

Every bit helps: The functional role of individuals in assembling any plant community, from the richest to monospecific ones

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Abstract

Plant trait-based ecology is a powerful extension of the attempt of community ecologists to unveil assembly mechanisms. However, the two main expected determinants of community assembly, niche and neutral processes, can be confused under this framework. Here, we propose to move from trait-based to *phenotype-based community ecology*, accounting for the variation between individuals (phenotypes affected by the abiotic and biotic environment, and vice versa), and explicitly considering their ability to compete with or facilitate its neighbours. This would shift our focus from species' niche responses to niche specialization of phenotypes, reducing the space for neutrality at the finest scales. The current assembly framework, based mainly on niche complementarity and using species-average functional traits, has been developed exploring mega-diverse communities, but it fails at describing poor plant communities. Under this framework, monospecificity would be interpreted as an arena where functionally similar individuals compete, consequently leading to regular patterns, which are rarely found in nature. Our niche specialization framework could help explaining coexistence in rich plant communities, where the higher fraction of functional variation is found between species, whereas the intraspecific trait variation dominates in poor species and monospecific communities. We propose a guide to conduct massive phenotyping at the community scale based on the use of visible and near-infrared spectroscopy. We also discuss the need to integrate the so-called plant's eye perspective based on the use of spatial pattern statistics in the current community ecology toolbox.

KEYWORDS

coexistence, neutrality, niche specialization, phenotypes, phenotypic variation, poor plant communities

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1 | FROM PLANT TRAIT-BASED TO PHENOTYPE-BASED COMMUNITY ECOLOGY

The emergence of trait-based plant ecology (Lavorel & Garnier, 2002; Shipley et al., 2016) is the conceptual consolidation of the idea that plant attributes, i.e., functional traits (Violle et al., 2007), rather than taxonomic identity or phylogenetic relationships, are responsible for community assembly and ecosystem processes (Shipley et al., 2016). This approach, rooted in Grime's pioneer work (Grime, 1979), offers a valuable venue to explain the deterministic mechanisms affecting community assembly (Vellend, 2010), including niche partitioning (Hutchinson, 1961), dispersal, abiotic and biotic assembly rules (Götzenberger et al., 2012), ecological filters (Shipley, 2010a) or habitat segregation at the scales where individuals interact via both competition and facilitation (Pulla et al., 2017). Although this trait-based approach was very efficient for describing community structure and dynamics at relatively coarse spatial scales (Diaz et al., 2004), and helped to solve the overlap between proposed mechanisms, it is imprecise at the finest scales where individuals interact (Lawton, 1999; Vellend, 2010). At these scales, neutral processes seem to be dominant (Hubbel, 2001; McGill, 2010), giving opportunity to stochastic events to rule out community structure (Chase, 2014, but see Pescador et al., 2020).

Following the long-standing taxonomic perspective, the functional variability of plants was summarized using species-level means (mean field approach sensu Violle et al., 2012), where all individuals of a given species were characterized with the mean value of any functional trait, independently of genotype, age, health status, abiotic environment or neighbourhood. Recent evidence revealed the critical role of functional trait variation within species, or intraspecific trait variation (hereafter ITV), in addition to the variation between species (hereafter BTV) for explaining the fine-scale community structure where plant–plant interactions prevail (Albert et al., 2010; Hulshof & Swenson, 2010; Albert et al., 2011; Violle et al., 2012). In a comprehensive meta-analysis, Siefert et al. (2015) found that a very significant fraction of the plant functional variation in nature corresponds to ITV, which, in some cases, may be even more important than BTV for community assembly (Messier et al., 2010; Violle et al., 2012). A solid theoretical and empirical picture is emerging on the relevance of ITV to explain plant coexistence (Messier et al., 2010; Bolnick et al., 2011) and how such intraspecific variability should be measured and incorporated in the toolbox of community ecologists (Mitchell & Bakker, 2014). For instance, the explicit consideration of ITV in realized assemblages reduced the importance attributed to stochasticity at the finest scales (Chase, 2014). This suggests that ITV adjusts the whole community functional response to microsite abiotic heterogeneity (see Pescador et al., 2015 in Mediterranean alpine communities). Such scaling down of the functional variability has proven to be very promising to generate new insights on the processes governing community assembly, especially at the finest spatial scales (see Violle et al., 2012; Sides et al., 2014; Carmona et al., 2015; Guzmán-M et al., 2018), but it may also allow the explicit

consideration of the functional role of individuals, and their trait plasticity, in coexistence (Muthukrishnan et al., 2020).

Phenotypic variation among individuals is the necessary substratum (effect) or result (response) of many biological processes (Herrera, 2009). This eco-evolutionary playground in which ecological processes and microevolution are merged (Agrawal, 2001; Rudman et al., 2018) determines the maintenance of genotypic differences within a population. Accordingly, this interplay would also determine a finite set of phenotypes conforming *multiscapes*, i.e. spatial realizations of genotype–phenotype distributions (sensu Aguirre et al., 2018), in which acclimation and/or adaptation may be very fast, for instance in response to microsite habitat heterogeneity, specific neighbourhoods or microbiome heterogeneity (Aarssen, 1989; Agrawal, 2001; Pfennig et al., 2010; Wund, 2012). In this sense, any individual plant may respond by adjusting its phenotype along ontogeny, mainly through phenotypic plasticity (Ashton et al., 2010; Matesanz & Valladares, 2014), clearly indicating that individual-level functional variation is not only genetically based but also driven by the biotic and abiotic environment. Previous evidence showed the genetic structure of *Thymus loscosii*, a rare but locally abundant plant, to be related to the abundance of the widespread congener *Th. vulgaris* at very fine scales in semi-arid Spain, suggesting that interactions with relatives may affect the realized plant spatial phenotypic and genetic structure (Matesanz et al., 2011). Although this ubiquitous variation among individuals, which may be very large (Messier et al., 2017; Carvalho et al., 2020), is currently being translated to community ecology (Bolnick et al., 2011; Crawford et al., 2019), its role for species coexistence at the neighbourhood scale is unclear (Banitz, 2019). Species interactions are affected by this phenotypic variation among individuals, having profound effects on community composition that need to be included in the current assembly paradigm (Ashton et al., 2010). This is precisely the spatial scale where proposed deterministic mechanisms usually fail (Chase, 2014) and neutrality gains weight through stochastic demography and dispersal (but see Kelly et al., 2008; Blonder et al., 2018). Although the coexistence literature uses species as the interacting units (but see Muthukrishnan et al., 2020) and communities are the result of dynamic populations/species living together (HilleRisLambers et al., 2012; Blonder et al., 2018), realized assemblages actually are phenotypes interacting and responding to microsite heterogeneity. This leads to the image of community assembly as a race at the interspecific level between the exclusion of poorly adapted species (species filtering) and a race at the intraspecific level between phenotypes evolving, an idea mathematically developed by Shipley (2010b; ch. 5). Although the relevance of plasticity in interaction outcomes and species coexistence is clear (see Abakumova et al., 2016; Pérez-Ramos et al., 2019), in those studies the phenotype is considered an experimentally induced response to the neighbourhood, rather than an effect in the assembly process.

Plant functional traits may be used to infer interspecific plant–plant interactions (Morueta-Holme et al., 2016) if all the individuals belonging to a certain species are identical from a functional perspective. The strength and sign of the interaction would be related to the similarity

between co-occurring species, with more functionally similar species competing more intensively (Webb et al., 2002), and to trait hierarchies, where species with more extreme values compete more intensively (Mayfield & Levine, 2010). This between-species phenotypic variation would affect the functional structure of the whole assemblage in the surroundings of each individual plant (Chacón-Labela et al., 2016). However, a realized plant assemblage is more than a combination of interacting species or populations. Variation within populations, either genetic or environmentally driven, may not only be large but also differ among species, so that species-level data would fail to capture key variation that may contribute to coexistence (Clark, 2010). Therefore, a plant community should be seen as a collection of phenotypes, i.e. individual functional realizations, that results from both genetic differences and phenotypic plasticity. These functional realizations may belong to the same species or not, but are interacting with other individuals in their neighbourhoods (Aarssen, 1983; Crawford et al., 2019). Since the ability of individual plants to recognize species identities among competitors is unknown, we should move from plant trait-based community ecology to what could be named *phenotype-based community ecology* (Carmona et al., 2015; Escudero & Valladares, 2016; Figure 1). In its simplest form, this would involve accounting for the variation between individuals, i.e. individual traits or phenotypes affected by the abiotic and biotic environment and vice versa (Violle et al., 2012), and explicitly considering the ability of each individual to compete with (Falster & Westoby, 2003) or facilitate (Schöb et al., 2012) its neighbours, regardless of the species it belongs to (Clark, 2010). Gravel et al. (2006) proposed a model to

achieve the niche–stochasticity reconciliation simply by locating these two apparently opposed ideas in a continuum. A set of complementary and redundant species can stably coexist with abundances determined by environmental heterogeneity and immigration. Obviously, this scaling down from populations (species) to individuals (phenotypes) would lead to a move from the species’ niche response to the niche specialization of phenotypes (see Araujo et al., 2011), reducing the space for neutrality in this continuum.

Although a huge effort has been devoted to explaining mechanisms promoting plant diversity maintenance and coexistence, a significant fraction has been conducted on very rich communities, such as mega-diverse tropical forests (Wright, 2002; Swenson, 2013). However, to our knowledge, far fewer studies have tried to unveil the mechanisms explaining coexistence and assembly in species-poor communities with a high degree of physiognomic and phylogenetic convergence (e.g., heathlands dominated by Ericaceae species or Mediterranean rockrose shrublands dominated by Cistaceae species), and even less in monospecific ones. This is especially remarkable, for instance, in the case of plant communities occurring in relatively productive and benign environments, such as natural and almost monospecific pine forests in temperate or Mediterranean climates (Figure 2). The current paradigm suggests that monospecificity would be the result of a competitive exclusion (Hardin, 1960) but if all the individuals in these assemblages were functionally equivalent, competition would lead to spatially regular distribution patterns, which are rarely found in nature (but see Rietkert & van de Koppel, 2008).

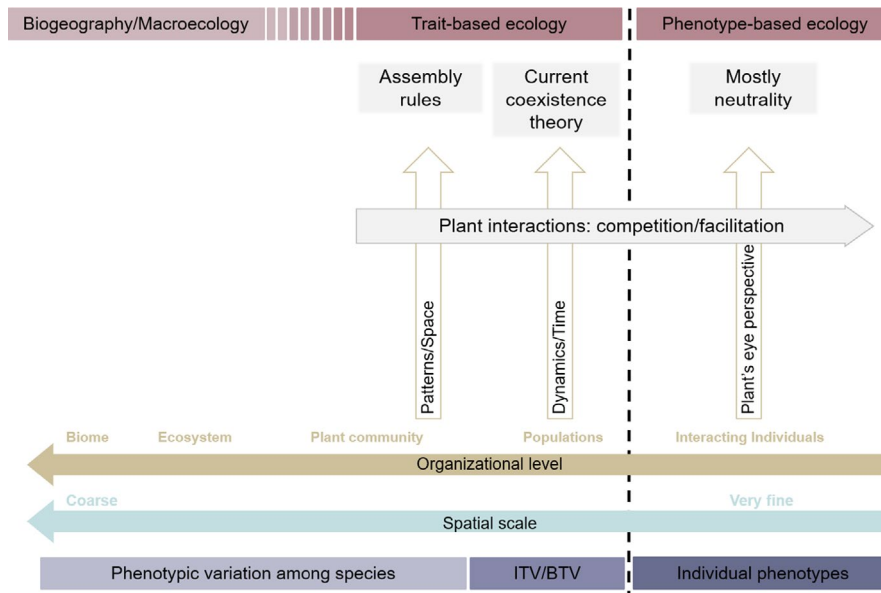


FIGURE 1 Conceptual framework to integrate plant functional trait variation along spatial scales and organizational levels. Plant trait-based ecology gives support to the so-called Coexistence Theory, which emphasizes the competitive variation in time (dynamics) among co-occurring species (fitness differences) and to the assembly rules, which are more focused on the variation in patterns among species in a niche complementarity scenario. They basically agree in giving weight to the confrontation between species entities. In the biological range in which plant communities are the dominant unit, the relative importance of the intraspecific trait variation limits the variation among species, which may become very low if the number of species in the assemblage is very low. Fine spatial scales, which have been proposed to be the domain of stochastic process (i.e. neutrality) basically consist of interacting individuals. Since evidence of species–species recognition is limited, our phenotype-based framework provides space for eco-evolutionary dynamics, recognizing that the phenotype is the unit for assembly. ITV: intraspecific trait variation, BTW: between-species trait variation

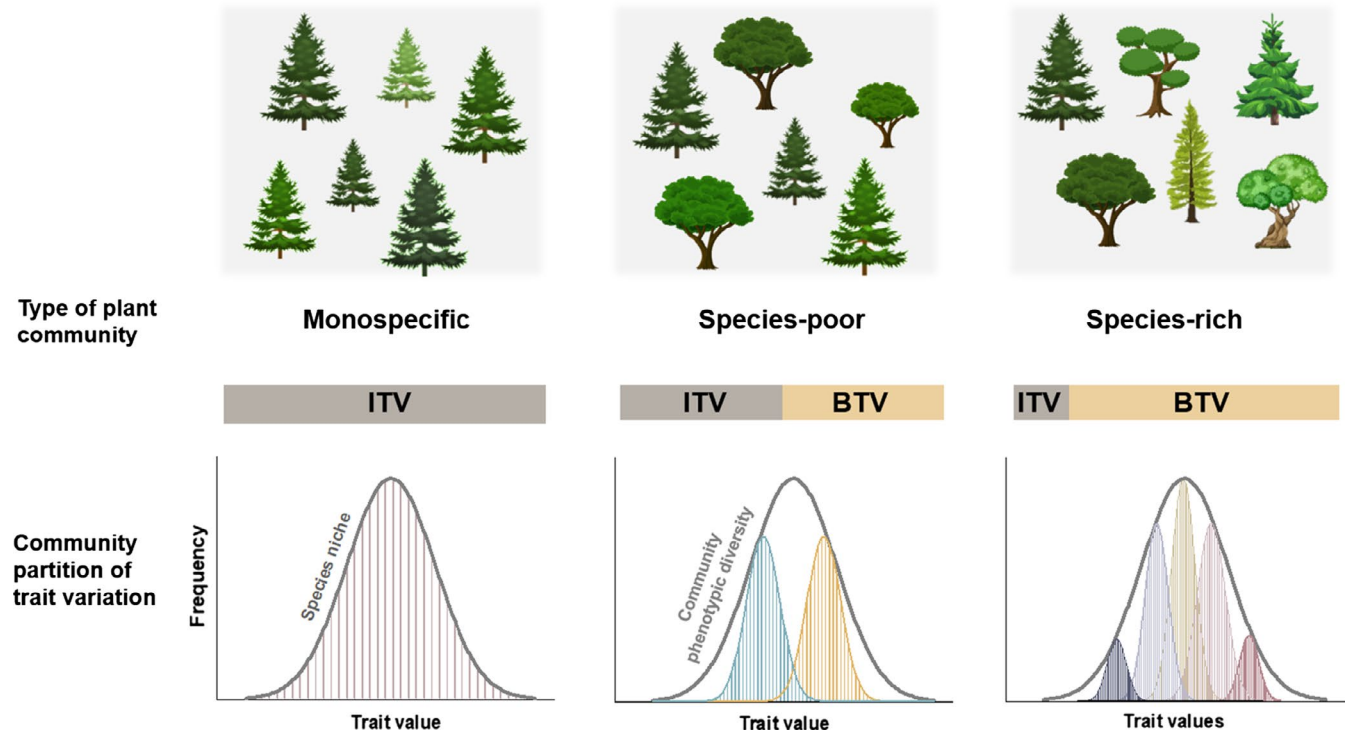


FIGURE 2 Plant communities vary from those composed of many co-occurring species (e.g., wet tropical forests and Mediterranean dwarf scrublands) to species-poor (e.g., temperate mixed forests or Mediterranean rockrose scrublands) and monospecific ones (e.g., Scotch pine forests). Since community assembly depends basically on the individual phenotypic variation and there is no evidence of species–species recognition in the field, we propose to scale down the idea of species–niche complementarity to the phenotype's niche specialization. In this novel framework, rooted in the idea that functional diversity comprises different components at contrasting spatial and biological scales (Carmona et al., 2015), species-rich communities distribute their functional variation for specific traits giving more weight to the between-trait component, i.e. variation among species (right panel) and minimizing within-species variation. Conversely, monospecific communities are structured around intra-trait variation (left panel). Note that our panels present trait spaces and conceptual connections with the species and phenotype niches

The explicit consideration of plant communities as a sum of different phenotypes belonging to one, few or many different species without abandoning the long-standing deterministic niche perspective (MacArthur & Levins, 1967; Wright, 2002; Borchert et al., 2015) could offer a powerful tool to introduce this type of poor assemblages in the current assembly picture. From this perspective, individual phenotypes and not species would share a common ground for interacting, i.e. physical/microsite space, maximizing the differences and functional complementarity between coexisting individuals. Plant neighbourhoods would be built following the principle of niche complementarity (Bolnick et al., 2011), with a certain level of phenotypic niche differentiation, and competition between neighbours would be minimized by maintaining complementary phenotypes (Ashton et al., 2010). This would suggest that the smaller the number of coexisting species in a realized assemblage, the larger the phenotypic variation among conspecifics required for stable coexistence. Conversely, when the number of coexisting species is large, the stochastic dilution effect (Wang et al., 2016) would allow most phenotypic variation in the community to occur among species (more importance of BTV). This species richness gradient from monospecific to poor and, finally, to very rich communities will determine the relative importance of ITV vs BTV (Figure 1). If the

number of coexisting species is very low, individual phenotypes should be different enough to minimize competition between neighbours of the same species (Albert et al., 2011). On the contrary, if species number is high, a larger fraction of BTV necessary to explore complementary niches would be accounted for by competition with other species, minimizing differences within species, simply because the probability to live together with a conspecific is lower. In this sense, most dominant species show important functional differences among individuals (Bolnick et al., 2011) with some phenotypes specialized to be competitive in a certain region of the niche space occupied by the whole species, and others being more prone to establish facilitative interactions elsewhere (e.g., Michalet et al., 2011). Our conceptual framework could be extended to clonal plants considering that each ramet would be a different phenotypic realization of a genotype, in turn depending on the biotic neighbourhood and fine soil heterogeneity.

2 | MASSIVE PHENOTYPING

Generating sufficient data to evaluate predictions of niche phenotype complementarity in whole assemblages is clearly

a challenge. Massive phenotyping, i.e. the characterization of morphological, physiological, or phenological attributes in all individuals in a community, may help to deepen our understanding on assembly mechanisms in plant communities, independently of their taxonomic richness. However, this massive phenotyping has rarely been conducted in community ecology (Granier & Vile, 2014), and clear guidelines on how to conduct it in full communities are needed (see Losapio et al., 2018). Approaches to massively measure functional traits in the field and determine molecular contents in the lab can be summarized into three categories (White et al., 2012): (i) direct laboratory analyses, which requires measurements of all the individuals in a plant community, often being too time-consuming (Carmona et al., 2015); (ii) proximal (remote) sensing and imaging, which often has spatial and spectral resolutions that do not allow successfully distinguishing individuals and establishing correlations with functional traits; and (iii) calibration models based on visible–near infrared (Vis–NIR) spectrometry, with measurements taken directly in the plants. Although we acknowledge the extraordinary potential of field-based high-throughput phenotyping platforms (HTPPs; Araus & Cairns, 2014; Araus et al., 2015), they have only been used in monospecific crops, and their extrapolation to natural and complex plant communities seems challenging. Thus, we encourage the use of available alternatives. Vis–NIR spectroscopy is an inexpensive, regularly used and easy technique to calibrate numerous plant functional traits (Montes et al., 2007; White et al., 2012; Araus & Cairns, 2014). Vis–NIR spectra capture the physical and chemical characteristics of the samples, either vegetative plant tissues, harvested seeds or other plant organs (see Pupeza et al., 2020). Using chemometrics analysis and calibration models, different plant functional traits, including those below-ground, can be determined on the basis of a single spectrum which could be collected in the lab or directly in the field in less than one minute. While the precision of these indirect alternatives may be lower than those obtained with direct analysis, the fast, cost-effective, and non-destructive nature of Vis–NIR spectroscopy may overcome these limitations and justify its use (Araus et al., 2015). The possibility to measure literally thousands of individuals for several functional traits and species gives an enormous potential to this technique. Furthermore, the availability of portable Vis–NIR devices for in situ monitoring provides new opportunities to characterize phenotypes in the field at an unknown scale without harming individuals (de la Roza-Delgado et al., 2017). To illustrate its feasibility, we show Partial Least Squares (PLS) regression models on three leaf traits, namely specific leaf area, leaf thickness and leaf dry matter content, developed for pines in a well-conserved monospecific *Pinus sylvestris* stand on the treeline of the Sierra de Guadarrama National Park (Spain; Figure 3). Our models provide calibrations with R^2 higher than 0.8 in some cases (range 0.5–0.83), which can then be used to phenotype literally thousands of individuals in the field by taking their individual Vis–NIR needle spectra.

3 | NEIGHBOURHOOD PLANT'S PERSPECTIVE

Working with fully-mapped communities would provide a framework to explore the existence of niche complementarity and differentiation among individual phenotypes. The so-called plant's eye perspective (sensu Aarssen, 1989; Murrell et al., 2001), centred on the response or effect of individual plants in realized assemblages, leads to evaluating the phenotypic differentiation in each neighbourhood at different scales. For example, recent studies in different species-rich communities, using brand-new spatial pattern tools, have shown how the taxonomic (e.g., Wiegand et al., 2007; Pescador et al., 2019 for point and shape patterns), phylogenetic (Gusmán et al., 2018) and functional diversity (Chacón-Labela et al., 2016) are non-randomly organized around individuals of different species. Using the same framework, if we measure several functional traits in all individuals, we might be able to assess, for instance, the relative importance of ITV vs BTV in the assembly of neighbourhoods around each individual. In fact, using plant height in a mapped Mediterranean dwarf shrubland and null models accounting for the abiotic heterogeneity (Chacón-Labela et al., 2016), we found that individuals of most species were surrounded by less between-species trait diversity (BTV) for height than expected (unpublished data). However, the neighbourhoods of most species were neutral with respect to ITV. At larger spatial scales, the neighbourhoods still repelled BTV but had more ITV than expected, i.e. most species were accumulators of ITV.

We are aware that the acquisition of individual information on specific traits in a whole mapped community is challenging, but when feasible it would allow evaluating the existence of functional/phenotypic complementarities at the scale of neighbourhoods (see Baraloto et al., 2010 for a discussion of the costs and benefits of sampling functional traits in a reduced set of individuals vs all). The current toolbox of spatial pattern analyses offers diverse techniques to deal with all individual phenotypes mapped and/or characterized functionally (Wiegand & Moloney, 2014; Velázquez et al., 2016; Wiegand et al., 2017).

4 | CONCLUSIONS

The impressive growth of what was initially called functional plant ecology (see Violle et al., 2007), rooted in the powerful idea that plants exert their effect and affect their surroundings by their functional attributes, has helped to explain how communities are assembled, a hot topic in ecology (Escudero & Valladares, 2016). Because of the ambiguity of this name, Shipley et al., (2016) rephrased the discipline as plant trait-based ecology. Here, we propose a new framework in which the role given to species and populations (Götzenberger et al., 2012; HilleRisLambers et al., 2012) is scaled down to the variation among individuals and the recognition of the existence of a phenotype niche specialization (Clark, 2010). This phenotype-based community ecology offers a complete and valid venue to deal with coexistence, not only in

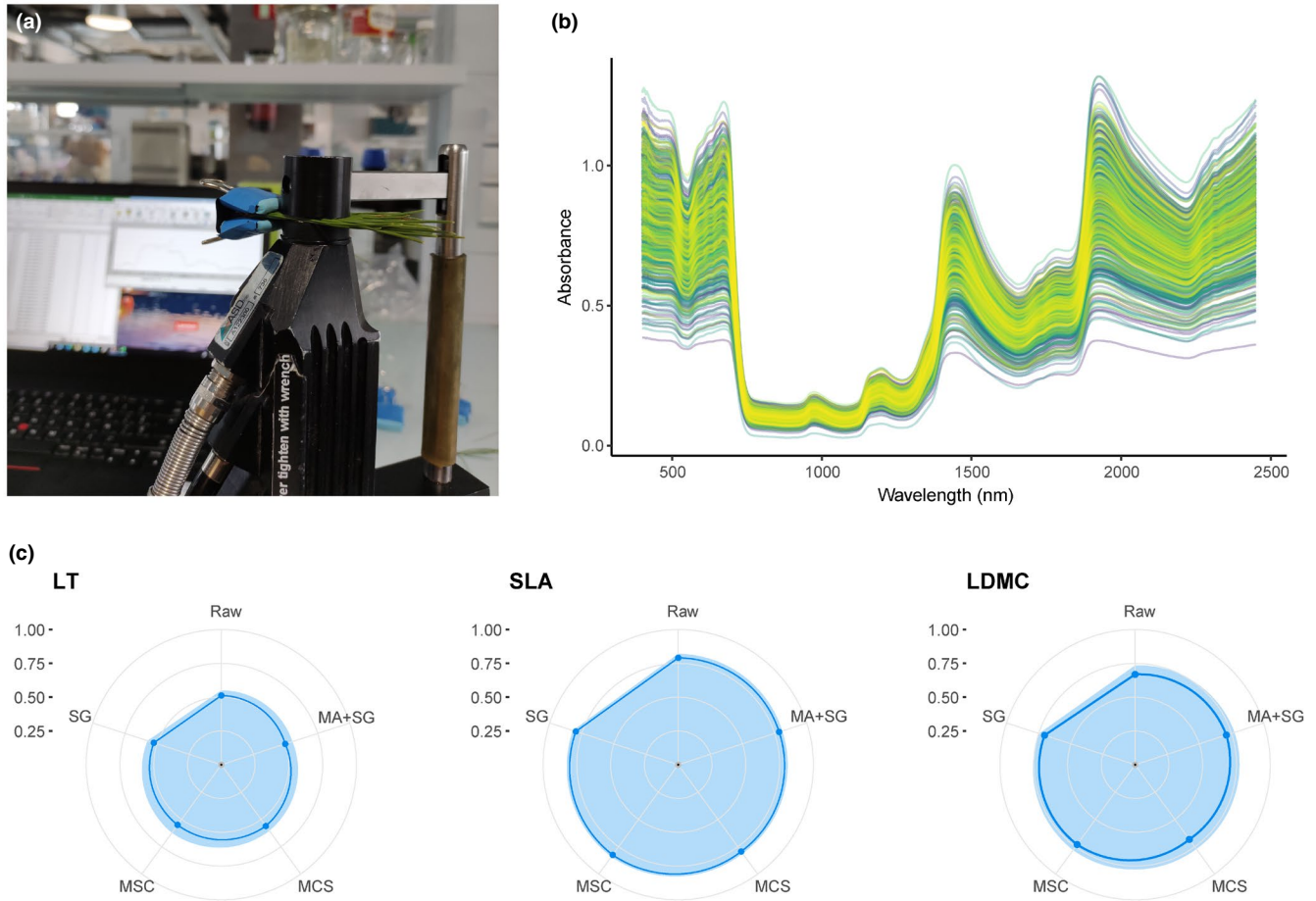


FIGURE 3 An example of massive phenotyping using visible–near infrared (Vis–NIR) spectrometry. Massive phenotyping with Vis–NIR absorbance spectra of *Pinus sylvestris* needles of 170 trees from a forest stand located at the tree-line of the Guadarrama National Park (1,900 m a.s.l.; lat. 40.81° N, long. 3.95° W). (a) Detail of contact probe with the ASD leaf clip connected to an ASD LabSpec 4 spectrometer (Malvern Panalytical, Malvern, UK) used to capture the absorbance spectra. (b) Vis–NIR absorbance spectra in the region 400–2,500 nm captured from leaves of 170 pines (c) Polar plots representing PLS (partial least squares) regression model results for three functional traits (LT, leaf thickness; SLA, specific leaf area; LDMC, leaf dry matter content) using Vis–NIR absorbance leaf spectra as independent variables. For each functional trait, five models were built and validated a total of 10 times with 70% and 30% of the samples, respectively, using raw data and four spectral pre-processing techniques (MA+SG, moving averages + Savitzky–Golay transformation; MCS, mean centering-scaling; MSC, multiple scatter correction; SG, Savitzky–Golay transformation). Coloured dots of each polar plot represent the average squared correlation of prediction (R^2_p) while the coloured polygons indicate the standard deviation achieved in each case

rich communities but also in poor and monospecific ones. If communities are very rich, most of the functional variability will fall within the so-called BTV, with a very residual participation of ITV. However, with few species, most of this functional variation, which can be as high as in the case of rich communities, will be accounted for by ITV.

After the explicit recognition that evolutionary and ecological processes can operate at the same scale, massive genomic data are opening the door to study eco-evolutionary dynamics (Rudman et al., 2018). While this can help to detect deterministic mechanisms behind phenotypic change, massive phenotyping is still needed. Our conceptual framework aims to connect plant community ecology to eco-evolutionary processes. Although phenotypes are complex mixtures of effects and responses, they represent the ecological adjustment of any genotype to local conditions, including interacting neighbours and microsite conditions. Phenotypes can be labelled

with a taxonomic recognition such as species identity but, in fact, they try to minimize competition by differentiating their niche.

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AUTHOR CONTRIBUTIONS

AE conceived of the main idea and led the writing of the manuscript, with support from SM and DSP. DSP analyzed the data presented in Figure 3. All other authors contributed to the discussion of the ideas presented in this paper.

DATA AVAILABILITY STATEMENT

Data for Figure 3 of this study are openly available via Figshare (Pescador et al., 2021): 10.6084/m9.figshare.14402108.

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