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Responses of competitive understorey species to spatial environmental gradients inaccurately explain temporal changes

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Abstract

Understorey plant communities play a key role in the functioning of forest ecosystems. Under favourable environmental conditions, competitive understorey species may develop high abundances and influence important ecosystem processes such as tree regeneration. Thus, understanding and predicting the response of competitive understorey species as a function of changing environmental conditions is important for forest managers. In the absence of sufficient temporal data to quantify actual vegetation changes, space-for-time (SFT) substitution is often used, i.e. studies that use environmental gradients across space to infer vegetation responses to environmental change over time. Here we assess the validity of such SFT approaches and analysed 36 resurvey studies from ancient forests with low levels of recent disturbances across temperate Europe to assess how six competitive understorey plant species respond to gradients of overstorey cover, soil conditions, atmospheric N deposition and climatic conditions over space *and* time. The combination of historical and contemporary surveys allows (i) to test if observed contemporary patterns across space are consistent at the time of the historical survey, and, crucially, (ii) to assess whether changes in abundance over time given recorded environmental change match expectations from patterns recorded along environmental gradients in space. We found consistent spatial relationships at the two periods: local variation in soil variables and overstorey cover were the best predictors of individual species' cover while interregional variation in coarse-scale variables, i.e. N deposition and climate, was less important. However, we found that our SFT approach could not accurately explain the large variation in abundance changes over time. We thus recommend to be cautious when using SFT substitution to infer species responses to temporal changes.

Keywords: Temperate forest; Herb layer; Tree regeneration; Global change; Nitrogen deposition; Canopy; Spatiotemporal resurvey data; Cover abundance; Chronosequence; forestREplot

Introduction

The importance of understorey plant communities and their key role in the functioning of forest ecosystems are increasingly recognized (Nilsson & Wardle, 2005; Gilliam, 2007; Thrippleton, Bugmann, Kramer-priewasser, & Snell, 2016). One important influence of the understorey is its effect on tree regeneration; each tree in the overstorey has recruited in and passed through this forest layer as a seedling. Through the initial competitive interactions with the regeneration of overstorey tree species, the understorey community acts as a filter and may have long-term impacts on forest overstorey structure and composition (George & Bazzaz, 1999; Royo & Carson, 2006). Opportunistic, fast-growing understorey plant species develop high abundances when resource availability is high, leading to reduced seedling growth and survival, and even complete failure of the tree regeneration (George & Bazzaz, 1999; Balandier, Collet, Miller, Reynolds, & Zedaker, 2006; Royo & Carson, 2006). Thus, it is important for forest managers to understand which (combinations of) environmental factors mainly drive the abundance response of these competitive species.

Understorey species' distribution and abundance are first of all determined by the local-scale environment. The overstorey community can determine the composition and abundance of understorey plants by controlling resources and conditions on the forest floor (Härdtle, Oheimb, & Westphal, 2003; Gilliam, 2007; Li et al., 2012; Nieto-lugilde et al., 2015). Overstorey opening results in increased light availability at the forest floor, but can also improve nutrient and water availability and temperature conditions for understorey plants (Barbier, Gosselin, & Balandier, 2008; Wagner, Fischer, & Huth, 2011). This may lead to a shift in species composition, with a higher cover of light-demanding, competitive species (Degen, Devillez, & Jacquemart, 2005; Naaf & Wulf, 2007; Kelemen, Mihók, Gálhidy, & Standovár, 2012). Understorey

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