

A plant trait-based response-and-effect framework to assess vineyard inter-row soil management

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ABSTRACT

Biodiversity impacts ecosystem properties and the ecosystem services provided by those ecosystems. As a result, promoting plant diversity in agricultural systems has been a key issue in agriculture over recent years. In this context, weeds have an important role in maintaining field biodiversity, when it is balanced with their potential negative impact on crop production. Functional trait diversity, rather than the diversity of species *per se*, is a facet of biodiversity most directly related to species and community responses to management practices, with subsequent consequences for ecosystem services. Trait-based approaches, originally developed in the field of comparative ecology, allowed the description of weed species responses to management practices in annual crop systems. Here, we aimed to extend the trait-based approach to the spontaneous vegetation of vineyards. First, we propose a brief summary of current knowledge about weed communities in vineyards. Then we show how the relationships between management practices, weeds and grape vines can be translated into a response-effect framework: soil management practices (tillage, cover crops, spontaneous vegetation) can be considered as environmental filters that determine the composition and structure of vegetation, which, in turn, modify grapevine growth conditions in the vineyard. Finally, we tested this framework in a Mediterranean vineyard where, for 2 years, we characterized the responses of different components of weed communities (taxonomic and functional composition) in three inter-row management practices (tillage, cover crops and mowing spontaneous vegetation) and their effects on several grapevine processes (vine yield, vine leaf water potential and assimilable nitrogen in must).

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Introduction

Biodiversity impacts ecosystem properties and the ecosystem services provided by those ecosystems (Diaz and Cabido 1997; Tilman et al. 1997; Chapin et al. 2000; Cardinale et al. 2012). As a result, promoting plant diversity (specific or genetic) in agricultural systems has been a key issue in agriculture over recent years, as it has been proposed for natural ecosystems (Tilman, Wedin, and Knops 1996; Cardinale et al. 2012; Litrico and Violle 2015). In this context, weeds have an important role in maintaining field biodiversity, when it is balanced with their potential negative impact on crop production (Storkey 2006). More precisely, weeds are a major problem in crop production either through competing for resources or by reducing crop quality (Naylor and Lutman 2002). At the same time, weeds can in some cases provide additional services to provisioning service of yield (such as pollination, limitation

of soil erosion, “traps” for disease agents). The use of key ecological concepts is an important requirement for quantifying the positive contribution of weeds to ecosystem services without compromising crop yield (Storkey 2006). Related to this, management of vegetation co-occurring with cultivated plant diversity (such as weeds, spontaneous vegetation or cultivated cover crops) will permit us: (i) to identify assembly rules of complex weed communities; (ii) to recognize groups of species that respond similarly to a set of management practices; and (iii) to interact with biotic and abiotic components of the agro-system (Navas 2012).

Most studies in weed ecology have focused on the taxonomic characterization of the composition and structure of weed communities (Storkey and Westbury 2007; Fried, Norton, and Reboud 2008). However, functional trait diversity, rather than the diversity of species *per se*, is a facet of biodiversity most directly related to species

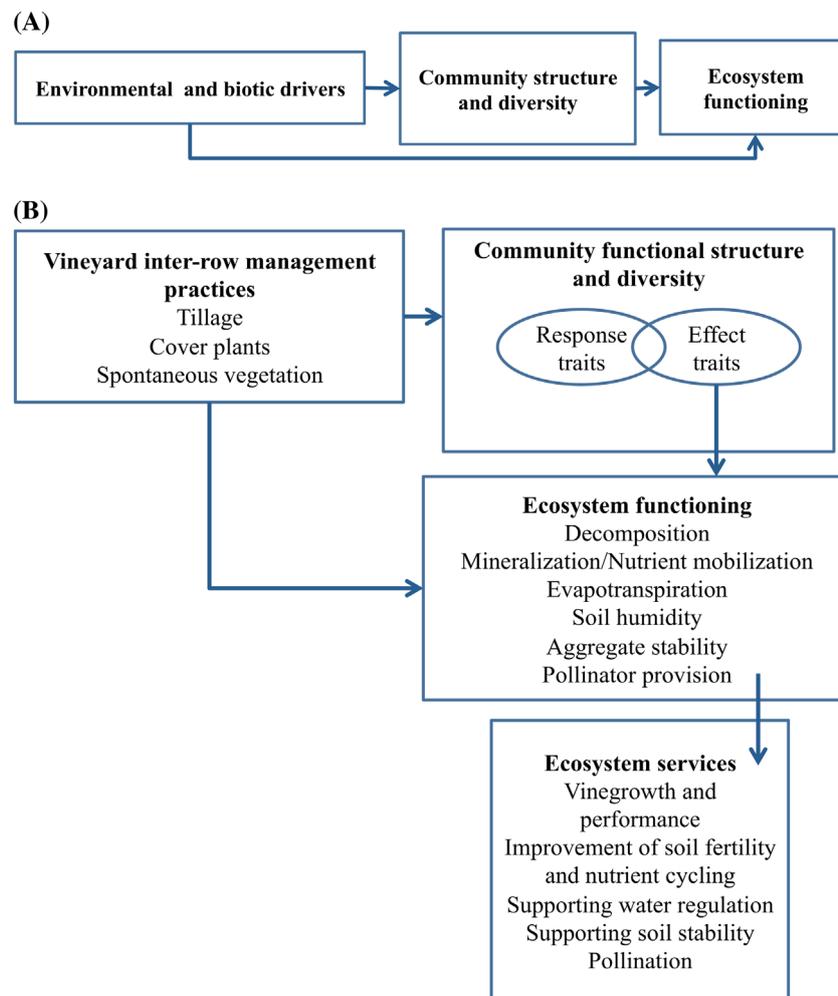


Figure 1. (A) The response-and-effect framework representing the communities responses to biotic and abiotic drivers and their effects on ecosystem functioning and ecosystem services (Lavorel and Garnier 2002; Suding et al. 2008). (B) Adaptation of the above framework to the effects of different inter-row soil management in the vineyards (such as tillage, cover plants and spontaneous vegetation) to species traits and their effects on different ecosystem processes and ecosystem services.

and community responses to management practices, with subsequent consequences for ecosystem services (Naeem and Wright 2003; Cadotte, Carscadden, and Mirotnick 2011). Trait-based approaches, originally developed in the field of comparative ecology have permitted the description of weed species responses to management practices in annual crop systems (Booth and Swanton 2002; Garnier and Navas 2011; Gunton, Petit, and Gaba 2011; Gaba et al. 2014).

The aim of this paper is to extend the trait-based approach to the spontaneous vegetation of perennial cropping systems, namely vineyards. Only a few studies have dealt with the taxonomic characterization of weed communities in those systems (Gago, Cabaleiro and Garcia 2007; Monteiro and Lopes 2007; Tesic, Keller and Hutton 2007; Steenwerth et al. 2016) and none of them have applied a trait-based approach. According to the response–effect framework (Figure 1A; Lavorel and Garnier 2002; Suding et al. 2008; Lavorel 2013), environmental drivers act as filters, sorting species according to the value of their traits (*response traits*), which results in a functional structure of communities that drives the functioning of ecosystems (*effect traits*). The ultimate

goal of response–effect analyses is the formulation of parsimonious quantitative relationships expressing the different ecosystem processes in relation to particular traits (Lavorel and Garnier 2002). So, to apply this framework, it is important to use arguments about scaling through the community level by integrating two components: (i) how a community responds to changes, and (ii) how this modified community affects ecosystem processes (Suding et al. 2008; Dawson and Chapin 1993). This response–effect framework has been tested and successfully applied in grasslands to understand how the different intensity levels of land-use impact ecosystem services through the changes in vegetation but it has not yet been tested in cultivated systems (Gross et al. 2008; Minden and Kleyer 2011).

Moreover, this approach provides a mechanistic understanding of the linkages between biodiversity and ecosystem functioning (Renting et al. 2009). As some trait values vary with environmental conditions and agricultural management practices (*response traits*) and can affect ecosystem functioning (*effect traits*), this framework could further be used to develop particular trait-based management strategies that can be implemented in

farming systems to increase multiple ecosystem services as well as to manage trade-offs among ecosystem services in agriculture (Wood et al. 2015). Most research has focused on using traits to understand how biodiversity in agricultural systems responds to management practices, rather than on understanding how biodiversity impacts agroecosystem services. In this paper, we start with a brief summary of current knowledge about weed communities in vineyards. Then we show how the relationships between management practices, weeds and grape vine can be translated in a response–effect framework: soil management practices (tillage, cover crops, spontaneous vegetation) can be considered as environmental filters that determine the composition and structure of vegetation, which, in turn, modify grapevine growth conditions in the vineyard. (Figure 1B). Next, we tested this approach in a Mediterranean vineyard where we characterized during 2 years the responses of different components of weed communities (taxonomic and functional composition and dynamics) in three inter-row management practices (tillage, cover crops and managed spontaneous vegetation) and their effects on several grapevine processes (vine yield, vine leaf water potential and assimilable nitrogen in must).

Vineyard management inter-row practices as a gradient of disturbance and competition intensity

Before the 1970s, vegetation between vine rows was traditionally managed by mechanical weeding based on soil tillage. Following the generalized use of chemical weed control and the disappearance of tillage, important shifts in weed community composition were observed between the 1970s and the 1990s (Barralis, Cloquemin and Guérin 1983; Maillet 1980). However, health and environmental concerns about the impact of chemicals and deep tillage have recently promoted changes in weed management practices (Monteiro and Moreira 2004; Moreira 1994). Currently, grape growers can choose between two main weed control methods, as alternatives to chemical control, used exclusively or in combination: reduced tillage in inter-rows and/or the use of a plant cover (temporary or permanent, spontaneous or sown, in rows or inter-rows) (Gago, Cabaleiro, and García 2007). The practice of cover cropping is currently increasing in vineyards (Teasdale 1996; Monteiro and Lopes 2007; Moonen and Bàrberi 2008; Giese et al. 2014) as it provides various ecosystem services in relation to the soil (erosion), the crop (control of vegetative development, and the resulting conditions of yield formation and disease development) and the environment (limited use of pesticides as herbicides or fungicides) (see Ripoche et al. 2011 for related references). But introducing a second crop as a green cover can lead to undesirable competition for soil resources such as water and nitrogen (Celette, Gaudin, and Gary 2008) and affects the issue of trade-off between

provisioning and regulating ecosystem services. For this reason, vineyards represent a relevant model, in which inter-row soil management ranges from regular soil cultivation (tillage), as in annual crops, to mowing spontaneous vegetation, as in semi-natural permanent grasslands.

Gaba et al. (2014) proposed a comparative description of the environmental gradients created mainly by an annual cropping system. Here, we represent three inter-row vineyard management practices (tillage, cover crop and spontaneous vegetation) as a double gradient of soil disturbance and competition intensity with tillage being the most disturbed habitat based on Grime's theory (Grime 1979). Tillage corresponds to high disturbance, defined according to White and Pickett (1985) as “any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability or the physical environment” (Figure 2A). The outcome of tillage varies with respect to both characteristics of the operation, such as depth, number of passes and the characteristics of the soil that is being tilled (see Gaba et al. 2014 for a detailed description). At low levels of disturbance, strong competitors exclude competitively inferior species and communities are dominated by a few species. Intermediate levels of disturbance can disrupt competitive hierarchies by increasing levels of mortality and in that way making free space available for the recruitment of competitively inferior species (Connell 1978). These patterns are also affected by spatio-temporal variability in disturbance: how often a disturbance occurs (i.e. frequency), how large the disturbance is (i.e. area or extent) and time since the last disturbance (i.e. time). When the extent of disturbance is considered, areas that are too large will eliminate all species, areas that are too small will have little or no impact, whereas disturbed areas of intermediate size may disrupt competitive exclusion and allow the establishment of new species in the disturbed patches (Wilson 1994).

Studies in annual crop systems described tillage as a filter that influences weed species composition and weed seed distribution in the soil seed bank (e.g. Cousens and Moss 1990; Cardina, Herms and Doohan, 1991). According to Grime's theory, tillage treatment will result in less diverse communities dominated by a small number of species whereas an intermediate disturbance (corresponding to vegetation cover treatment frequently mowed) will result in more diverse and equitable communities (Grime 2006). Under low disturbance, corresponding to the spontaneous cover, competitive exclusion by the dominant species is expected to occur (Navas and Violle 2009), due to light, nutrient or water competition (Figure 2A). At low intensities or frequencies of disturbance there is a balance between competitive exclusion and loss of competitive dominant species by disturbance. As indicated in Figure 2A, we assumed that the intensity of soil tillage (from no tillage treatments to conventional tillage treatments) corresponds to a disturbance

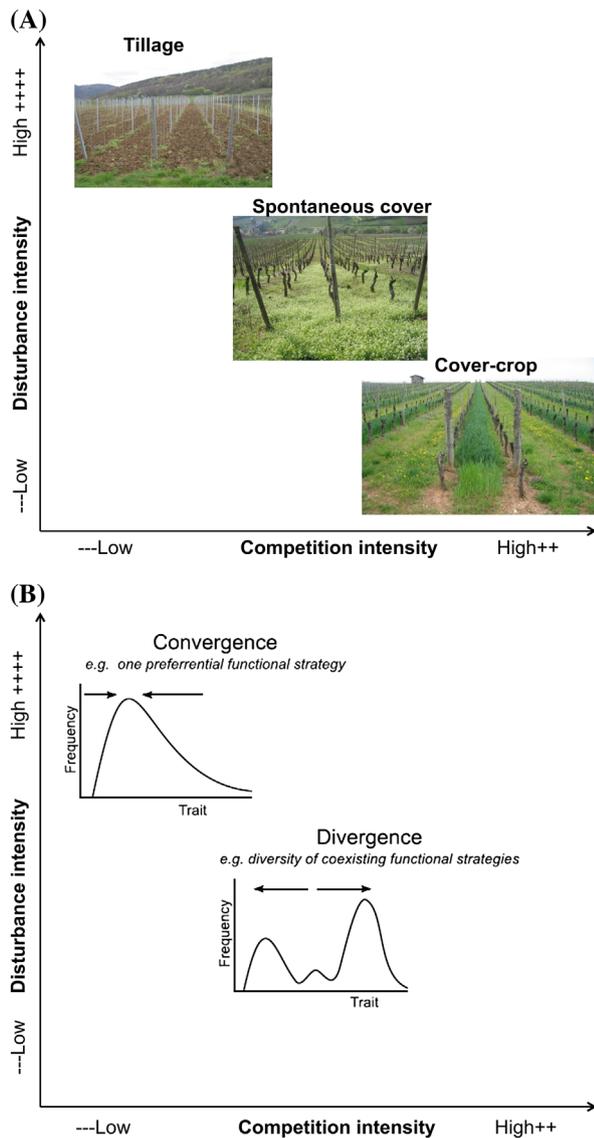


Figure 2. (A) Representation of three inter-row soil management in vineyards according to disturbance–competition intensity hypothesis proposed by Grime (1979). (B) Hypothesis about how soil inter-row management practices determine the functional structure of the communities. High disturbance, corresponding to tillage treatment, leads to shift in community weighted-trait and decreasing functional diversity (trait convergence). Vegetation cover will favour strong biotic interactions, selects individuals depending on their differences in trait values, and leads to increasing functional diversity (trait divergence according to niche differentiation hypothesis).

gradient, whereas the degree of vegetation cover, from spontaneous vegetation (with varying and irregular cover according to the weed species) to sowed cover crop (with the sowed species being implanted to be the dominant species) corresponds to a competition intensity gradient (for light, nutrient or soil water content).

Effects of different inter-row management practices on the composition and structure of weed communities and ecosystem functioning

The effects of different inter-row soil management practices in vineyards on communities' composition and structure and ecosystem processes have been discussed

in the literature (synthesis in Table 1). Conflicting results were found considering the effects of tillage on plant diversity and composition, possibly as a result of community fluctuations and initial seed stocks rather than deterministic changes in community composition (for example Derksen et al. 1993; Gago, Cabaleiro, and García 2007; Légère, Stevenson, and Vanasse 2011 found that plant cover crop showed a much lower number of weed species, mostly therophytes (Beuret and Neury 1990; Maillet 1980) irrespective of soil management technique). A limitation of using plant cover (spontaneous or sown) is the competition for resources including water, soil nutrients and light, which can compromise vineyard vigour, at least over the short term before possible accommodation. However recent studies on intercropping in vineyards have shown that in some situations, water stress may not be greater than in bare soil vineyards (Celette, Gaudin, and Gary 2008). The advantage of some cover crops is the possibility to use them to manage weeds through several mechanisms. First, competition between weeds and cover crops for light and soil resources will occur to varying degrees based on the vineyard environment and management (Fredrikson, Skinkis, and Peachey 2011). Second, allelopathic suppression of weeds has been observed upon decomposition of legume residues, such as clovers (Dyck, Liebman, and Erich 1995; Liebman and Davis 2000) and non-leguminous residues, such as cereal rye.

On the other hand spontaneous cover treatment can be chosen as a costless trade-off for the winegrowers between improving soil properties, limiting mechanical work and maintaining vine production. According to the objectives of winegrowers (limiting weed competition when resources are limiting or improving soil structure and improving soil bearing capacity or forcing the vineyard to develop deep rooting with interesting side effects such as a better capacity to access water), the management of the spontaneous treatment should be adapted each year in agreement with the climatic constraints: for example, the number and dates of mowing could be adapted and the spontaneous treatment may be retained or not.

Functional structure of weed communities and response traits to different management practices and resources availability

The functional characterization of weed responses to specific components of management has been successfully developed in several recent studies (Booth and Swanton 2002; Storkey 2004, 2006; Gunton, Petit and Gaba 2011; Fried Kazakou and Gaba 2012; Navas 2012) showing that for annual crop species, the phenological traits of weeds (timing of emergence) are one of the key drivers of weed community assembly in responses to crop sowing dates and harvest dates. However, in the case of perennial cropping systems, only taxonomical diversity indices of weed species have been used to compare the effect

Table 1. A summary of different studies testing the effects of different inter-row soil management practices on communities' composition and structure, pollination and arthropod diversity, soil properties (organic matter accumulation, fertility, erosion), water conservation and availability and vine vigour and grapevine yield.

Agroecosystem properties	Inter-row soil management practices in vineyards				References
	Tillage	Cover crop	Spontaneous vegetation		
Plant species diversity and abundance	↘	↘	↗		Gago, Cabaleiro and García 2007; Baumgartner, Veilleux and Steenwerth 2007; Lososova, Danihelka and Chytrý 2003; Monteiro et al. 2008; Monteiro et al. 2012; Ingels et al. 2005; Fredrikson, Skinkis and Peachey 2011; Olmstead et al. 2012; Smith 2006; Porcova and Wikler 2014; Pal 2004; Song, Ryou and Cho 2004; Ferreira et al. 2012; Miglecz et al. 2015; Sanguankeo and León 2011; Steenwerth et al. 2016
Pollinator and arthropod diversity	↘	↗	↗		Sanguankeo and León 2011; Baños-Picón et al. 2013
Soil organic matter/Soil fertility	↘	↗	↗		Steenwerth and Belina 2010; Smith 2006; Ingels et al. 2005; Smith et al. 2008; Jordan, Bjorkman and Vanden-Heuvel 2016; Ferreira et al. 2012; Song, Ryou and Cho 2004
Soil erosion	↗	↘	↘		Baumgartner, Veilleux and Steenwerth 2007; Sweet and Schreiner 2010; Guerra and Steenwerth 2012; Battany and Grismer 2000;
Aggregate stability	↘	↗	↗		Celette et al. 2005; Maigre 2002; Morlat and Jacquet 2003; Morlat and Chaussod 2008
Water conservation/availability		↗ or ↘			Caspari, Neal and Naylor 1997; Celette, Gaudin and Gary 2008; Gulick et al. 1994; Monteiro et al. 2008; Morlat 1987; Ruiz-Colmenero, Bienes, and Marques, 2011
Vine vigour and grapevine yield	↗	↗ or ↘	↗ or ↘		Zalameña et al. 2013; De Vetter, Dilley, and Nonnecke 2015; Jordan, Bjorkman, and Vanden-Heuvel 2016; Susaj et al. 2013; Guerra and Steenwerth 2012; Baumgartner, Veilleux and Steenwerth 2007; Bibiana and Steenwerth 2012; Sweet and Schreiner 2010; Ingels et al. 2005; Song, Ryou, and Cho 2004; Sanguankeo, Ramon and Malone 2009; Rodriguez-Lovelie, Soyer and Molot 2000; Morlat and Jacquet 2003; Caspari, Neal and Naylor 1997; Geoffrion 2000; Maigre and Aerny 2001; Lopes et al. 2011

Note: ↗ or ↘ indicates the direction of agroecosystem properties according to the treatment.

Table 2. Responses trait to different soil management practices.

Response traits	Soil management practices			
	Tillage	Shade effect	Vegetation cover	
			Low nutrients effect	Drought effect
Whole plant traits				
Grime strategy	R	C	S to C	S to C
Life form	A			
Plant height	low	high	low	low
Clonality	low			high
Potential growth rate	high	high or low	low	low
Leaf traits				
Specific leaf area (SLA)	high	high or low	low	low
Leaf size (LA)	high	high or low	low	low
Leaf dry matter content (LDMC)	low	high or low	high	high
Leaf N and P concentration (LNC, LPC)	high	high or low	low	low
Litter N and P concentration	high	high or low	low	low
Leaf life span	short	long	short	long
Stem and below-ground traits				
Stem dry matter content (SDMC)	low	high or low	high	high
Specific root length	low	high or low		high or low
Diameter of fine roots	low		high	
Root depth	low	high	high	high
Nutrient uptake strategy	high		low	
Regenerative traits				
Seed mass	low	high	–	high
Dispersal mode				
Onset of flowering	early		–	early
Seed number	high	low	low	low

Notes: Adapted from Garnier, Navas, and Grigulis (2016) by considering species traits responses to a disturbance gradient (from tillage to no tillage management) or a resource (light, nutrient, soil water) gradient corresponding to different types of vegetation cover. Grime's strategies: R for ruderal, C for competitive and S for stress-tolerant. Life forms: A indicates annual species.

of different management practices so far (e.g. Barralis, Cloquemin, and Guérin 1983; Dastgheib and Frampton, 2000 for vineyards) whereas functional traits were only used very recently to assess the services of sown cover crops (Gamour et al. 2015).

According to the response–effect framework, response traits to environmental filters change a community's functional structure and diversity and so impact ecosystem processes through changes in the representation of ecosystem-effect traits (Suding et al. 2008; Figure 1A). It has been assumed that the most abundant species are often more functionally important simply because of greater representation (Grime 1998; Garnier et al. 2004; Balvanera, Kremen, and Martinez-Ramos 2005). This assumption forms the basis of the dominance hypothesis proposed by Grime (1998) under the name of the *mass-ratio hypothesis*, suggesting that community effects on ecosystem functioning are mainly determined by the traits of the dominant species. Garnier et al. (2004) described the functional structure of a community through value and range of traits by an estimator known as the Community Weighted Mean (CWM). The CWM represents the average trait value for a unit of biomass within a community. In other cases, species functional effects may not scale as directly with abundance due to non-additive interactions, as suggested by the *niche complementarity hypothesis* (Petchey and Gaston 2006). According to this hypothesis, environmental filtering may affect functional trait diversity (i.e. trait convergence or divergence) within communities through mechanisms such as complementarity resource use (Petchey and Gaston 2006).

In Table 2 we provide a summary of the response of traits according to different inter-row soil management and the corresponding sources. Based on previous results in other environments (for a review see Garnier, Navas and Grigulis 2016), highly disturbed habitats select species with rapid completion of the life cycle and high fecundity (low seed mass, onset of flowering at the end of favourable season, low reproductive height), corresponding to the ruderal species strategy (R) (Grime 1979; Table 2). An intermediate disturbance condition favours the coexistence of competitive species and stress-tolerant species (due to the resources limitation) (Mackey and Currie 2001). Unproductive low-disturbance habitats select perennial species with slower plant growth, longer life spans, denser tissues, in which resources are conserved more efficiently. Stress-tolerant species (S) allocate resources to maintenance and defences, such as anti-herbivory (Grime 2001). Finally, productive habitats (no disturbed and no stressed habitats) select mostly species for the ability to pre-empt resources by foraging (competitors, C) (Table 2). Competitors are primarily composed of species with high relative growth rate, short leaf life span, relatively low seed production, and high allocation to leaf construction. They persist in high-nutrient and low-disturbance environments. Hence, in contrast to the denser tissues, low specific leaf area and concomitantly slow growth of stress-tolerators (Poorter and van der Werf 1998; Poorter and Jong 1999; Weiher et al. 1999), both competitors and ruderal species are characterized by high specific leaf area and faster relative growth rates (resulting from greater internal conductivity and lesser investment in structural tissues), with

ruderal species investing more in the reproductive phase of the life cycle (Table 2).

We assume that in tillage treatments, tolerance and escape are the two types of responses that species will adopt resulting in small size, with high growth rates (as found for example in Storkey 2006; Fried, Kazakou and Gaba 2012). Plants growing in nutrient-poor or dry environments will increase their ability to access soil resources (by increasing root biomass or their capacity to fix atmospheric nitrogen). In cover crop treatments, it is expected that the less competitive weed species will be excluded, and only some competitive species that can rapidly reach a high size (relative to the cover crop), high specific root length and depth, and efficient nutrient-use strategies or pre-empting capacities would be able to survive. Alternatively, we assume that spontaneous species having different traits and using resources differently from the cover crop could also survive (e.g. early flowering weed species able to produce seeds before the closure of the canopy of the cover crop).

In addition, we hypothesize that disturbance (represented by tillage treatment) acts as a strong filter resulting in the convergence of traits within communities (i.e. reduction in trait variation with increased disturbance), whereas cover crop and spontaneous vegetation will result in fewer similar species in the communities according to the limiting similarity hypothesis (Figure 2B). This means that the functional divergence (i.e. the degree to which the distribution of species abundances in niche space maximizes total community variation in functional characters) of the different weed species is the combined result of species separate niches and complementarity in resource use.

Effect traits of weed communities and services on vineyard ecosystems

Several studies have shown that many ecosystem properties (for example above-ground net primary productivity, litter decomposition, soil nitrogen, soil water content,

digestibility) are shaped by the traits of dominant species and/or functional diversity of communities (see Garnier, Navas, and Grigulis 2016 for a detailed review). These numerous studies were conducted in diverse ecosystems (secondary succession, grasslands, forests or serpentine ecosystems) but none of them considered perennial cropping. Recently, Gamour et al. (2015) discussed how the trait-based approach could be extended to assess the services delivered in cover-cropped banana cropping systems and identified which effect traits are related to these services.

Here we adapt the synthesis about traits and ecosystem services proposed by de Bello et al. (2010) to assess the contribution of vegetation species traits to different ecosystem services related to vineyards (Table 3). Following de Bello et al. (2010), we consider that there is a group of traits such as growth form, canopy density and plant size as well as the root system that are involved in water regulation and soil stability. We assume that leaf and litter traits influence vine growth and soil fertility through an increase in the decomposition and mineralization processes (as shown for tree species by Wardle, Bonner and Barker 2002). In order to expand the trait-services approach to services such as pollination (with different trophic groups involved) we should consider different trophic levels (Lavorel et al. 2013). To date, this approach has never been tested in vineyards or any other agricultural system (except in grasslands). The challenge for future works is to establish the linkages between traits and services to provide a basis for practical agroecosystem management and decision-making.

A case study: short-term dynamics of weed communities in response to different soil management and effects in vineyard performance in southern France

In Mediterranean regions, adaptation to climate fluctuations is a recurrent management problem in agricultural production (Ripoche et al. 2011). In perennial

Table 3. Species traits relating to different ecosystem services important for the vineyards.

Agroecosystem services	Trait effects	Ecosystem properties
Vine growth and performance	Growth form and size; plant size (-); LDMC (-); SLA (+); litter N and P concentration (+); N fixing species (+); root depth; root length	Decomposition, mineralization, nutrient mobilization
Improvement of soil fertility and nutrient cycling	Growth form; plant size (-); LDMC (-); SLA (+); LNC (+); litter N and P concentration (+); N fixing species (+); root exudates; root length and biomass; onset of flowering (-)	Decomposition, mineralization, nutrient mobilization
Supporting water regulation	Growth form; plant size (+); canopy density (+); leaf area (+); phenology; root depth	Evapotranspiration
	Plant size (+); canopy density (+); growth form; litter amount (+)	Infiltration/maintenance of soil humidity
	Canopy size; growth form diversity (+); growth form composition	Surface water flow/run off
Supporting soil stability	Growth form; root depth; root density	Erosion prevention
Pollination	Flower traits (flower colour, peduncle length, corolla shape)	Pollinator provision

Notes: LDMC, Leaf dry matter content; LNC, leaf N concentration; SLA, specific leaf area.

The direction of the effect of the trait on the considered process(es) can be positive (+), negative (-) or variable when no indication is given. Adapted from de Bello et al. (2010) and Garnier, Navas, and Grigulis (2016)

systems, like vineyards, adaptation is possible through canopy management (Smart et al. 1991), fertilization, irrigation, or soil surface and intercropping management (Chiffot et al. 2006; Celette, Gaudin, and Gary 2008). However only 14% of vineyards in the Mediterranean regions are intercropped (Mezière et al. 2009), because wine growers in those regions fear occasional episodes of strong competition for water between the two crops and are reluctant to introduce cover crops despite the regulating services they would provide (Ripoche et al. 2011). In this study, we compare response traits of weeds in three management practices and test their links with agroecosystem properties. This first attempt to adapt the trait–response framework to vineyards may advocate how management practices can achieve target traits and those traits will be prone to achieve ecosystem properties and services (as suggested at the theoretical framework of Wood et al. 2015). We tested this framework in a Mediterranean vineyard where we characterized, during 2 years, the responses of different components of weed communities (taxonomic and functional composition) in three inter-row management practices (tillage, cover crops and mowing spontaneous vegetation) and their effects on several grapevine processes (vine yield, vine leaf water potential and assimilable nitrogen in must).

The field experiment is detailed in Guilpart, Metay, and Gary (2014). Grapevines (*Vitis vinifera* L. cv. Shiraz) were planted in 2002, in rows oriented northwest–southeast at a density of 3300 stocks per hectare (2.5 m × 1.2 m). Three treatments were designed to create a gradient of soil resources (water and nitrogen): (i) a first treatment was obtained by sowing a mix of annual *Medicago* species (*Medicago truncatula*, *Medicago rigidula*, *Medicago polymorpha*) in the inter-row during autumn 2009 (cover crop treatment hereafter); (ii) a second treatment with bare soil was obtained by mechanical weeding in the inter-row with three operations in spring (in April, May and June in 2010 and in March, April and June in 2011), (tillage treatment hereafter); (iii) permanent natural plant coverage between rows (spontaneous cover treatment) mowed twice a year. There was no fertilization or irrigation in these treatments. Treatments were applied as strips. Cover crop and tillage treatments were composed of 185 vine stocks (37 vine stocks per row and five rows) whereas spontaneous cover treatment was composed of 74 vine stocks (37 vine stocks per row and two rows).

Depending on the regime of disturbance due to practical operations in the vineyard, weed cover sampling was conducted at several dates during a year, especially before and after treatments and over at least 2 years to record weed communities early responses (measured traits are detailed in Figures 3 and 4). We also monitored vine yield and growth, and water and nitrogen grapevine status, as previous research has documented significant effects of cover crops on these key parameters (Ingels et al. 2005; King and Berry 2005; Tesic, Keller, and Hutton 2007). After calculation of several indices, their distribution was

tested for normality and \log_{10} transformed when required. A repeated ANOVA was performed to test the effect of three treatments, the effect of different sampling dates and their interaction as the different measurements made on the same plots at different dates were not independent. We tested the main effect of date and treatment, the additive effect and their interaction. The model best supported by the data was selected based on the Akaike Information Criterion (Burnham and Anderson 2002). Post-hoc tests were performed to test the effect of treatment or date on different variables. Statistical analyses were performed under R environment (R Development Core Team 2011) using the lme4, plotrix and multcomp packages.

Hypothesis 1: Inter-row management treatments as a gradient of disturbance and competition intensity

We first hypothesized that the three management practices represent a double gradient of disturbance and competition intensity, which acts as filters affecting composition, species richness and abundance. We expected that tillage treatment would favour a small number of dominant species (low Shannon indices) whereas vegetation cover would favour a higher number of species, equally abundant (high Shannon indices). Our results showed that diversity indices varied among the three management practices, and the sampling date (Figure 3). More precisely, spontaneous treatment showed the highest number of species with more than 14 species per m² observed on all the sampling dates whereas tillage treatment harboured the lowest number of species (with a mean of eight species) and the highest variation across dates (Figure 3A). Shannon diversity index was highest in the spontaneous treatment and lowest in the tillage treatment, indicating that in this treatment only a limited number of species were abundant (Figure 3B). High disturbance, corresponding to tillage treatment, resulted in less diverse communities dominated by a small number of species whereas an intermediate disturbance resulted in more diverse and equitable communities. Moreover, there are some species that are very tolerant to all treatments e.g. *Poa annua*, *Crepis sancta* and *Senecio vulgaris* in April 2010 and *Malva sylvestris* in May 2011, which have also been shown to be among the most generalist weed species able to withstand a large range of management and ecological conditions in annual arable fields (Fried, Petit, and Reboud 2010). Weed and cover crop biomass did not differ between the three treatments in April 2010 (Figure 3C). Spontaneous and cover crop treatments did not present significant differences during the three dates of measurements, but it is important to note that cover crop treatment presented high variability among the different plots (certainly due to the establishment difficulties of the cover crop in the first year). In the tillage treatment, biomass was destroyed just before measurements in May and June.

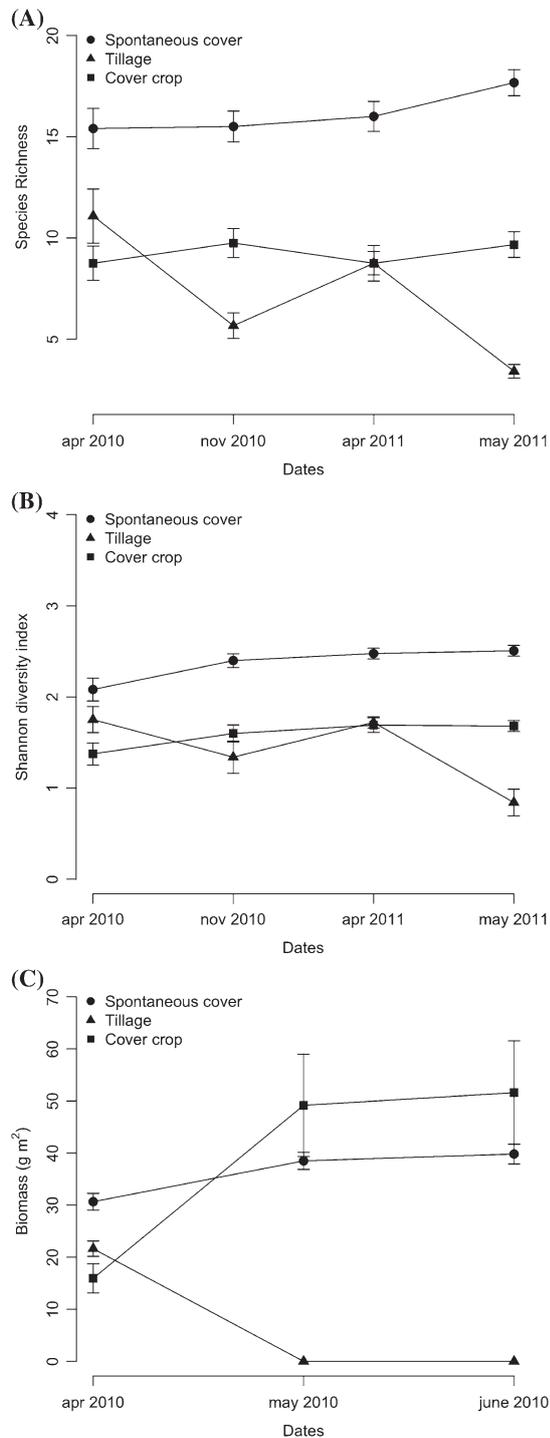


Figure 3. Temporal variations of (A) Species richness, calculated as the number of weed species per quadrat [$\chi^2_{\text{treatment}}: 54.947^{***}$ (post-hoc test: a, b, c); $\chi^2_{\text{date}}: \text{ns}$]. (B) Shannon diversity index, calculated as $-\sum [p_i \ln(p_i)]$, where p_i is the relative abundance of each weed species in a given quadrat [$\chi^2_{\text{treatment}}: 79.60^{***}$ (post-hoc test: a, b, c); $\chi^2_{\text{date}}: 2.75^*$]. (C) Weed species biomass estimated in the three treatments three times in 2010 with a destructive biomass removal from six quadrats of 0.85 m² each randomly selected closed to weed identification areas [$\chi^2_{\text{treatment}}: 79.60^{***}$ (post-hoc test: a, b, c); $\chi^2_{\text{date}}: 2.75^*$]. Mean values, standard errors, results of repeated two-way analysis of variance and post-hoc tests are given. Vegetation for richness and abundance was sampled four times between April 2010 and May 2011 (12 permanent plots of 1 × 1 m were established in each soil management system). For each record, species abundance was recorded using the Braun-Blanquet scale (Braun-Blanquet 1964) Traits values were obtained by the Leda trait base (Kleyrer et al. 2008).

Hypothesis 2: Functional composition and structure of weed communities respond to management treatments

The second hypothesis was about species response traits to different management practices: that tillage treatment will favour species with traits corresponding to ruderal strategy (high growth rate, traits favouring resources acquisition), whereas cover crop will favour competitive species. To test this hypothesis we characterized weeds functional composition in the three inter-row treatments. We choose traits reflecting species morphology, phenology and reproduction (traits values were obtained in standardized databases: Leda, BiolFlor and Badoma). We then calculated CWM (Garnier et al. 2004) and the Functional Richness Index, which represents the amount of functional space filled by the community (Villéger, Mason, and Mouillot 2008) for plant communities in the three treatments for all the sampling dates. Our results confirm the hypothesis that tillage treatment favoured species with trait values associated with extensive exploitation of productivity-related resources and fast growth (especially high specific leaf area values). CWM of all the traits varied significantly among the three treatments. Species from the tillage treatment showed the lowest reproductive height values (Figure 4A), the highest specific leaf area values (Figure 4B) and late onset of flowering (Figure 4C). The opposite pattern was found for species from the cover treatment. This pattern can be explained in part if we consider the early onset of flowering observed in plants for the cover crop treatment: species in this treatment tend to flower and produce seeds earlier in season than *Medicago* plants. Additionally, species in the cover plant treatment showed the higher reproductive height values as a response to competition for light. The results of this study agree with the findings of Flynn et al. (2009), Laliberté and Tylianakis (2012) and Guerrero et al. (2014), who showed that the intensification of land use reduced functional diversity and redundancy. We also tested whether tillage treatment (highly disturbed habitat) acts as a filter resulting in the convergence of traits within communities whereas plant cover (sown or spontaneous) vegetation will result in fewer similar species in the communities with large trait variability. We found that spontaneous vegetation treatment showed the highest functional richness whereas in tillage treatment functional richness decreased even when species richness increased (implying functional convergence, Figure 4D). Communities in spontaneous vegetation treatment presented high functional divergence, which indicates a high degree of niche differentiation, and so low resource competition. Hence, communities with high functional divergence may express increased ecosystem function, especially improvement of soil fertility and nutrient cycling, as a result of more efficient resource use (Mason et al. 2005).

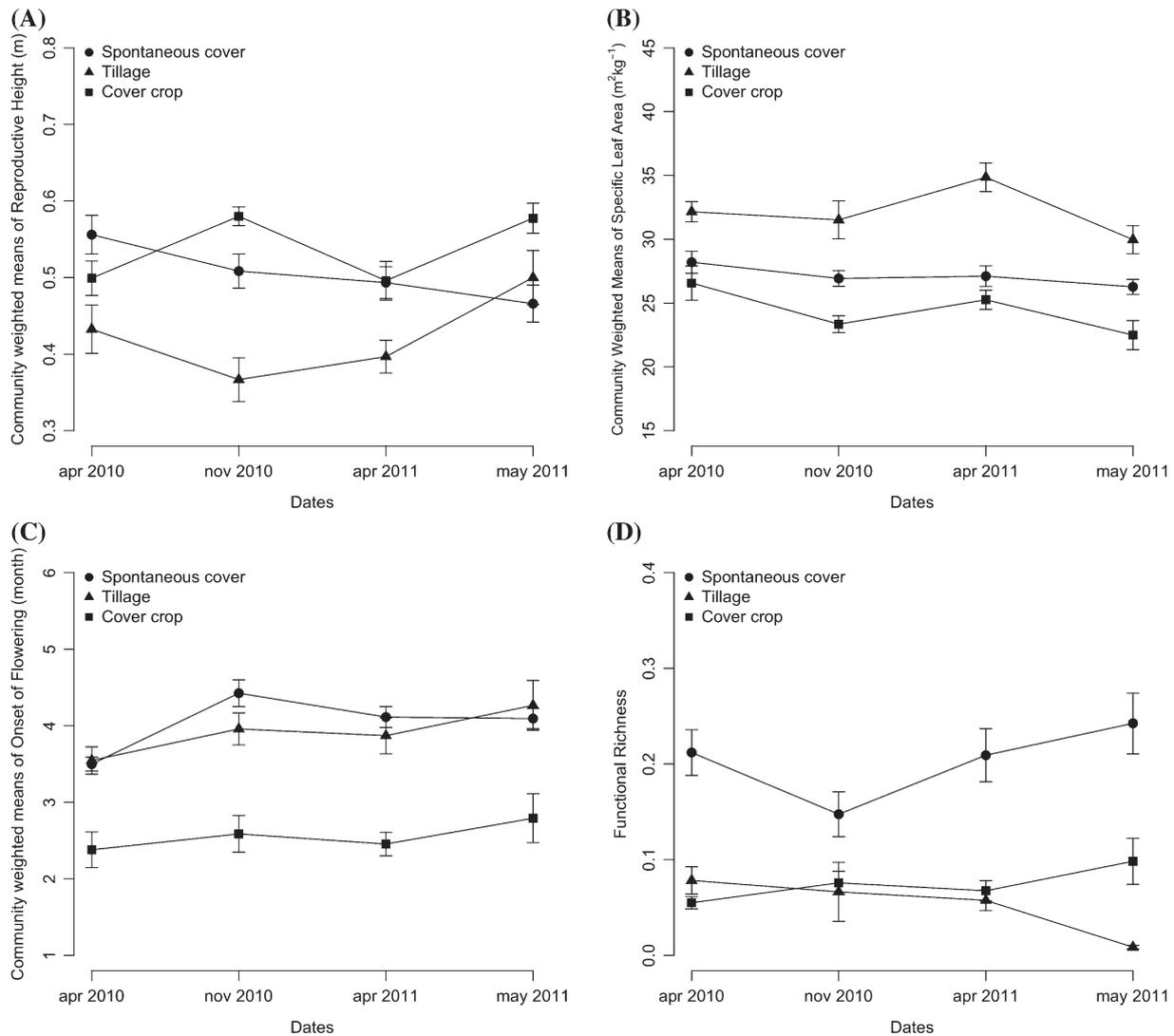


Figure 4. The functional structure of communities was assessed by calculating community-weighted means (CWM; Garnier et al. 2004): $CWM = \sum_{i=1}^s p_{ik} \times t_{ij}$ where t_{ij} is the value of the trait j for species i , and p_{ik} is the relative abundance of species i in community k . CWM represents the average trait value for a unit of biomass within a community and was used to describe changes in the functional structure of communities over time and across the different treatments. (A) Community-weighted means of reproductive height, measured at the time of seed dispersal, depicts species' carbon gain with respect to the plant's ability to compete for light (Westoby et al. 2002; Violle et al. 2009) [$\chi^2_{\text{treatment}}$: 30.03*** (post-hoc test: a, b, a); χ^2_{date} : ns; $\chi^2_{\text{treatment} \times \text{date}}$: 26.19***]. (B) Community weighted means of specific leaf area, calculated as the ratio between leaf area and leaf dry mass, is particularly important because it is directly related to resource economy (Wright et al. 2004). [$\chi^2_{\text{treatment}}$: 59.96*** (post-hoc test: a, b, c); χ^2_{date} : ns; $\chi^2_{\text{treatment} \times \text{date}}$: 1053***]. (C) Community weighted means of onset of flowering, a phenological trait associated with persistence in disturbed habitats, coded using month as a unit from 1 (January) to 12 (December) [$\chi^2_{\text{treatment}}$: 43.20*** (post-hoc test: a, a, b); χ^2_{date} : ns; $\chi^2_{\text{treatment} \times \text{date}}$: 43.24***]. (D) Functional richness across the three soil inter-row management treatments. Functional richness (FRci) represents the amount of functional space filled by the community. For multiple trait studies, functional richness estimates the volume filled in the dimensional space by the community of interest (Villéger, Mason, and Moullot 2008). Low functional richness indicates that some of the resources (α niches) potentially available to the community are unused (Mason et al. 2005). For a given functional trait c , functional richness in community i is calculated as: $FR_{ci} = \frac{SF_{ci}}{R_c}$, where SF_{ci} is the niche space filled by species within a community and R_c is the absolute range of the trait [$\chi^2_{\text{treatment}}$: 51.10*** (post-hoc test: a, b, b); χ^2_{date} : ns; $\chi^2_{\text{treatment} \times \text{date}}$: 15.44***]. Mean values, standard errors, results of repeated two-way analyses of variance and post-hoc tests are given.

Hypothesis 3: Species traits affect ecosystem properties

We hypothesized that different soil management practices in the vineyards would affect vine growth and performance. Although spontaneous cover is supposed to have a higher impact on vine yield compared with tillage; it is expected that the effect of the legume cover crop is intermediate after 2 years, as competition with

the vines is compensated by an increase in nitrogen supply and that the presence or the vigour of competitive weeds that may be present in spontaneous cover is reduced. However, spontaneous and tillage treatments presented significantly higher grapevine yields than the cover crop treatment around 4000 g/vine (which corresponds to about 12 t of grapes ha⁻¹ according to the density of vines per ha) in spontaneous and tillage

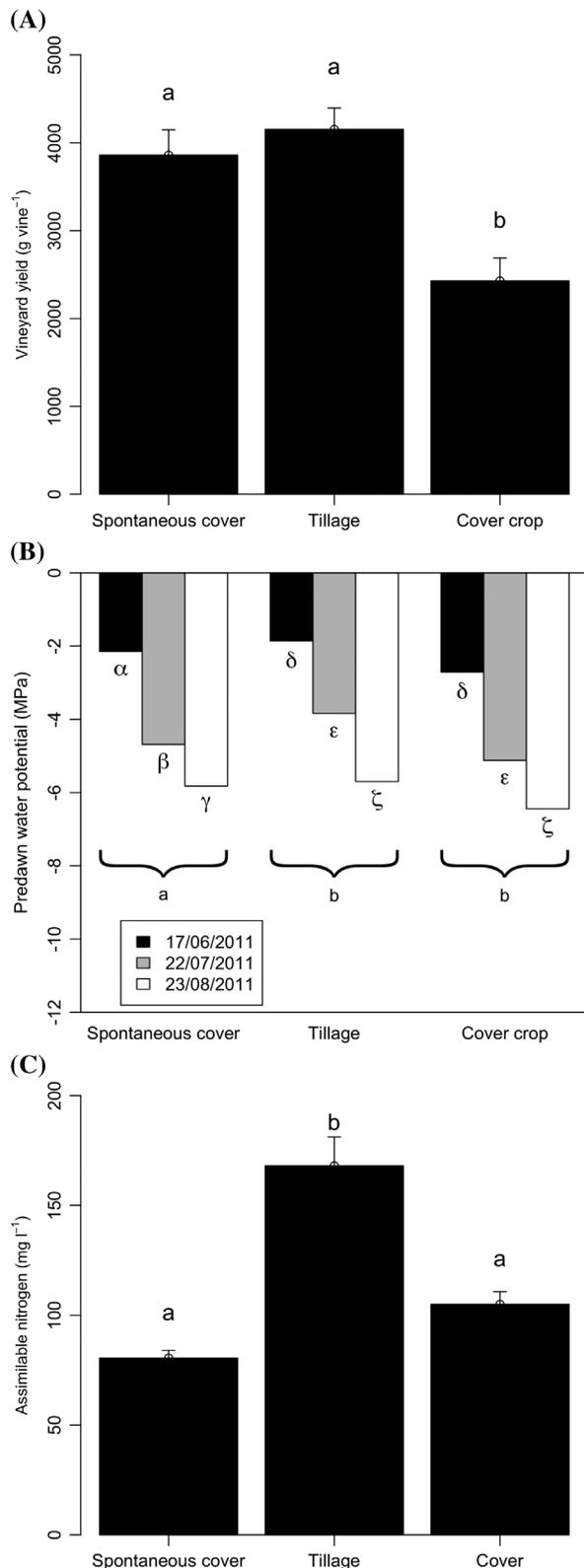


Figure 5. (A) Grapevine yield (kg vine⁻¹) [$\chi^2_{\text{treatment}}$: 510.2*** (post-hoc test: a, b, b)]. (B) Predawn leaf water potential during the most critical period for vine growth (MPa) [$\chi^2_{\text{treatment}}$: 22.1***, χ^2_{date} : 885***]. (C) Assimilable nitrogen in must (mg l⁻¹) across the three soil inter-row management treatments [$\chi^2_{\text{treatment}}$: 28.24***]. For a detailed description of the protocol see Guilpart, Metay, and Gary 2014). Mean values, standard errors, results of one-way analysis of variance and post-hoc tests are given.

treatments versus around 2500 g/vine (corresponding to 7.5 t grapes ha⁻¹) in the cover treatment) (Figure 5A). This result can be explained by the non-significant

differences in biomass of spontaneous and cover crops and the higher functional trait divergence (especially of specific leaf area, which corresponds to resource use). Pre-dawn leaf water potential, a dynamic indicator of the water stress undertaken by the vine, shows that cover treatment always created higher water stress conditions for the vine throughout the summer (-0.64 MPa in late August versus -0.57 MPa and -0.58 MPa for tillage and spontaneous treatment, respectively) (Figure 5B). Assimilable nitrogen in must was significantly higher at harvest at the tillage treatment (168 mg L⁻¹ versus 80 mg L⁻¹ and 105 mg L⁻¹ for spontaneous and cover treatment, respectively). For the latter two, the assimilable nitrogen content in must was below the threshold of 140 mg L⁻¹ generally considered as the threshold for nitrogen deficiency (Casalta, Sablayrolles, and Salmon 2013). Cover treatment based on legumes did not show any improvement in vine nitrogen nutrition even if there was a slight increase (Figure 5C), probably as a consequence of the water stress created by the cover crop. In this case, the most limiting factor is water (Figure 5B). We should notice that these measures have been realized only 2 years after the installation of the cover plant and spontaneous treatment, which is not a long enough period for vineyards to be adapted. In conclusion, both spontaneous and tillage treatments appeared acceptable as far as yield was maintained (at least) during this transient phase before vineyard adaptation possibly through different rooting. The advantage of the tillage treatment on one hand was that it seemed efficiently able to limit weed growth (see biomass data in Figure 3C) and consequently maintain both an adequate water status for the vine and a high level of assimilable nitrogen. On the other hand, spontaneous vegetation treatment can be chosen as a costless trade-off for the winegrowers between improving soil properties, limiting mechanical work and maintaining vine production.

Lavorel and Grigulis (2012) proposed a framework based on alpine grasslands, differing in their management regimen, corresponding to a gradient of management intensity: intensive management practices (like mowing and fertilization) favour species with traits values associated with high-resource acquisition (high specific leaf surface for example), and so influencing ecosystem processes and services (such as net primary productivity and rapid biochemical cycles). In our study, we found a positive relationship between specific leaf area, CWM and vineyard yield (Figure 6): communities dominated by species with high specific leaf area are linked to higher yield than communities dominated by species with low specific leaf area. This result, found for the first time in perennial crop systems like vineyards, allows direct testing of the trait–service link and the hypothesis presented in Figure 1B. This hypothesis should be tested on other ecosystem properties such as decomposition and mineralization. Our hypotheses are that intensive management practices, like tillage, act as

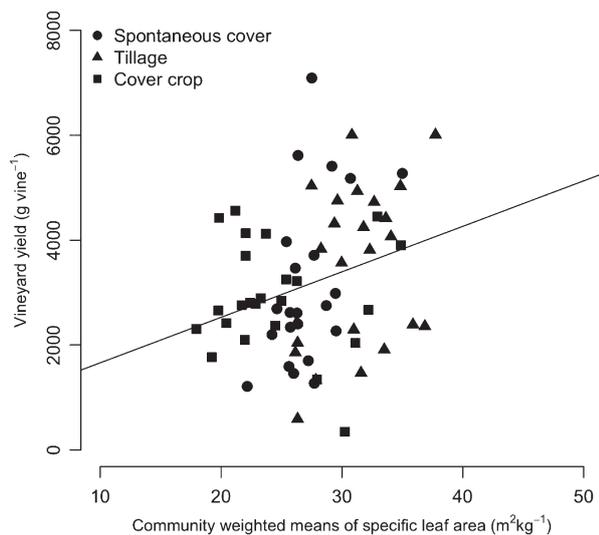


Figure 6. Relationship between communities weighted means of specific leaf area and vineyard yield across the disturbance–competition intensity gradient. Open white circles, tillage treatment communities; black circles, spontaneous vegetation communities; triangles, cover crop communities. Spearman correlation coefficient $r = 0.25^*$. Regression equation: $y = 86.79x + 792$ ($r^2 = 0.276$).

filters for species traits favouring high growth rates, rapid nutrient mobilization and then rapid decomposition and mineralization. As a consequence, resource availability is high and vineyard yield increases. Our results for yield did not clearly distinguish tillage treatment and spontaneous vegetation cover. There is a high variability in each treatment, which requires characterization of resources in more details for each community in order to interpret the results.

Conclusion and perspectives

In this paper, we introduced a trait-based framework to assess vineyard inter-row soil management. The case study was the first attempt to establish a direct relationship between functional traits and ecosystem services in perennial crop systems. The results confirm our initial objective that the functional characterization of community responses to different management practices could be a key issue to design the management of inter-row communities. As illustrated using the vineyard as our case study, this trait-based framework has the potential to improve the understanding of weed community assembly, integrate its effects on crop production and allow an adaptation of different soil management practices. Applying this framework requires us to:

- (i) Characterize and position the different management practices along a double gradient of disturbance and resource
- (ii) Recognize groups of species that respond in a similar way to a set of management practices
- (iii) Identify and measure traits that are closely related to functions and processes across the

resource and disturbance gradients (*response traits*) as different functional traits of important issues for different services and ecosystem processes (see Table 3);

- (iv) Compare the vegetation diversity and ecosystem function(s)/service(s) resulting from the different management practices;
- (v) Test the linkages between traits and services (*effect traits*) and establish quantitative relationships. These relationships would make it possible to use traits to scale from individual plants and communities to the ecosystem level function.

Our response-and-effect framework can help when choosing the best “ideotypes”, i.e. the species with the required traits to provide several services while limiting competition with the crop as proposed in Table 3. Our study is supported by a characterization of spontaneous flora but the results can be extended to design both sown and spontaneous cover-cropped grapevine systems. In the first case, this method can help to choose the most adequate cover crop species or mixture of cover crop species to sow and how to manage it. Yet, the added value of the plant trait-based response-and-effect framework lies in its ability to identify selective management practices that can drive the trajectories of the spontaneous community towards the best “ideotype”, so contributing to design more sustainable grapevine systems.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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