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Consequences of past climate change for species engaged in obligatory interactions

Conséquences des changements climatiques passés sur les espèces en interactions obligatoires

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ABSTRACT

Obligatory interactions between species are fundamental to ecosystem functioning and are expected to be particularly sensitive to climate change. Although the effect of past and current climate changes on individual species has been thoroughly investigated, their effect on obligatory interactions has been overlooked. In this review, we present predictions about the effects of climate change on obligatory interactions and illustrate these predictions with examples from the literature. We focus on abrupt past climate change, especially during the Quaternary, because knowing past responses is useful for understanding and predicting the response of organisms and ecosystems to the current climate change. We also pinpoint the need for better time calibration of demographic events from genetic data, and for more studies focused on particularly suitable biological models. We hope that this review will stimulate interaction between the earth sciences and the life sciences on this timely topic.

RÉSUMÉ

Les interactions obligatoires entre espèces sont fondamentales au fonctionnement des écosystèmes et sont particulièrement sensibles aux changements climatiques. Bien que l'effet des changements climatiques passés et présents sur les espèces prises individuellement soit l'objet de nombreuses études, l'effet sur les interactions obligatoires est mal connu. Dans cette revue, nous exposons les attendus concernant les effets des changements climatiques sur les interactions obligatoires et les illustrons avec des exemples pris dans la littérature. Nous nous sommes focalisés sur les changements climatiques abrupts passés, en particulier du Quaternaire, car ils permettent de comprendre et de prédire la réponse des organismes et des écosystèmes au changement climatique actuel. Par ailleurs, nous insistons sur la nécessité d'une meilleure calibration temporelle des évènements démographiques à partir des données génétiques et sur le besoin de concentrer les efforts sur un nombre réduit de modèles biologiques particulièrement propices. Nous espérons que cette revue stimulera les interactions entre sciences de la terre et sciences de la vie sur ce thème d'actualité.

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1. Introduction

Climate fluctuation has been one of the main forces driving the dynamics of biodiversity on Earth. The response of ecosystems to climate changes is thus a central issue in the evolution of life and can only be understood through detailed analyses of the relationships between organisms and environment and among organisms. Biotic interactions are the mechanisms that link together the individual pieces and they must be understood simultaneously at proximal (ecological mechanisms) and ultimate (evolutionary processes) levels.

Obligatory interactions, i.e., interactions in which at least one partner depends on the other, are among the most fundamental to the functioning of ecosystems. They are either mutualistic, i.e., interactions that are beneficial for the interacting species, or parasitic, i.e., interactions that are beneficial for one species but detrimental to the other. Reciprocal benefits improve the ecological success of the interacting species and, at the ecosystem level, play key roles in nutrient cycles and energy flow. Mutualistic and parasitic interactions both generate biodiversity, by accelerating speciation (Hoffmeister and Martin, 2003; Margulis and Fester, 1991; Mereschkowsky, 1926), and maintain biodiversity, as specialization facilitates coexistence (Poisot et al., 2011). In the context of global change, mutually beneficial interactions are important for the functioning and stability of ecosystems (Danovaro et al., 2008). Moreover, mutualisms are key factors in the adaptation and survival of species, but obligatory mutualisms are more sensitive to environmental changes than facultative mutualisms (Kiers et al., 2010).

Obligatory interactions are expected to be particularly sensitive to climate change because the two partners may respond differently to changes but each still depends upon the other for its survival. Their sensitivity and their structuring role in ecosystems make them good models for studying the consequences of current and past climate changes at the scale of the ecosystem. Understanding the mechanisms underlying responses of obligatory interactions to abrupt past climate changes should help us understand changes in ecosystems that are happening now and predict what may happen in the future.

The effect of current and past climate changes has been thoroughly investigated for species considered individually. Species and population histories are usually inferred either from the palaeontological record or from genetic data on current populations using phylogeography and population genetics (Hewitt, 2004; Vegas-Vilarrubia et al., 2011). Interest in the response of species communities to changes has grown only recently (Urban et al., 2012). In addition, reconstruction of past vegetation composition through pollen records, correlated with reconstruction of past climate fluctuation using physical and chemical proxies, allows to assess the intensity of past changes and the related response of ecosystems. However, the mechanisms underlying these responses are rarely investigated.

Most of the periodic climate fluctuations that occurred in the past are due to periodic variation in parameters of the Earth's orbit, called Milankovitch oscillations (Berger, 1988). Time scales of these climate fluctuations, ranging from tens of thousands of years to over a hundred thousand years, are likely to have driven evolutionary changes in species and populations. Milankovitch oscillations combined with tectonic organization are thus considered a major driver of evolution, shaping life history traits, interspecies interactions, and global patterns of biodiversity at different scales (Dynesius and Jansson, 2000; Webb and Bartlein, 1992).

In this paper, we review the potential effects of climate change on obligatory interactions, and search the literature for evidence of such effects in the recent past, mostly the Quaternary period. The paper is structured around three categories of effects of climate change on populations that are expected to have shaped the evolutionary history of obligatory interactions: fragmentation of populations, range shifts, and partner extinction due to extreme and abrupt climate events. For each category we first present the predicted response of populations in obligatory interactions, and then illustrate these responses with examples from the literature.

2. Fragmentation of populations

Climate fluctuation induces changes in temperature and rainfall that are spatially heterogeneous, because physical characteristics of the landscape strongly influence local environmental conditions. Thus, even if climate becomes globally unfavourable to a given species, this species can still be maintained in isolated places with particular microclimates. Areas with sharp altitudinal variation are classical examples, where species can cope with climate change by shifting their altitudinal range distribution, which requires migrating over much shorter distances than in flat landscapes (Loarie et al., 2009). Other examples are the possible maintenance of biota requiring humid conditions along riversides in otherwise dry landscapes (Born et al., 2011; Colyn et al., 1991), or the maintenance of warm-adapted biota on sun-exposed slopes in otherwise cold landscapes (Graham et al., 2005, 2006; Schonswetter et al., 2005). Landscape heterogeneity may thus allow the persistence of species or communities throughout cycles of climate change.

During glacial periods, forests were considerably more restricted at all latitudes than in the current interglacial period and some forest-restricted species managed to persist only in localized regions—referred to as forest refugia or glacial refugia—presenting relatively favourable (warm, wet) climatic conditions (Hewitt, 2000; Petit et al., 1999). As climates warmed after glacial periods, surviving populations expanded to reach their contemporary ranges. That places existed where populations of one or more species persisted during climatic fluctuations is widely accepted. The role of refugia, i.e. places where a community or a whole ecosystem persisted, is globally validated in ecosystems of temperate and boreal regions (Schmitt, 2007). For tropical regions, no consensus about the role of forest refugia in the dynamics of biodiversity during climate fluctuations has been reached. Current debate concerns two points. First, the role of refugia in the evolutionary diversification of tropical biota remains