



## Disentangling the effects of spatial proximity and genetic similarity on individual growth performances in Norway spruce natural populations

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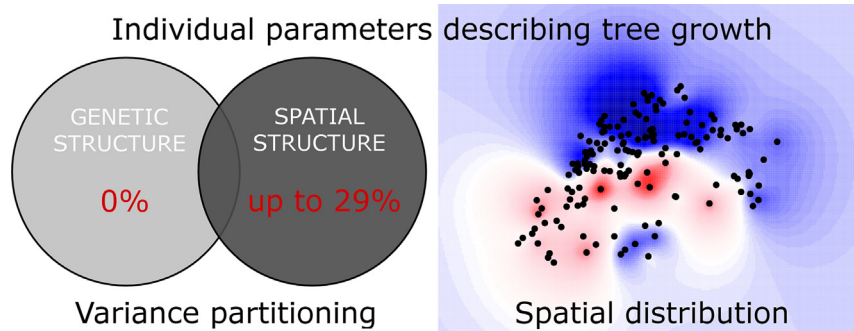
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### HIGHLIGHTS

- Need for multidisciplinary data to study individual trees' growth performances.
- Random slope mixed-effects models capture most variance in growth patterns.
- Microenvironmental variation is much more relevant than genetic structure in influencing individual growth patterns.

### GRAPHICAL ABSTRACT



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### ABSTRACT

Cambial growth is a phenotypic trait influenced by various physiological processes, numerous biotic and abiotic drivers, as well as by the genetic background. By archiving the outcome of such complex interplay, tree-rings are an exceptional resource for addressing individual long-term growth responses to changing environments and climate. Disentangling the effects of the different drivers of tree growth, however, remains challenging because of the lack of multidisciplinary data. Here, we combine individual dendrochronological, genetic and spatial data to assess the relative importance of genetic similarity and spatial proximity on Norway spruce (*Picea abies* (L.) Karst.) growth performances. We intensively sampled five plots from two populations in southern and central Europe, characterizing a total of 482 trees. A two-step analytical framework was developed. First, the effects of climate and tree age on tree-ring width (TRW) were estimated for each individual using a random slope linear mixed-effects model. Individual parameters were then tested against genetic and spatial variables by Mantel tests, partial redundancy analyses and variance partitioning. Our modelling approach successfully captured a large fraction of variance in TRW (conditional  $R^2$  values up to 0.94) which was largely embedded in inter-

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individual differences. All statistical approaches consistently showed that genetic similarity was not related to variation in the individual parameters describing growth responses. In contrast, up to 29% of the variance of individual parameters was accounted by spatial variables, revealing that microenvironmental features are more relevant than genetic similarity in determining similar growth patterns. Our study highlights both the advantages of modelling dendrochronological data at the individual level and the relevance of microenvironmental variation on individual growth patterns. These two aspects should be carefully considered in future multidisciplinary studies on growth dynamics in natural populations.

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## 1. Introduction

Cambial growth is a complex quantitative trait influenced by several determinants such as climate, tree age, competition, disturbances (e.g. pathogen outbreaks, management, wildfires) as well as individual microenvironmental conditions and genetic background (Cook et al., 1990; Schweingruber, 1996). Although recent advances in genomics have discovered some genetic and epigenetic factors involved in growth processes of model plants (Busov et al., 2008), most of the genetic architecture of growth traits is still unknown for forest tree species (Grattapaglia et al., 2009). However, the available literature about common garden experiments and progeny trials showed that growth traits (e.g. height, diameter, tree-ring width, wood density) have moderate to high values of heritability (Cornelius, 1994; Hannrup et al., 2004; Klisz et al., 2016; Lind et al., 2018; Martinez Meier et al., 2008; Mihai and Mirancea, 2016; Quesada et al., 2017). The heritability of a phenotypic trait is the essential prerequisite for potentially adaptive responses (Lind et al., 2018; Ritland and Ritland, 1996). Heritability should be ideally estimated *in situ* (Kremer et al., 2014; Ritland, 1996), because it can be easily overestimated when assessed under controlled environmental conditions, and this bias can be even larger for complex traits (Castellanos et al., 2015; Ritland, 2000). A potential first step in this direction is to jointly analyse quantitative trait variation and genetic relatedness in natural conditions (Ritland, 1996, 2000). The extent of relatedness between two individuals reflects their coancestry (that is how many common ancestors do they share and how much these ancestors are distant in time) and the resulting probability of their alleles being identical by descent (Wang, 2017; Weir et al., 2006). Related individuals have more similar genotypes with respect to unrelated ones and, thus, they are expected to show also more similar phenotypes for quantitative traits (Falconer and Mackay, 1996). Over the last decades, substantial improvements in genotyping techniques and genetic analyses gave to population genetic studies a greater power to address ecological questions (Selkoe and Toonen, 2006). Although hyper-variable microsatellites often do not provide any information about potentially adaptive responses (King et al., 2013), they are considered as almost ideal markers to estimate relatedness, and study demographic processes in general, with high resolution power (Hardy, 2003; Weir et al., 2006).

Generating genetic data is currently far easier than obtaining a deep phenotypic characterization of numerous individuals (Araus and Cairns, 2014). The recent development of high throughput phenotyping techniques has started to fill this gap, at least in controlled conditions for annual species or, for forest trees, at the seedling stage (Araus and Cairns, 2014; Fiorani and Schurr, 2013; Furbank and Tester, 2011). However, a deep phenotyping of a large number of forest trees in natural conditions remains challenging. An available option is taking advantage of dendrochronology to characterize growth performances through individual annual tree-ring width (TRW) data (Heer et al., 2018). For this purpose, a shift in the classical dendrochronological perspective is required. Indeed, the traditional dendrochronological approach mainly aims at finding the within-population common climatic signal, by reducing the amount of unwanted noise through some useful but potentially controversial procedures (for a detailed discussion of their advantages and limitations see Carrer (2011)). In dendrochronological studies few

individuals per site are usually sampled (~20/site), preferentially selecting old dominant trees, which are supposed to present the best signal to noise ratio (Fritts, 1976). Tree-ring series are then standardized to remove age-related and low-frequency trends determined by non-climatic factors, and to homogenize growth rates and variances (Cook, 1985). Finally, standardized tree-ring series are usually averaged into a unique site chronology (Cook and Kairiukstis, 1990). Whereas this approach is ideal for reconstructing past climate, it prevents characterizing the whole range of individual growth performances and responses to climate (Carrer, 2011) and eventually predicting how trees may cope with climate change (Redmond et al., 2017). Carrer (2011) proposed an individual-based dendrochronological approach after finding out that investigating the whole range of individual responses outperforms the classical method to obtain more robust and reliable estimates of mean growth-climate correlations. Additionally, Galván et al. (2014) suggested the adoption of new protocols for sampling all adult trees within a circumscribed area, to better quantify how climate affects individual tree growth.

Recent dendrochronological studies underlined the relevance of individual-based linear mixed-effects models to quantify and disentangle the effects of different drivers of growth (Galván et al., 2014; Hereş et al., 2012; Linares et al., 2010; Macalady and Bugmann, 2014; Primicia et al., 2015; Redmond et al., 2017). Such individual-based models offer the possibility of estimating model parameter both at the population and individual level. However, the above-mentioned studies were mainly focused on the mean effect of each driver at the population level, whereas inter-individual variation was poorly investigated. In contrast, we argue that the individual parameters obtained by such modelling approach can be considered as a new type of tree-ring based phenotypic traits (see Housset et al., 2018). In fact, such parameters describe how individual trees respond to specific yearly-based drivers of growth (e.g. age, climate), while holding constant the others. In this way, inter-individual variation of sensitivities to drivers of growth could be explicitly quantified (Albert et al., 2011) and linked to factors that are time-constant (e.g. genotypes) or measured occasionally (e.g. microenvironmental features, competition).

In our study we assess whether sharing the same microenvironment and/or genetic characteristics influences inter-individual variation of growth performances within natural populations of Norway spruce (*Picea abies* (L.) Karst). To our knowledge, King et al. (2013) is the only study that tried to answer a similar question, assessing whether genetic relatedness or climate affect TRW variation along forest trees' altitudinal transects. In their work, 115 Norway spruce individuals from five populations were genotyped with five microsatellite markers (SSRs). The authors visually compared genetic relatedness and growth synchronicity, concluding that among-population TRW variation is more climate- than genetic-driven at regional scale. Here, we embrace the change in perspective suggested by recent dendrochronological literature to switch from a classical population-based approach to a deep individual-based exploration of growth dynamics. We intensively sampled within-population phenotypic variance in five plots collecting dendrochronological data from 482 trees. All individuals were genotyped at 11 SSRs to thoroughly characterize the genetic structure within each plot. We develop an individual-based analytical framework to quantify inter-individual variation of TRW and assess the effects of different

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