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Shifts in the regeneration niche of an endangered tree (*Acer opalus* ssp. *granatense*) during ontogeny: Using an ecological concept for application

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Summary

Most of our knowledge regarding ontogenetic niche shifts in plants has been derived from studies involving only two or unconnected life stages. Approaches covering a broader range of different life stages are still needed to fully understand the implications of ontogenetic niche shifts for plant regeneration dynamics. We investigated ontogenetic shifts in the endangered Mediterranean tree species *Acer opalus* ssp. *granatense* (*A. opalus*) comparing the environmental characteristics of individuals of different ages with those of a random sample of available microsites. In addition, since herbivory could be a limiting factor, herbivory damage was quantified. Differences in environmental characteristics between locations of individual plants and randomly selected points became larger with plant age, suggesting that the regeneration niche of *A. opalus* shifts during ontogeny, undergoing a contraction. The presence of shrubs and adult trees, the depth of the litter layer, and herbivory were the main factors influencing these changes. *A. opalus* can germinate in all available microhabitats its seeds can reach, but saplings establish and grow only in a subset of microhabitats, which represent a change in tolerance to extrinsic factors. Old saplings establish under the canopy of shrubs, far away from tree cover that could block light required in the oldest stage. Therefore, temporal changes in the nature and strength of plant–plant interactions are also occurring. The ecological concept of niche shifts reveals the microsites with higher probabilities of long-term sapling survival of *A. opalus*: shrub cover involves an array of environmental changes crucial for the successful establishment of *A. opalus* saplings under stressful Mediterranean conditions, from microhabitat amelioration to herbivory protection.

Zusammenfassung

Der größte Teil unseres Wissens über ontogenetischen Nischenverschiebung bei Pflanzen wurde in Untersuchungen gewonnen, die nur zwei oder nicht verbundene Lebensabschnitte berücksichtigen. Es werden immer noch Ansätze benötigt, die eine größere Bandbreite von verschiedenen Lebensstadien abdecken, um Implikationen von ontogenetischer Nischenverschiebung für die Dynamik der Pflanzenregeneration zu verstehen. Wir untersuchten ontogenetische Veränderungen bei der gefährdeten mediterranen Baumart *Acer opalus* spp. *granatense* (A. opalus)

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indem wir die Umweltcharakteristiken von Individuen verschiedenen Alters mit denen von einer zufälligen Auswahl von verfügbaren Mikrohabitaten verglichen. Zusätzlich wurde die Beschädigung durch Herbivorie quantifiziert, da Herbivorie ein limitierender Faktor sein könnte. Die Unterschiede in den Umweltcharakteristiken zwischen den Standorten individueller Pflanzen und zufällig ausgewählten Standorten wurden mit zunehmenden Pflanzenalter größer, und lassen vermuten, dass sich die Regenerationsnische von A. opalus verändert indem sie sich verkleinert. Das Vorhandensein von Büschen und ausgewachsenen Bäumen, die Tiefe der Streuauflage und Herbivorie waren die Hauptfaktoren, die diese Veränderungen beeinflussten. A. opalus kann in allen verfügbaren Mikrohabitaten keimen, die von den Samen erreicht werden, aber die Schösslinge etablieren sich und wachsen nur in einem Teil der Mikrohabitate, was eine Änderung der Toleranz gegenüber äußeren Faktoren darstellt. Ältere Schösslinge etablieren sich unter der Deckung von Büschen, weit weg von einem Kronendach, welches das Licht blockieren könnte, das im ältesten Stadium benötigt wird. Deshalb finden auch zeitliche Veränderungen in der Art und Stärke von Pflanzen-Pflanzen-Interaktionen statt. Das ökologische Konzept der Nischenverschiebung lässt die Mikrohabitate erkennen, die eine höhere Wahrscheinlichkeit für ein langfristiges Überleben von A. opalus Schösslingen aufweisen: Buschdeckung beinhaltet eine Reihe von Umweltveränderungen, die für eine erfolgreiche Etablierung von A. opalus Schösslingen unter den schwierigen mediterranen Bedingungen entscheidend sind, wie die Verbesserung des Mikrohabitats und der Schutz vor Herbivorie.

Keywords: *Acer opalus* spp. *granatense*; Mediterranean mountain; Ontogenetic shift; Regeneration niche; Tree regeneration

Introduction

To a large extent, the abundance and distribution of plant species are determined during early regeneration stages, when seedlings and saplings are most vulnerable to their immediate environment (Kitajima & Fenner, 2000; Zoladeski & Maycock, 1990). Thus, it is not surprising that the so-called ''regeneration niche'' (characteristics of the environment at the time of establishment; Grubb, 1977) is crucial for understanding the composition, structure, and dynamics of plant communities in a variety of environments (Silvertown, 2004). Recent studies suggest that the regeneration niche changes over the life cycle of individuals (Chase & Leibold, 2003; Miriti, 2006). These changes, known as ontogenetic niche shifts (Parrish & Bazzaz, 1985), have been widely explored in animal ecology (e.g. Amundsen et al., 2003; Post, 2003). However, knowledge regarding ontogenetic niche shifts in plants is much more limited. The studies available have analysed only two life stages, often unconnected, such as seeds and seedlings (Schupp & Fuentes, 1995), seedlings and mature trees (Cavender-Bares & Bazzaz, 2000), or juveniles of different ages (Espelta, Riba, & Retana, 1995). Approaches involving a broader range of different life stages are still needed to understand fully whether ontogenetic niche shifts drive the spatial distribution and successional dynamics of plant communities (Grubb, 1977).

Plants do not actively seek ideal habitats, but they exhibit distinct differences in tolerances to extrinsic factors at different developmental stages (Franco & Nobel, 1989; Miriti, 2006; Parrish & Bazzaz, 1985), causing changes in niche dimension. A niche expansion occurs when species requirements are stricter in earlier stages, whereas a niche contraction would indicate that requirements are stricter in later stages of development. Parrish and Bazzaz (1985) considered niche expansion the most common situation for plants, since species requirements were usually narrow at the germination stage and broader at the seedling and adult stages. Contrary to this, niche contraction could limit the establishment of a plant by restricting it to a subset of environmental characteristics within the potential scenarios that can be occupied by the species.

The demographic responses of different stages to abiotic and biotic conditions will be expressed in different ways (e.g. differential mortality rates of seedlings, and differential growth or reproductive allocation of larger plants, Miriti, 2006; Parrish & Bazzaz, 1985). Such ontogenetic constraints are often critical in understanding the whole dynamic of a plant population in which a particular stage needs specific conditions not shared by other life stages. A paradigm to the significance of ontogenetic changes is that shifting conditions alternatively favour positive or negative interactions among plants different in size (Callaway, 1995; Holmgren, Scheffer, & Huston, 1997; Holzapfel & Mahall, 1999). Whatever the case, proper knowledge of ontogenetic niche changes is essential from both a basic and applied standpoint in order to increase our understanding of the processes underlying niche shifts as well as to establish appropriate management and restoration plans that consider the microsites where the species has higher probabilities of long-term survival.

The Mediterranean tree *Acer opalus* ssp. *granatense* (Boiss.) Font Quer and Rothm (hereafter *A. opalus*) is an ideal species to evaluate ontogenetic niche shifts because: (i) the wind dispersal of its seeds facilitates the