completely symmetric. In the other (Sim = 1), the link is completely asymmetrical so that, for example, A is fully nested in B.

It follows that if O(A,B) is understood as a measure of interaction intensity (either direct or indirect) between species A and B, then we can define a measure of strength summarising how strongly other species may potentially interact with A, measured as the weighted sum of the proportion of the geographical distribution of $B_{1..n}$ that overlaps with species A. Thereafter, this measure will be termed strength in (S_{in})
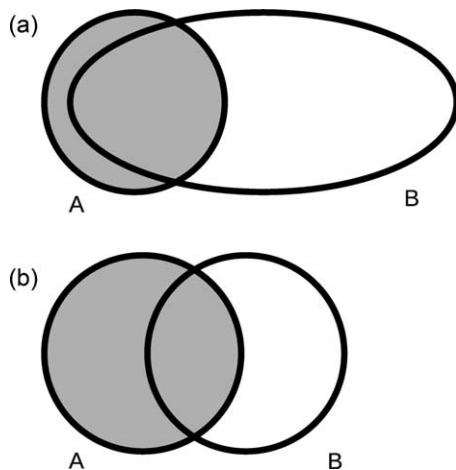

Figure 1. Graphical representation of symmetry in the geographical distribution between pairs of species: (a) species A depends strongly on species B, but species B does not depend strongly on species A; (b) species A and B depends moderately and equally on one another.

$$S_{in}(A) = \sum_{i}^{n} O(B_i, A) \quad (4)$$

Species sensitivity to the loss of links in the network
The previous measures of degree (k) and strength (S_{in}) provide indices allowing the quantification of the robustness of small sets of interacting species to the loss of highly connected species. A third measure, herein termed strength out (s_{out}), measures the sensitivity of individual species to the loss of nodes in the network. Strength out does not contribute to measuring network robustness; it measures how dependent a species might be, given the potential interactions with other species: a high s_{out} implies that the target species is highly dependent on other species, while low s_{out} implies the opposite. Strength out can be measured as the weighted sum of the proportion of the geographic distribution of species A that overlaps with $B_{1..n}$

$$S_{out}(A) = \sum_{i}^{n} O(A, B_i) \quad (5)$$

Network robustness
The former measures are focused on the properties of summed pairs of interacting species. To assess the overall robustness of networks we need to investigate the collective properties of degree (k) and strength (s_{in}). Following Dunne et al. (2002b), network robustness can firstly be investigated by examination of the frequency distribution of the species degree k_i. That is, the frequency distribution of the number of species a given species interacts with. Formally, the distribution P(k) gives the proportion of species in the network having degree k. Typically P(k) follows an exponential or power law (scale-free) distributions. Scale-free distributions depict networks in which most species are poorly connected with one another whereas a few species are well connected. In the ecological literature, such well-connected species are termed keystones, whereas in the network literature they are termed hubs. Scale-free degree frequency distributions are expected to be very robust to random loss of species, because most species are poorly connected in the network thus being unlikely removed by chance. However, they are very sensitive to the chirurgic removal of species with high k degree (Albert et al. 2000). In contrast, networks with exponential degree distributions, whereby a great proportion of species is highly connected with other species, are more sensitive to random removal of species.

Secondly, network robustness was investigated by examination of the frequency distribution of the species strength s_i. That is, the frequency distribution of the sum of dependencies between pairs of species (our measure of S_{in}). The distribution of $P(s_{in})$ is expected to generally have the same properties as P(k) (Barrat et al. 2004).

Modelling exposure of individual species to climate change

Species exposure to climate change was measured as $\delta = r_i t_{future} - r_i t_{baseline}$, where r is the distributional range of species i at time t. In order to calculate δ, individual species

potential distributions were modelled with ensemble forecasting (Araújo and New 2007) based on four widely-used bioclimatic envelope modelling techniques: 1) generalized linear models assuming a binomial error distribution (GLM, McCullagh and Nelder 1989); 2) mahalanobis distance (MD, Farber and Kadmon 2003); 3) maximum entropy (MaxEnt, Phillips and Dudík 2008); and 4) genetic algorithm for rule prediction (GARP, Stockwell and Peters 1999). Maximum entropy and GARP were parameterised using the default options in MaxEnt and Open Modeller GARP. Internal evaluation of the models was performed with a data split procedure, whereby 70% of the occurrence data was randomly split and used for calibration of the models and the remaining 30% were used for cross-evaluation of the models; this procedure was repeated 50 times thus generating a 50-fold cross-validation of model results. For species with range size <10 cells, rather than performing a 50-fold cross validation, each of the n cells with presence records were deleted once and the analyses were repeated n times. Model accuracy was measured using the average True Skill Statistic (Allouche et al. 2006). This analysis was performed to check if grossly implausible projections were being made (i.e. TSS <0.3). No species was removed based on this criterion and because measures of accuracy on non-independent data do not provide a reliable benchmark for evaluation of projections of species distributional changes under climate change (Araújo et al. 2005a), we instead used an unweighted consensus of the four modelling techniques. Projections agreeing at least half of the times were retained. With such approach potential errors associated with individual model projections are thus smoothed out in the consensus (Araújo et al. 2005b, Marmion et al. 2009). Nevertheless, final projections for current and future periods were obtained with all known records of occurrence, because bioclimate envelope models have been shown to be extremely sensitive to incompleteness of data in the calibration set (Araújo et al. 2009). Models were fitted with the BIOENSEMBLES software (Diniz-Filho et al. 2009).

Assessing co-variation between robustness and exposure to climate change

The two measures of network robustness can be compared against measures of exposure of species to climate change. Such comparison allows addressing the question of whether species with disproportionate contribution to network robustness, or species that are particularly sensitive to the loss of links in the network, are less or more exposed to climate change than species with minor contributions to network robustness or with small dependence on network structure.

The case study

The species distributions used to illustrate the framework included records of presence and absence for 58 amphibians, 91 reptiles (Gasc et al. 1997), 233 breeding birds (Hagemeijer and Blair 1997), and 186 mammals (Mitchell-Jones et al. 1999). Data represents the majority of terrestrial vertebrates of Europe (only mammals and birds with life-cycles highly dependent on water bodies were removed). The geographic grid used is based on that of the Atlas Florae Europaeae (Lahti and Lampinen 1999), with cell boundaries typically following the 50 km lines of the Universal Transverse Mercator (UTM) grid, except near the border of the six-degree UTM zones and at coasts. Data were converted to the AFE grid system by identifying unique (although sometimes approximate) correspondence between cells in these grids. The mapped area (2089 grid cells) excludes most of the eastern European countries (except for the Baltic States) because of low recording efforts in these areas (Williams et al. 2000).

The bioclimate envelope models were constructed with three variables (mean temperature of the coldest month (°C), mean temperature of the warmest month (°C), and mean annual summed precipitation (mm)) thought to reflect two properties of the climate – temperature and water – that have known roles in imposing constraints upon species distributions as a result of widely shared physiological limitations (Hawkins et al. 2003, Whittaker et al. 2007). Variables were also checked for collinearity using principal components analysis (PCA). The mean temperature of the warmest month (highest loading in PCA 1) was nearly orthogonal with mean summed precipitation (highest loading in PCA 2). The mean temperature of the coldest month was characterised with a vector 45 degrees from PCA 1 and 2.

Climate parameters were derived from an updated version of climate data provided by New et al. (2000). The updated data provides monthly values for the years 1901–2000 in a 10′ grid resolution (Schroter et al. 2005). Average monthly temperature and precipitation in grid cells covering the mapped area of Europe were used to calculate mean values of three different climate parameters for the period 1961–1991 (referred to as 'baseline data'). Future projections for 2020–2050 (referred to as the 2050 scenario) were based on climate model outputs from HadCM3 and made available through the Intergovernmental Panel on Climate Change (IPCC) Data Distribution Centre (<ipcc-ddc.cru.uea.ac.uk >). The modelled climate anomalies were scaled based on the A1FI scenario (Nakicenovic and Swart 2000).

Results

Network structure

Co-occurrence networks in the four groups of terrestrial vertebrates reveal different biogeographical structures (Fig. 2). Amphibians (median range size =79) have a co-occurrence network hub (i.e. with species highly connected to other species) in the Iberian Peninsula and another centred in central Europe. Reptiles (median range size =86) have two Mediterranean hubs (Iberian and Balkan peninsulas) and third centred in central Europe. Birds and mammals (median range sizes =389 and 187 respectively), have a slightly more diffuse network structure with a main hub in central Europe. Nevertheless, for birds, two smaller hubs are detected in the SW Mediterranean (including parts of the Iberian Peninsula and islands west of Italy) and
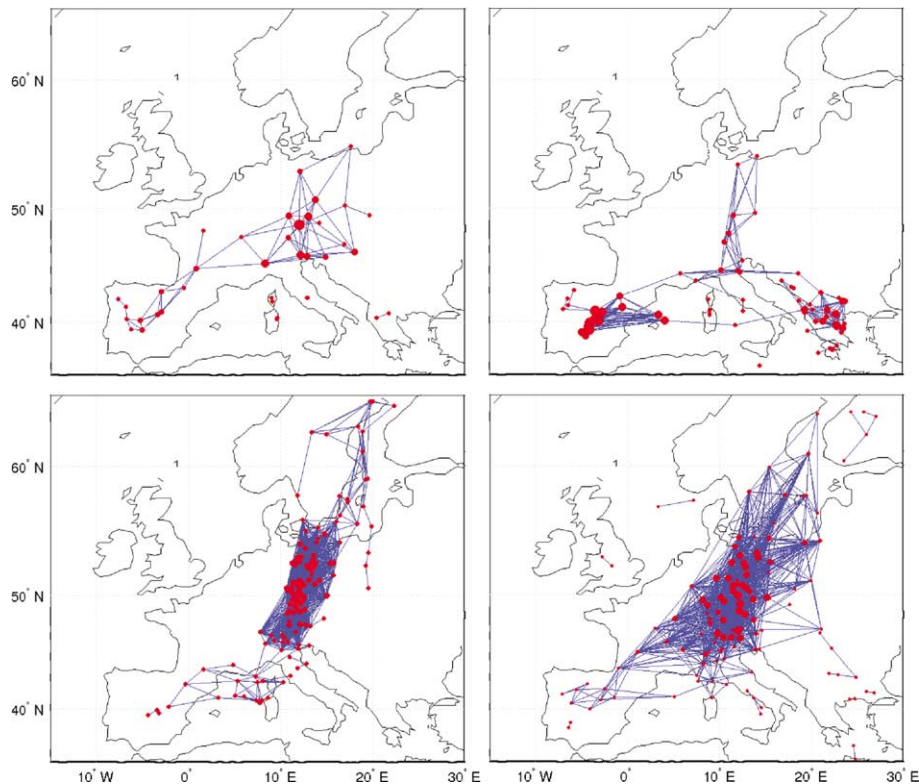
Figure 2. Spatial networks of co-occurrence among the European amphibians, reptiles, birds and mammals after removal of non-significant links (step 3 of the methods), and setting a threshold just below the percolation point (step 4 of the methods, Supplementary material Fig. A1). Circles represent the centroids of species distributions in a lat long coordinate system, and their sizes are proportional to the species degree (i.e. the number of links every species makes with other species). Lines represent the links between species. From top left to bottom right: amphibians; reptiles; birds; and mammals.

Scandinavia. Mammals have a more diffuse central European network structure extending to parts of Scandinavia with a small hub recorded in the Iberian Peninsula. Notice that Fig. 2 plots nodes (species) and links (level of co-occurrence just below the percolation threshold, Supplementary material Fig. A1), with nodes being located at the centre of each species range. Because species with restricted ranges are mainly in the south and to a smaller extent in the north, and species with wide ranges occur throughout most of Europe, central European hubs mainly represent the centroids of species that are widespread across Europe, whereas southern or northern hubs represent faunas nested in smaller regions.

Network robustness

Even though the spatial distribution of nodes and links varies between the four taxonomic groups, the empirical degree distribution $P(k)$ (for definitions see Table 2) displays a power-law-like distribution that is typical of many complex networks (Fig. 3). Departures to a perfect power law distribution do exist in our results, however. This is particularly true for birds and, to smaller extent, mammals since both taxa have more species with high degree k_i than expected. In other words, they have more species well connected in the network than expected from a typical power law distribution.

The frequency distribution of species strength $P(s_{in})$ (for definitions see Table 2) also reveals a power-law-like distribution for amphibians, reptiles and mammals, with the distribution of strength (in) for birds displaying no clear structure (Fig. 3). Inspection of the frequency distribution of the pairwise symmetries of co-occurrence between species (the measure used to calculate measures of strength, Table 2), further reveals the existence of a left-skewed distribution for most pairwise combinations of species (Fig. 4). In other words, most pairwise interactions (of co-occurrence) between species are asymmetrical.

Species sensitivity to network loss

Strength (out) is best characterised by a bell-shaped-like distribution (Fig. 4). The distribution of s_{out} for amphibians is slightly skewed to the left, meaning that a great proportion of species are expected to be sensitive to the loss of nodes in the network. The tendency for left (negative) skews is recorded also for birds and mammals but the degree of skewness is generally low for all taxa (Fig. 4).

Network properties and climate change

The two measures of species' contribution to network robustness, degree (k) and strength (s_{in}), display similar
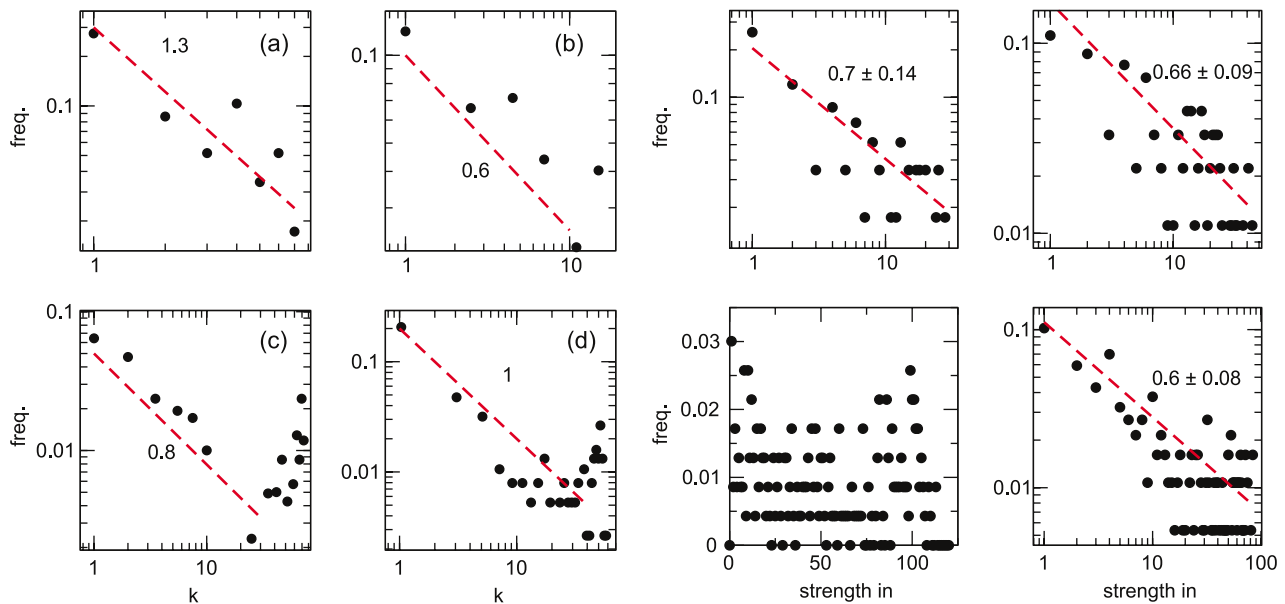
Figure 3. Distribution of degree (left panel), as defined by the probability of one species interacting with k species, and strength (in) (right panel) values, as defined by the sum of dependencies between the set of species $B_{1,n}$ with species A. In the panels: a) stands for amphibians; b) for reptiles; c) for birds; and d) for mammals. In random networks the degree and strength (in) distributions follows a Poisson distribution (or exponential if the number of nodes keeps growing), but in complex networks nodes tend to have few interactions and few nodes are more connected than expected by chance. This heterogeneous distribution of degree and strength (in) is often described by a power law function. In a log–log plot, such as that above, this relationship is given by a linear slope for the entire range of degree and strength (in) values. The distribution of degree and strength (in) values was processed using a standard rebinning procedure described by Adami and Chu (2002). The distributions of strength (in) for birds does not follow a power-law like distribution, thus we show the results without log-scaling the x axis.

properties when compared against species' exposure to 21st century climate change (Fig. 5). Essentially, amphibians, birds and mammals display a triangular relationship with over-dispersion of range-change values (δ) for species with low contribution to overall network robustness (low k and s_{in}). Species with high k degree and s_{in} strength tend to covary near the horizontal line of no-range-change, which means that as species become more important to overall network robustness they are also projected to be less impacted by climate change. This relationship is particularly marked for birds and mammals and for the measure of strength (s_{in}). For reptiles the pattern is slightly different with a clear tendency for species gaining range as a consequence of climate change being also the species that contribute more to robustness of the networks (Fig. 5).

When examining the measure of species sensitivity to network loss (s_{out}) against projected climate change impacts on species, no clear pattern emerges (Fig. 5). If anything, there is a tendency for species with intermediate strengths (s_{out}) to over-disperse towards intermediate values, but this may well be a consequence of the quasi-random distribution of strength (s_{out}) values (Fig. 4). Nevertheless there seems to be a tendency for amphibian and reptile species with high dependence on network structure (high s_{out}) to be generally positively affected by climate change (a few exceptions for amphibians). In contrast, the bird and mammal species that gaining or losing more with climate change tend to have low dependences on network structure.

Discussion

This study provides an approximation to using network analysis for assessments of climate change impacts on species. If one accepts that broad-scale interactions are reflected in patterns of overlapping distributions between species, then results invite the interpretation that 1) most pairs of interacting species had asymmetrical interdependencies, 2) most species displayed weak links thus a tendency for individualistic behaviour, and 3) networks describing the geographic pattern of co-occurrence among European vertebrate species displayed general properties shared by other complex networks, namely a power-law (i.e. scale free) distribution of degree (k) and strength (s_{in}), with the notable exception of networks for birds and mammals (the latter departing from scale free distribution only for k) (see also Azaele et al. 2010). Networks with scale-free distributions are particularly robust to random losses of nodes (Albert et al. 2000, Kaiser-Bunbury et al. 2010), while being sensitive to losses of well-connected hubs in the network (Albert et al. 2000). Having characterised the typology of the networks and identified the hubs that glue them together the question that follows is whether with climate change, such hubs would be affected. Here, species more exposed to climate change tended to be poorly connected to other species within the network (low k and s_{in}), while the more connected species tended to be less exposed to climate change. Low connectance for highly exposed species and high connectance for species with low exposure to climate change is good news. Poor connectance,
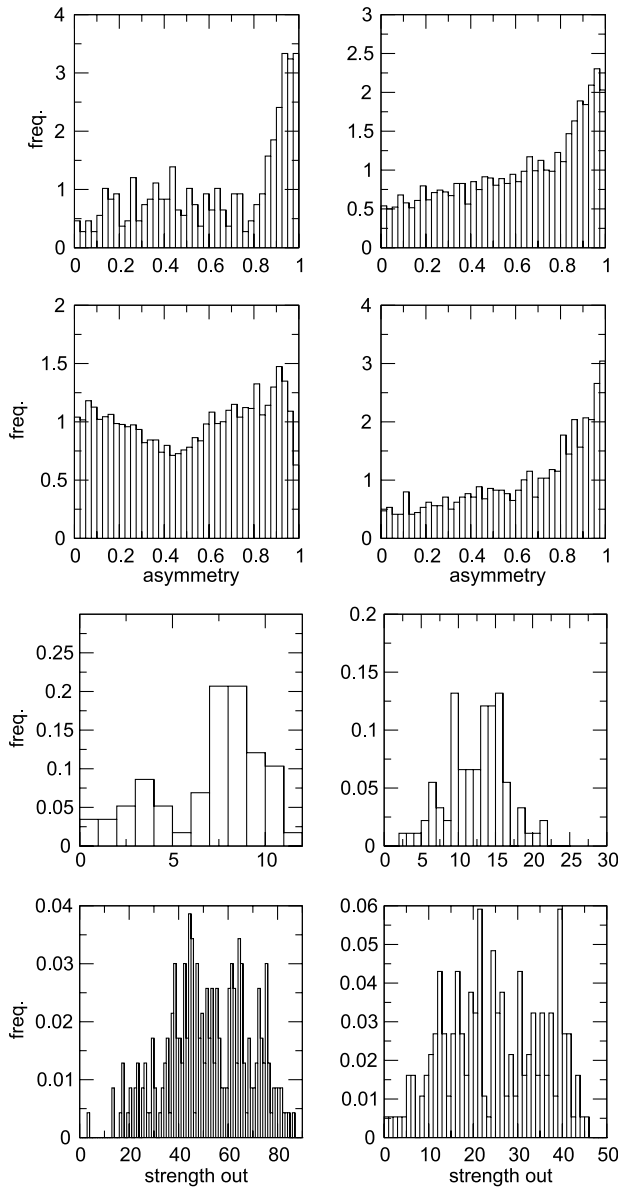
Figure 4. Frequency distribution of asymmetry values between pairs of species, and strength (out), as defined by the sum of dependencies between species A and $B_{1,n}$. In each panel from top left to bottom right: amphibians, reptiles, birds and mammals.

or low distributional overlap, makes the networks species belong to more robust to climate change because species are unlikely to be strongly associated with the distribution of other species in the network. It also indicates that while projections assuming individualistic responses of species to climate change are warranted for most cases, the general properties of interaction networks must be examined in order to anticipate which species would exert greater influence on the others and which would be more dependent on linkages with other species in the network. In other words, while most species display low connectance or overlap with other species, some species do have a high degree of connectance, thus supporting the hypothesis that strong interdependencies exist between species (but see the cautionary note below). Our framework provides one way to begin exploring the consequences of climate change on
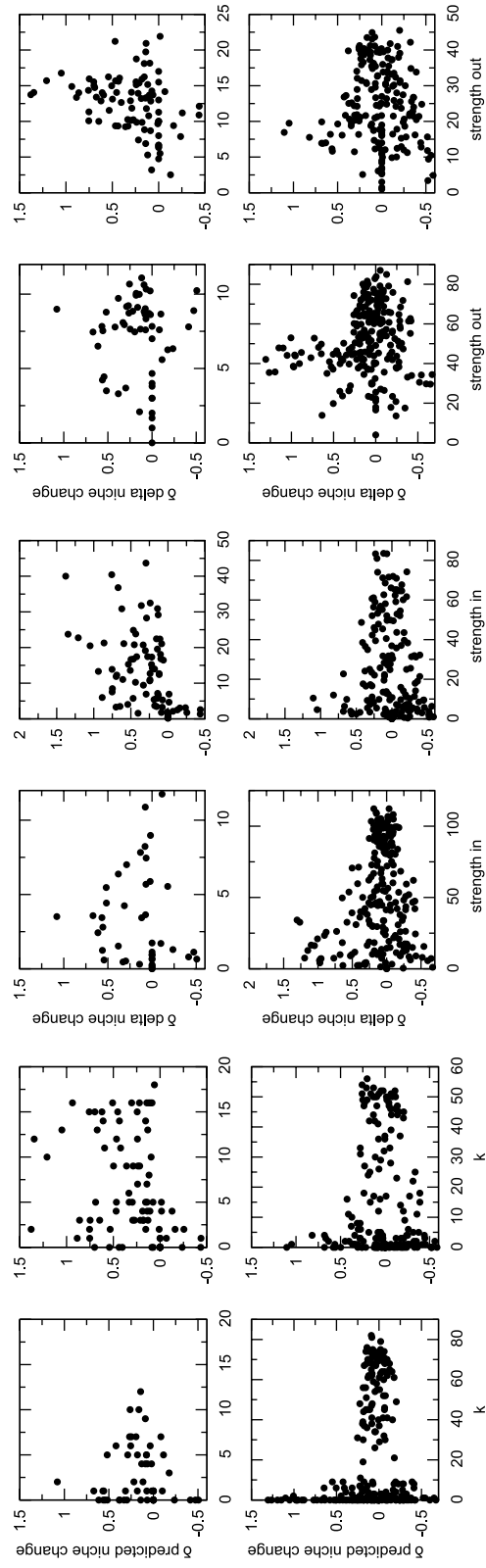

Figure 5. Species degree (k), strength (s_{in}) (degree to which focal species are needed by other species), and strength (s_{out}) (degree to which focal species needs other networked species), plotted against the projected change (δ) in the potential distribution of species under climate change. When δ values are >0 the species are projected to expand their ranges under climate change; when δ values are <0 contractions are projected. In each panel from top left to bottom right: amphibians, reptiles, birds and mammals.

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complex networks of co-occurring species. The critical question is whether co-occurrence networks provide inferences about functional properties of networks that would be useful for biodiversity assessments of climate change impacts.

The proposed framework rests on several assumptions that are largely untested and obviously are debatable; for example, that the strength of the interactions between two species can be inferred from the number of sites where both species coexist. Although co-occurrence networks are blind to the specific types of interactions involved, they do capture the essential fact that in order to interact, species must typically coexist. One exception is competitive exclusion, whereby spatial non-overlap is the outcome of strong negative interactions. Spatial networks of co-occurrence may thus be interpreted as summarizing potential interactions between species rather than actual ones. All other things being equal, one would expect regions with highly spatially dependent faunas to indicate the existence of functional interactions between species more so than faunas with lower spatial interdependences.

To avoid amalgamating likely and the unlikely interactions, as inferred from patterns of co-occurrence among species, we proposed a methodology based on 1) removal of links that may arise by chance alone, and 2) further removal of links preventing the emergence of clear network structure through inferences based on percolation theory (Table 1). The proposed methodology rests on the assumption that all species are either directly or indirectly connected in ecological systems and that spatial co-occurrence among species is, at partly, a consequence of functional interactions. Obviously, this is not always the case and species might co-occur due to shared physiological limitations or shared historical contingencies. For example, interaction hubs among amphibians and reptiles in the Mediterranean are likely to reflect mechanisms of parapatric speciation and long-term population persistence in glacial refugia that were not followed by inter-glacial expansion, possibly due to philopatry and limited dispersal (Gasc et al. 1997, Holman 1998, Araújo et al. 2008). The use of co-occurrence networks for practical assessments of biodiversity and climate change would thus require that an additional step 3) is implemented to screen for the ecological realism of the inferred interactions. Such screening would involve basic considerations of scale (e.g. what is the minimum spatial resolution required to infer interactions from co-occurrence patterns for particular groups of organisms?), as well as consideration of relevant aspects of the auto-ecology of the species (e.g. what organisms are likely to interact with one another?).

Previous attempts to factor biotic interactions into assessments of climate change impacts on species distributions are difficult to generalize as they typically involved a limited number of species in experimentally controlled environments (Davis et al. 1998, Suttle et al. 2007, Harmon et al. 2009), or use modelling approaches that require information that is generally unavailable for most species (Araújo and Luoto 2007), or tools that are conceptually incapable of handling interactions where they operate, i.e. in geographical space (see for discussion Baselga and Araújo 2009, 2010).

The proposed framework is a first attempt to handle a complex problem using the theoretical framework and analytical toolboxes of network analysis and bioclimatic modelling. We hope our contribution will motivate others to test the predictions and assumptions of the framework herein proposed, particularly the proposed inferences about network robustness and species sensitivity to loss of network links using co-occurrence networks. It is clear that not all potential interactions are real, and in some cases it may be more useful to explore bipartite networks that restrict analysis to co-occurrence of preselected taxa based on known functional relationships (Bascompte et al. 2006, Berg et al. 2009). But the important question is whether the general patterns emerging from coarse biogeographical analysis of networks reflects underlying patterns in nature. In other words, if the general structure of hubs and links in the network is maintained when actual interactions, rather than potential ones, are considered. A recent paper, showed that patterns of species co-occurrence at coarse geographical continental scales exhibit strong signals of interspecific interactions (Gotelli et al. 2010). The authors revealed that community-wide patterns of spatial segregation among Danish breeding birds could not be attributed to the patchy distribution of habitat, or to gross differences in habitat utilization among ecologically similar species. They proposed that conspecific attraction in concert with interspecific territoriality may result in spatially segregated distributions of ecologically similar species at larger spatial scales when habitat patch size is limited. Finally, they also showed that the effects of species interactions on community assembly were pervasive and could be discerned at grain sizes up to four orders of magnitude larger than those of individual territories. More examples support the view that spatial co-occurrence allows inferences to be about interactions among species. For example, Azeaele et al. (2010) demonstrated the usefulness of examining co-occurrence networks to uncover functional relationships between plants in forest ecosystems. Another study empirically investigated the extent to which trophic relationships between species could be uncovered through the analysis of bipartite predator-prey co-occurrence networks (Bell et al. 2010). The results of Bell et al. (2010) are encouraging in that the feeding behaviour of the studied polyphagous beetles and spiders could be inferred with their particular implementation of co-occurrence networks. More studies investigating the extent to which co-occurrence networks can help infer functional interactions among species are obviously needed (see also Heikkinen et al. 2007, Meier et al. 2010), but our prediction is that if errors arising from the simplified assumptions of co-occurrence networks are randomly distributed across taxa and regions, then functional networks based on verifiable interactions between species would not change the overall patterns emerging from co-occurrence networks. This should be particularly true at coarse resolutions where 'ecological noise' is reduced (Lawton 1999).

Conclusion

The challenges posed by a rapidly changing climate and its consequences on biodiversity, requires a concerted effort of

scientists in different disciplines. In this paper we have advanced an idea that builds on the interaction between network theory and bioclimatic modelling to generate a simple framework that can be use as a first approximation to tackle this challenge. We believe that network theory provides a suitable and powerful framework to address the complexities of climate change impacts on biodiversity, which in concert with simple co-occurrence matrices (the fundamental unit of analysis in community ecology and biogeography, Gotelli 2000) can pave the way to incorporate species interactions into the analysis of species responses to climate change and further our understanding of the effects of climate change on biodiversity.

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