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Disentangling the roles of climate, propagule pressure and land use on the current and potential elevational distribution of the invasive weed *Oxalis pes-caprae* L. on Crete

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Abstract

Climatic warming and land use change are likely to facilitate range expansions in invasive plant species, although the ability to predict such changes requires a better mechanistic understanding of the biological limits of populations. The introduced weed *Oxalis pes-caprae*, a significant pest of cultivation in many Mediterranean-type ecosystems, presents a suitable case study. The species distribution in the Mediterranean Basin closely follows that of olive cultivation, limited to below 600 m; yet its potential to colonise vulnerable areas at higher elevations has yet to be adequately assessed. To investigate the possibility, plant performance was assessed by experimentally sowing *O. pes-caprae* bulbils along an altitudinal gradient in the Lefka Ori mountains, Crete. The survivorship and bulbil biomass of the resulting plants all declined significantly with elevation, irrespective of soil type, initial bulbil size or seasonal variation. Whilst plants survived vegetatively up to 1400 m, seasonal bulbil productivity, likely to be critical to population viability, exceeded that of the sown bulbil biomass only below 750 m. These data indicate that the current elevation of *O. pes-caprae* is close to, but not at, its current climatic limit, and that low propagule pressure and scarcity of suitable habitat probably also act to limit the altitudinal distribution. Plant performance was correlated strongly with the duration of spring snow cover. Despite a 2 °C difference in mean spring temperatures in the 2 years of study, the predicted elevational change was only 37 m higher in the milder conditions. Overall, our results suggest that while *O. pes-caprae* performance is strongly linked to climate and is currently close to its climatic limit on Crete, there is limited scope for further spread unless land use and/or propagule pressure change at higher elevations. For this species, these elements are likely to be more significant drivers of invasion risk than the predicted changes of future climates.

Keywords: Altitude; Biological invasions; Climate change; Land use change; Population viability; Propagule pressure

Introduction

Invasions by non-native species often severely compromise the biodiversity, ecological functioning and economic value of invaded ecosystems (Mack et al., 2000; Hulme, 2006). Future global changes, such as

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climatic warming and an increased tendency towards human-dominated land use, are likely to favour invasive species and exacerbate their impacts (Dukes and Mooney, 1999; Vilà et al., 2006b). The Mediterranean region is often considered to be particularly susceptible to the combined effects of biological invasions and anthropogenic disturbance (Sala et al., 2000; Gritti et al., 2006); yet few experimental studies have attempted to examine the relationship between land use and climate on the distribution of alien species (Becker et al., 2005; Thuiller et al., 2006).

Correlative models suggest that climate is a major constraint on the distribution of many alien plant species (e.g. Kriticos et al., 2005; Dunlop et al., 2006). Whilst several studies have suggested likely range shifts based on such analyses (e.g. McDougall et al., 2005; Thuiller et al., 2005; Gritti et al., 2006), the ecological processes that limit plant distribution often remain largely unknown. However, the power of correlative assessments is reduced when the species range is not at equilibrium with the current climate (Hulme, 2005), propagule dispersal is limited, or where environmental gradients (e.g. agricultural land use and climate) are spatially confounded (Willis and Hulme, 2002).

Elevation appears to be an important correlate of alien species richness (Ullmann et al., 1995; Becker et al., 2005; McDougall et al., 2005) as well as distribution (Kitayama and Mueller-Dombois, 1995) and is often used as a proxy to explore the role of climatic limitation (Körner, 2007). Yet, low numbers of alien species at higher elevations may also reflect reduced propagule supply (Aragon and Morales, 2003), lower disturbance frequency (Kitayama and Mueller-Dombois, 1995) or simply the time since introduction (Becker et al., 2005). Thus, disentangling the relative importance of climate, habitat availability and propagule supply on the potential for invasion under a future warmer climate requires experimental rather than solely biogeographical (Thuiller et al., 2005) or observational (Becker et al., 2005; McDougall et al., 2005) approaches. Experimental sowing of species within and beyond their existing distributional range provides a means to assess the relative roles of climate, propagule supply and edaphic factors (e.g. soil type) on species abundance and performance (Carter and Prince, 1985; Willis and Hulme, 2002; Akasaka and Tsuyuzaki, 2005; Ramirez et al., 2006; Paiaro et al., 2007). Yet, in contrast to the numerous observational studies linking alien species elevational distributions to climatic limits (e.g. Kitayama and Mueller-Dombois, 1995; Aragon and Morales, 2003; Arevalo et al., 2005; Becker et al., 2005; Daehler, 2005; McDougall et al., 2005; Pauchard and Alaback, 2004), relatively few experimental approaches have been undertaken to examine alien plant species distributions along elevational gradients (Willis and Hulme, 2002; Akasaka and Tsuyuzaki, 2005; Paiaro et al., 2007).

In this study, experimental sowing of the Bermuda buttercup *Oxalis pes-caprae* L. (Oxalidaceae, hereafter *Oxalis*) along an elevation gradient on the Mediterranean island of Crete is used to examine the relative roles of climate, propagule supply and soil type on current distributional limits. While it is trivial to identify that climate presents an absolute limit to species elevational distribution, the key question is whether this physiological constraint coincides with the current limits. Thus the objective is to test whether the current distribution limit is absolute and determined uniquely by physiology through plant survivorship or is a demographic limit, reflecting constraints on plant population persistence. In the former case, the species response to future climatic changes may be predicted from a knowledge of bioclimatic surfaces or plant physiological models. Demographic limits are likely to occur at lower elevations than those imposed by physiological constraints and thus species response may also be conditional on changes to habitat suitability and propagule supply (Hulme, 2003). *Oxalis* is particularly well suited to these questions since it is a serious widespread economic weed of Mediterranean agriculture (Hulme et al, 2008), causes oxalate poisoning in livestock if eaten in sufficient quantities (Gimeno et al., 2006), and reduces both native species richness (Vilà et al., 2006c) and net primary production (Petsikos et al., 2007) where it occurs. The regional distribution is well described by bioclimatic niche models (Thuiller et al., 2005) and thus the responsiveness of *Oxalis* to climate will be essential information for predicting future risks and guiding management.

Materials and methods

Study species

Oxalis, a native to the Cape Region of South Africa, is an invasive alien weed in Italy, Greece, the Iberian Peninsula and North Africa, and beyond the Mediterranean basin in Portugal, south-west England, California, Florida, Australia, India and New Zealand (Vilà and Gimeno, 2007). The species was introduced to Crete in 1880 (Rackham and Moody, 1996), and is now prolific in anthropogenic habitats where the frequency of disturbance is high and the soil well-drained and fertile, especially in olive (*Olea europaea* ssp. *europaea* L.) groves and on other cultivated land (Rackham and Moody, 1996). The current distribution of *Oxalis* on Crete follows the boundaries of olive cultivation closely and has an altitudinal limit of 600 m above sea level (Turland et al., 1993), a pattern that is likely to have been facilitated by disturbances such as ploughing (Sala et al., 2007). Further colonisation is probably limited by poor dispersal of the bulbils away from