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Article

Network modelling is strictly required for predicting climate change impacts on biodiversity

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Abstract
Robust models are pivotal to the prediction of future climate change impacts on biodiversity. A move must be made away from individualistic models of single species toward the implication of synergistically interacting species. The focus should be on the indirect effects due to biotic interactions. Thanks to these kinds of models, counterintuitive results for species could be achieved, emerging from complex biotic feedbacks involving that species-specific expectations are not of necessity consistent with those of their community. In this paper, the proposed approaches can tackle some important limitations of commonly-used individualistic models, as they can: a) deal with an optionally large number of species, b) take into account biotic interactions, c) forecast indirect effects caused by climate change.

Keywords biotic interactions; climate impact models; ecological communities; indirect effects; scenarios simulations.

1 Introduction
Over the next decades, climate change will be one of the major drivers affecting diversity, composition, structure and functioning of ecological communities. Specific changes will include shifts in ecologically crucial factors, such as temperature, rainfall, solar irradiance and wind (Zhang and Chen, 2011). These aspects of climate change are likely to have deep effects on natural communities, with also potential feedbacks from communities to climate (Wu and Zhang, 2012).

Global surface temperature has increased by 0.74 °C on average over the last century with greater warming on land surfaces than on oceans (IPCC, 2001). Future warming is likely to be between 1.1 °C and 6.4 °C by the end of the 21th century, depending on the projection scenario (IPCC, 2001).

An urgent issue is predicting the effects of increased temperature on ecological communities across the globe. Climate change will affect patterns and processes of species and food webs in a variety of ways such as alteration of dispersal rates, spatial uncoupling of interactions and shifted phenology resulting in a rearrangement of species mutual interactions. Studies investigating the consequences of future climate changes
on species distributions often apply the assumption that species respond to climate changes in an individualistic way (Baselga et al., 2009; Heegaard and Vandvik, 2004; Tylianakis et al., 2007). Instead, climate-induced scenarios may cause unobvious local-scale alterations to the network of interactions among species, and biotic interactions may complicate the broad-scale control that the environment has on a species’ distribution (Suttle et al., 2007). The indirect effects that are potentially sensitive to global climate change and the complex feedbacks that exist among species implicate that species-specific previsions are not necessarily consistent with those of their communities (Ferrier et al., 2006). Accordingly, single-species studies should be expanded to include a more general multi-species assessment based on some kind of synthesis of individualistic models (Ellis et al., 2007).

Changing individual species models to account for complex biotic interactions is challenging. Doing it without data hungry models is even tougher, and inevitably requires some kind of scaling from single species to whole interaction networks. In this paper, several network approaches are proposed that can tackle some important limitations of commonly-used individualistic models, as they can: a) deal with an optionally large number of species, b) take into account biotic interactions among species, c) forecast indirect effects caused by climate change.

2 Four Increasingly Complex Solutions
A full understanding of the effects of climate-induced scenarios on biotic communities necessarily requires the consideration of the whole interaction network among species (Ferrarini, 2012). This requires a methodological approach as follows (Fig. 1): climate change scenario → direct impact on each species → indirect impacts on all linked species → feedback impacts at community level.

This requires a $n \times n$ “climate-induced” interaction matrix whose off-diagonal elements $w_{ij}$ take into account the inter-specific effects of species $i$ upon species $j$ as primed by a climate change scenario, instead elements $w_{jj}$ take into account intra-specific effects (on growth, phenology and reproduction) of climate warming on single species.

In order to do this, I propose here the following methodological framework (Fig. 2) for network modelling of climate change impacts on ecological communities.
A quantitative network model of interacting species requires a precise estimate of the strength of species interactions induced by climate change, that could be unavailable for most species. On the other hand, a qualitative network model would lose information about strength of interactions. Moreover, a semi-quantitative model could encapsulate “hard” data (e.g., species coverages) based on precise statistical estimates, with “soft” data (e.g., theorized effect of temperature increase on single species), resulting in an overall parsimonious model of the community dynamics under a climate change scenario. The qualitative and semi-quantitative approaches are also worthy where the climate parameters required to feed into the network model are lacking or limited. This often happens for limited-in-size study areas whose extension is smaller or comparable to the spatial resolution of available climatic maps. Instead, most broad-scale studies use coarse resolution (e.g. 50 km × 50 km) data, and can be fed with quantitative climate projections (e.g. Worldclim data).

2.1 Qualitative networks

If precise predictions are not a requirement, I suggest that qualitative models could offer an alternative and cost-effective method for predicting biotic responses to climate change. A qualitative approach, like loop analysis (LA; Puccia and Levins, 1985), would provide predictions on the probable direction of change in species abundances, and would be suitable if only the direction of the effects of climate perturbations is required, not their magnitude (Ferrarini, 2012). The strength of this approach would be in its generality, and its ability to address the complex, nonlinear effects that feedbacks among species determine on single species and on the whole network of species.

LA uses signed digraphs to represent networks of interacting variables. System variables are depicted as nodes in the graph, and each connection between two nodes represents a non-zero coefficient of the
community matrix. Press perturbations may act by changing one or more parameters in the growth rate of the
variables. Taking the inverse of the community matrix provides an estimate of the direction of change in the
equilibrium level of variables in response to these parameter changes. The element \( a_{ij} \) of the matrix represents
the effect of variable \( j \) on the growth variable \( i \), when the following equation is solved for a moving
equilibrium:

\[
\frac{dX_i}{dt} = f_i(X_1, X_2, \ldots, X_n; C_1, C_2, \ldots, C_h)
\]

where \( X_1, \ldots, X_n \) represent the variables and \( C_1, \ldots, C_h \) the parameters. Responses of abundances or biomass are
arranged in a table of predictions whose signs show the predicted direction of change. The entries in a table
denote variations expected in all the column variables when parameter inputs affect each row variable.

For the purposes of this paper, interacting variables (nodes) would represent species, while sign (+, 0, -) of
induced connections among species could emerge from the following schema: let’s suppose that climate
change favors species \( i \) and disfavor species \( j \), this causes species \( i \) to likely expand its niche hindering species
\( j \), in case they are in contact. Since each species can undergoing 3 kinds of climate-induced effects (positive,
negative, null), a couple of species can undergo: (+1, -1) interaction when one species is favorite and the other
one disfavored; (-1, -1) interaction when they are both favorite or disfavored; (0, 0) represents no interaction
(when the 2 species are both indifferent to climate change). Furthermore, there might be self-damped terms
associated to density-dependent control (organisms with spatial limitations) or continuous supply of the
species from outside the system.

2.2 Semi-quantitative networks

Fuzzy cognitive maps (FCM; Kosko, 1986) are particularly useful for applications where relationships
between concepts cannot be expressed in exact mathematical equations (Ferrarini, 2011a; Ferrarini, 2011b).
Biological and environmental quantities and their causal interactions are often described in relative and vague
terms. A large proportion of the ecological information is represented in this way, and cannot be used as an
input to data-driven mathematical or statistical models. The main advantage of FCM relies in its ability to
represent such fuzziness.

FCM are semi-quantitative networks which describe the behaviour of a system in terms of concepts
(nodes); each concept represents a variable (e.g., species' abundances) or a characteristic of the system. Values
of nodes change over time, and take values in the interval [0, 100]: a value of 0 means that the factor is absent,
a value of 100 means that the factor is present to the maximum possible extent, while a value of 50 represents
the actual level of system variables. The causal links between nodes are represented by directed weighted
edges that illustrate how much one concept influences the interlinked concepts, and the causal weights of the
interconnections belong to the [-1, +1] interval. The strength of the weight \( w_{ij} \) indicates the degree of influence
between concept \( C_i \) and concept \( C_j \). The value of each concept at every simulation step is calculated as follows:

\[
A_j(t) = A_j(t-1) + \sum_i A_i(t-1) \cdot w_{ij}
\]

where \( A_j(t) \) is the value of concept \( C_j \) at time \( t \), \( A_j(t-1) \) is the value of concept \( C_j \) at time \( t-1 \), \( w_{ij} \) is the weight
of the interconnection from concept \( C_i \) to concept \( C_j \).

For the purposes of this paper, while values of the generic \( i \)-th species \( C_i \) at time \( T_0 \) (actual surface cover)
and diagonal values \( w_{ij} \) (direct effects due to climate change) might be assessed through in situ monitoring, off-
diagonal \( w_{ij} \) values (climate-induced indirect effects) could be stochastically simulated. Instead of just using
\(<+1, 0, -1> \) values as depicted above for quantitative networks, off-diagonal might be simulated using \( n \)
simulations by varying off-diagonal values of a random increase up to 100% for favored species, and a random
decrease up to 100% for disfavored species, subsequently achieving both the average expected dynamic and the expected deviations.

2.3 Quantitative networks
If also the strengths of induced interactions among species are known, a dynamical system of \( n \) interacting species under climate change impact behaves as follows:

\[
\frac{d\bar{S}}{dt} = \varphi(\bar{S}, t)
\]

where \( \bar{S} \) is the number of individuals (or the total biomass) of the generic \( i \)-th species. If we also consider inputs and outputs from outer ecosystems, we must write:

\[
\frac{d\bar{S}}{dt} = \varphi(\bar{S}, t) + \bar{I} + \bar{O}
\]

This can be modelled and simulated using a system of canonical linear equations, as follows:

\[
\begin{align*}
\frac{dS_i}{dt} &= a_{i1}S_i + \ldots + a_{in}S_n + I_i + O_i \\
&\ldots \\
\frac{dS_n}{dt} &= a_{1n}S_1 + \ldots + a_{nn}S_n + I_n + O_n
\end{align*}
\]

that can also be written in a compact form

\[
\frac{d\bar{S}}{dt} = A*\bar{S} + \bar{I} + \bar{O}
\]

where

\[
A = \begin{pmatrix}
a_{11} & \ldots & a_{1n} \\
\ldots & \ldots & \ldots \\
a_{n1} & \ldots & a_{nn}
\end{pmatrix}
\]

is the matrix of the unitary-time effect on \( S_i \) due to unitary \( S_j \), with initial values

\[
\bar{S}_0 = \langle S_1(0), S_2(0), \ldots, S_n(0) \rangle
\]

and co-domain limits

\[
\begin{align*}
S_{i\text{min}} &\leq S_i(t) \leq S_{i\text{max}} \\
&\ldots \\
S_{n\text{min}} &\leq S_n(t) \leq S_{n\text{max}}
\end{align*}
\]

The parameters of such equations could be determined through \textit{in situ} experiments specifically for each study area, or through laboratory experiments where climate variables are accelerated and parameters are extracted specifically for each species and for each kind of interaction.

2.4 Quantitative networks incorporating spatial dimension
If also spatial arrangements of species are known, we need partial differential equations (PDEs). Let \( S(x, y, z, t) \) measure species’ biomass (or number of individuals) at time \( t \) and at the generic location \( <x, y, z> \),
the climate-induced dynamical system of \( n \) spatially-explicit interacting species becomes:

\[
\begin{align*}
\frac{\delta S_1}{\delta t} &= a_{i1}S_{i(x,y,z)} + \ldots + a_{in}S_{n(x,y,z)} + I_{i(x,y,z)} + O_{i(x,y,z)} \\
\ldots
\frac{\delta S_n}{\delta t} &= a_{1n}S_{1(x,y,z)} + \ldots + a_{nn}S_{n(x,y,z)} + I_{n(x,y,z)} + O_{n(x,y,z)}
\end{align*}
\]

(10)

While this kind of network modelling is data hungry, it allows to achieve spatially-explicit predictions of climate change impacts on biotic communities.

3 Conclusions

Animals and plants are embedded in complex networks of interactions with other organisms, and the ways in which climate change works across the whole community is much more complex than the simple direct effects on single species. Local biotic interactions among species complicate the broad-scale control that climate has on species dynamics, and climate change scenarios is likely to cause unobvious alterations to the network of interactions among species. This is particularly true at local scale, where biotic interactions are cardinal to the community response (Trivedi et al., 2008).

Hence, the proposed approaches to the prevision of climate change effects on biotic communities focus on the importance of ecological indirect effects (Krivtsov, 2004; Salas and Borrett, 2011) based on the rationale that climate change determines direct effects on single species, thence inducing complex feedbacks at community-level and leading to indirect effects and unexpected outcomes as well.

References


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