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Original article

Plants on the move: The role of seed dispersal and initial population establishment for climate-driven range expansions

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ABSTRACT

Recent climate change will presumably allow many plant species to expand their geographical range up to several hundred kilometres towards the poles within a few decades. Much uncertainty exists however to which extent species will actually be able to keep pace with a rapidly changing climate. A suite of direct and indirect research approaches have explored the phenomenon of range expansions, and the existing evidence is scattered across the literature of diverse research subdisciplines. Here I attempt to synthesise the available information within a population ecological framework in order to evaluate implications of patterns of seed dispersal and initial population establishment for range expansions. After introducing different study approaches and their respective contributions, I review the empirical evidence for the role of long-distance seed dispersal in past and ongoing expansions. Then I examine how some major ecological determinants of seed dispersal and colonisation processes - population fecundity, dispersal pathways, arrival site conditions, and biotic interactions during recruitment - could be altered by a rapidly changing climate. While there is broad consensus that long-distance dispersal is likely to be critical for rapid range expansions, it remains challenging to relate dispersal processes and pathways with the establishment of pioneer populations ahead of the continuous species range. Further transdisciplinary efforts are clearly needed to address this link, key for understanding how plant populations 'move' across changing landscapes.

1. Introduction

The 20th century experienced the strongest global warming of the last millennium, and future temperature rises are likely to exceed this trend with a predicted increase between 1.8 °C and 4 °C until 2100 (Solomon et al., 2007). The potential impact of modern rapid climate change on the distribution and conservation of biodiversity is the object of great concern. One major consequence is that plant and animal species worldwide are moving to higher latitudes and elevations in response to shifts of the environmental conditions to which they are adapted (Parmesan, 2006). Model-based projections suggest that the expected climatic conditions would permit many species to expand their current distribution range several hundred kilometres towards the poles within only a few decades (e.g. Skov and Svenning, 2004; Jump et al., 2009). Much uncertainty exists however to which extent species will actually be able to achieve such large-scale range expansions in pace with a rapidly changing climate. The answer to this question has wide-ranging ecological and evolutionary consequences spanning from the population to the biome level. Thus, the expansion process can strongly affect the range-wide genetic structure of species and the adaptive potential of their populations (Excoffier et al., 2009). The differential migration capacity of species should result in considerable reshufflings of local communities and regional species pools (Ackerly, 2003; Jackson et al., 2009). And the expansion of biomes such as the boreal forests will directly influence future climate, be it as a mitigating (e.g. by sequestering CO_2) or an exacerbating (e.g. reducing albedo) force (Bonan, 2008).

It is broadly accepted that range expansions depend on the populations residing at the colonisation front, or 'leading edge' (Thuiller et al., 2008; Murphy et al., 2010). Hence, predicting the expansion potential of a species requires a sound understanding of the ecological and micro-evolutionary key processes that occur in these populations (Hampe and Petit, 2005). Two processes are necessarily involved in a range expansion: 1) the dispersal of individuals (propagules in the case of plants) beyond the current range limit and 2) the establishment and growth of resulting

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pioneer populations. Both processes contain a strong stochastic component, usually escape direct observation and therefore are extremely difficult to measure in nature (Nathan et al., 2003; Nathan, 2006; Simberloff, 2009). A suite of direct and indirect research approaches have been used to explore the phenomenon of range expansions, and the existing evidence is scattered across the literature of various research disciplines spanning dispersal ecology, palaeoecology, landscape genetics, phylogeography, invasion biology, climate change research and different branches of dispersal and distribution modelling.

Great progress has been made in combining some of the above disciplines, and these interdisciplinary efforts have considerably helped refine our understanding of species range dynamics (Petit et al., 2004; Botkin et al., 2007; Hu et al., 2009). For instance, a rapidly growing number of phylogeographical studies combines molecular surveys with palaeoecological data and/or species distribution modelling exercises (e.g., Cheddadi et al., 2006; Alsos et al., 2009; Liepelt et al., 2009). Other examples are the rapidly growing field of 'invasion genetics' (Estoup and Guillemaud, 2010), studies at the interface between dispersal ecology and invasion research (Gosper et al., 2005) or those that merge invasion and climate change biology (e.g., Gallien et al., 2010). A greater gap appears however to persist between disciplines that focus on past range dynamics and those that investigate primarily ongoing expansions. And little interdisciplinary research has to date been specifically dedicated to populations at the leading edge of expanding species ranges. Hence, we are lacking a general framework that integrates the many intrinsic and extrinsic factors that can determine the success or failure of a species to keep pace with a rapidly changing climate.

The aim of this essay review is to synthesise some of the scattered information upon range expansions within a population ecological and micro-evolutionary framework, in an attempt to examine the role of seed dispersal and initial population establishment for this process. After introducing different study approaches and their respective contributions, I will review the empirical evidence for the role of (long-distance) dispersal in past and ongoing range expansions. Then I examine how some major ecological determinants of dispersal and colonisation processes - population fecundity, dispersal pathways, arrival site conditions, and biotic interactions during recruitment - could be altered by a rapidly changing climate.

This paper draws largely on knowledge derived from extra-tropical woody plants, since these organisms count with the most detailed empirical records and have served as models for important paradigms related with the topic of this paper (e.g., Rejmanek and Richardson, 1996; Petit et al., 2004; Svenning and Skov, 2004; Hu et al., 2009). Moreover, the importance of trees for sustaining life in general and biodiversity in particular can hardly be overstated. Forests cover ~30% of the land surface (~42 million km^2), store ~45% of terrestrial carbon, and contribute ~50% of terrestrial net primary production (Bonan, 2008). Hence, the impact of future climate changes on the distribution and conservation of biodiversity will depend to a great extent on the reaction of trees and the ecosystems they sustain.

2. Contributions from different research fields

Linking patterns of seed dispersal and plant recruitment with colonisation events at a landscape to continental level requires integrating processes that occur at very different spatial and temporal scales (Kollmann, 2000; Nathan, 2006). Therefore complementary research approaches are needed to shed light on the diverse processes and conditions involved in a successful range expansion (Fig. 1). And while the capacity of species to experience rapid large-scale range expansions is likely to be ultimately determined by mechanisms acting at the landscape to regional level (such as habitat availability and connectivity), these cannot be understood without a sound knowledge of local-scale biological phenomena (such as patterns of plant fecundity or disperser abundance).

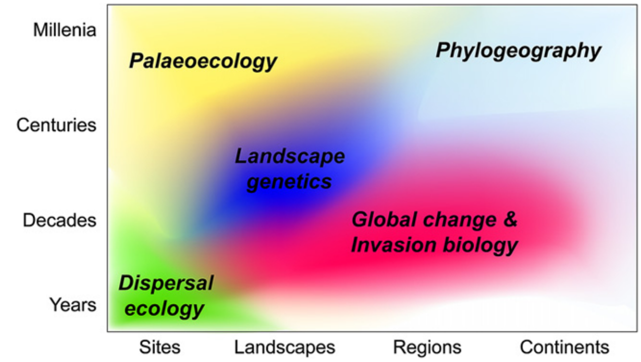

Fig. 1. The complementary empirical research approaches treated in this review that are contributing to extend our understanding of climate-driven range expansions.

Field studies are indispensable for monitoring spatio-temporal patterns of colonisation and related population dynamics. Moreover, ecological field studies help understand the scenario in which seed dispersal and plant recruitment occur. This includes biotic and abiotic determinants of key parameters such as plant fecundity, the behaviour of dispersal vectors, the fates of dispersed propagules, habitat conditions supporting plant establishment, etc. In brief, field studies provide baseline information for understanding why some few dispersal events result in the successful colonisation of new territories while the vast majority does not.

Population genetic studies help identify actual patterns of propagule dispersal that cannot be measured by field-based methods. Moreover, they inform about ecological and micro-evolutionary processes that accompany the establishment and growth of pioneer populations (Excoffier et al., 2009). A common denominator of all genetic approaches considered here is their explicit consideration of space. Analytical methods are as diverse as the spatio-temporal scales of interest (Hamrick and Trapnell, 2011). Studies that directly assess contemporary patterns of seed dispersal by means of parentage analyses usually operate at the level of local populations. Larger scales require indirect methods that infer historical patterns of dispersal from the spatial genetic structure of extant populations; this is the case with landscape genetics (Sork and Waits, 2010), phylogeography (Knowles, 2009) and invasion genetics (Estoup and Guillemaud, 2010).

Palaeoecology was the first field to highlight the dynamic nature of species ranges. The fossil record continues to play an important role, as it provides the time frame for reconstructions of past range expansions and serves as descriptor of past environments, critical information for disciplines such as phylogeography or the modelling of past species distributions (Nogués-Bravo, 2009). Moreover, palaeoecological data sometimes provide the only means to test hypotheses about range expansions (and to reveal their limitations in a stochastic world; see Jackson et al., 2009).

Invasion biology asks very similar questions to those addressed here, as climate-driven 'natural' range expansions are basically a special case of biological invasions (Petit et al., 2004; Estoup and Guillemaud, 2010): What makes a successful coloniser? Which species are particularly efficient? Which environments favour range expansions? How do pioneer populations perform? Which evolutionary processes do they experience? The discipline builds