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

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**Running title:** Responses and effects of weed communities in vineyards inter-row soil management

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45

## **Abstract**

Biodiversity impacts ecosystem properties and ecosystem services provided by those ecosystems. In this respect, weeds have an important role in maintaining field biodiversity, when balanced with their potential negative impact on crop yield and quality. Trait-based approaches, originally developed in the field of comparative ecology, allow describing weed species responses to management practices in annual crop systems. Here, we aimed at extending the trait-based approach to the spontaneous vegetation of perennial cropping systems, such as vineyards. We adapted the response-effect framework for perennial cultures and especially the vegetation for different soil management practices (tillage, cover crops, spontaneous vegetation) considered as alternatives to the use of herbicides. Soil management practices act as environmental filters that determine the composition and structure of vegetation, which, in turn, modify grapevine growth conditions in the vineyard. We tested this approach in a Mediterranean vineyard where we characterized during 2 years the responses of different components of weed communities (specific and functional composition and dynamics) 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).

**Keywords:** cover crop, functional traits, tillage, vineyard, weed communities

## **Introduction**

Biodiversity impacts ecosystem properties and ecosystem services provided by those ecosystems (Cardinale et al. 2012; Diaz and Cabido 1997; Chapin et al. 2000; Tilman et al. 1997). The underlying hypothesis is that species differ in the efficiency of resource use (resource use complementarity) and/or in how they modify the surrounding environment in ways that impact other species (Wood et al. 2015; Cardinale et al. 2012). As a result, improving plant diversity (specific or genetic) in agricultural systems has been a key issue in agriculture over recent years (Litrice and Violle 2015; Tilman, Wedin, and Knops 1996; Cardinale et al. 2012). In this context, weeds have an important role in maintaining field biodiversity, when it is balanced with their potential negative impact on crop yield and quality (Storkey 2006). More precisely, weeds are a major problem in crop production either through competing for resources or 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 etc.). The use of key ecological concepts is an important requirement for quantifying the positive contribution of weeds to maintaining biodiversity and ecosystem services without compromising yield must therefore be set in the context of these dis-services associated with weeds (Storkey 2006). Related to this, to manage co-occurring to cultivated plant diversity (weeds, spontaneous vegetation or cover crops) it seems essential to identify assembly rules of complex weed communities and to recognize groups of species that similarly respond to a set of management practices, interact with biotic and biotic components of the agro-system or affect the ecosystem functioning (Navas 2012).

Several studies have focused mostly on the taxonomic characterization of the composition and the structure of weed communities occurring in cropping systems to predict their response to agricultural management practices (Fried, Norton, and Reboud 2008; Storkey and Westbury

2007). However, functional trait diversity, rather than the diversity of species *per se*, is a facet of biodiversity most directly related to species responses on different management practices and thus consequences to ecosystem functioning (Naeem and Wright 2003; Cadotte, Carscadden, and Mirotchnick 2011). Trait-based approaches, originally developed in the field of comparative ecology, have permitted to describe weed species responses to management practices in annual crop systems (Booth and Swanton, 2002; Gaba, Fried, Kazakou, Chauvel and Navas 2013; Garnier and Navas 2011; Gunton, Petit and Gaba 2011).

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; Steenwerth, Calderón-Orellana, Hanifin, Storm and Mcelrone 2016; Tesic, Keller and Hutton 2007) and none of them have used the trait-based approach. According to the response-effect framework (Fig. 1a; Lavorel and Garnier 2002; Lavorel, 2013; Suding et al., 2008), environmental drivers act as filters sorting species according to the value of traits (**response traits**), which results in a functional structure of communities impacting ecosystem functioning (**effect traits**). The ultimate goal of response-effect analyses should be the formulation of parsimonious quantitative relationships expressing the different components of each ecosystem function in relation to particular traits (Lavorel and Garnier 2002). These relationships would make it possible to use traits to scale from individual plants and the communities they form to the ecosystem level (Dawson and Chapin 1993). So, to apply this framework, it is important to use arguments about scaling through the community level by integrating two components: (1) how a community responds to changes, and (2) how that modified community affects ecosystem processes (Suding et al. 2008). This response-effect framework has been tested and successfully applied in grasslands to understand how the different levels of land-use impact ecosystem services through the

changes in vegetation but not yet 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 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). However, most research 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 adapt the response-effect framework for perennial cultures and more specifically the vegetation under different soil management practices (tillage, cover crops, spontaneous vegetation) considered as alternatives to the use of herbicides between rows. We hypothesized that soil management practices act as environmental filters, which determine the composition and structure of vegetation, which in turn modify grapevine growth conditions in the vineyard (Fig. 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).

Insert Figure 1, here

## **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 caused changes in weed management practices (Monteiro and Moreira, 2004; Moreira, 1994). Currently, grape growers can choose between two main weed control methods, alternative 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 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 can lead to undesirable competition for soil resources such as water and nitrogen (Celette, Gaudin, and Gary 2008) and result in a problem 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. (2013) proposed a comparative description of the environmental gradients created mainly by 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 & 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" (Fig. 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. 2013 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, however, disrupt competitive hierarchies by increasing levels of mortality and thus making free space available for 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 intermediate areas may disrupt competitive exclusion and allow establishment of new species in the disturbed patches (Wilson 1994).

Studies in annual crops systems have described tillage as a filter that influences weed species composition and weed seed distribution in the soil seed bank (for example Cardina, Herms and Doohan, 1991; Cousens and Moss 1990). 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 (Grime 2006), due to light, nutrient or water competition (Fig. 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 Fig. 2a, we assumed that the intensity of soil tillage (from no tillage treatments to conventional tillage treatments) corresponds to a disturbance 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 well implanted and thus dominant species) corresponds to a competition intensity gradient (for light, nutrient or soil water content).

Insert Figure 2 here

## **Effects of different inter-row management practices on communities' composition and structure 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) (we focus on non chemical management methods). Conflicting results were found considering the effects of tillage on plant diversity and composition, possibly as a result of community fluctuations rather than deterministic changes in community composition (for example Derksen, Lafond, Thomas, Loeppky and Swanton, 1993; Legere, Stevenson, & Vanasse, 2011; Gago, Cabaleiro, and García 2007 found that plant cover crop showed a much lower number of weed species, mostly therophytes (Beuret and Neury 1990; Maillet 1980) irrespective to 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 vigor. 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 and Liebman 1994, Liebman and Davis 2000) and non leguminous residues, such as cereal rye (Weston 1996).

On the other hand spontaneous cover treatment can be chosen as a costless tradeoff 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), 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.

Insert Table 1 here

### **Functional structure and species 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; Fried, Kazakou and Gaba 2012; Gunton et al. 2011; Navas 2012; Storkey 2004; 2006) 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 of different management practices so far (e.g. Barralis et al., 1983; Dastgheib and Frampton, 2000 for vineyards) while functional traits were only used very recently to assess the services of sown cover crop (Gamour et al. 2015).

According to the response-effect framework, response traits to environmental filters change community's functional structure and diversity and thus impact ecosystem processes via changes in the representation of ecosystem-effect traits (Suding et al. 2008; Fig. 1a). It has been assumed that the most abundant species are often more functionally important simply due to 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). 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 favorable season, low reproductive height), corresponding to the ruderal species strategy (R) (Grime 1979; Table 2). An intermediate disturbance condition favors the coexistence of competitive species and stress-tolerant species (due to the resources limitation) (Mackey and Currie 2001). Unproductive habitats select perennial species with slower plant growth, longer life spans, denser tissues, in which resources are conserved more

efficiently (stress-tolerant S). Stress-tolerant species, found in low stress, low disturbance habitats, allocate resources to maintenance and defenses, such as anti-herbivory (Grime 2001). Finally productive habitats (no disturbed and no stressed habitats) select mostly annual 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, relatively low seed production, and high allocation to leaf construction. They persist in high nutrient and low disturbance environments. Thus, in contrast to the denser tissues, low specific leaf area and concomitantly slow growth of stress-tolerators (Poorter and Jong 1999; Poorter and van der Werf 1998; 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 et al. 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, while 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 would be able to maintain. Alternatively, we assume that spontaneous species having different traits and using resources differently than the cover crop could also maintain (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) act as a 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 to less similar species in the communities according to the limiting similarity hypothesis (Fig. 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 result of species separate niches and thus complementary in resource use.

Insert Table 2 here

### **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 controlled by the traits of dominant species or/and functional diversity of communities (see Garnier et al. 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 used 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 *via* an increase in the decomposition and mineralization processes (as shown for tree species by Wardle et al. 2002). In order to expand

the trait-services approach to services such as pollination (with different trophic groups are 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.

Insert Table 3 here

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

In Mediterranean regions, adaptation to climate fluctuations is a recurrent management problem in agricultural production (Ripoche et al. 2011). In perennial systems, like vineyards, adaptation is possible through canopy management (Smart et al., 1991), fertilization, irrigation, or soil surface and intercropping management (Celette and Gary, 2006; Chifflet et al., 2006). However only 14% of vineyards in the Mediterranean regions are intercropped, (Mezière et al. 2009) as 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 associate plant diversity in three management practices and test their links with agroecosystem properties. This first attempt to adapt the trait-response framework to vineyards may permit to demonstrate how management practices can achieve target traits and those traits will achieve goals for the rates of ecosystem properties and services (as suggested at the theoretical framework of Wood et al. 2015). More precisely we tested the effect of three management practices (tillage, managed spontaneous vegetation and cover crop) commonly used in Mediterranean vineyards on different components of taxonomic and functional diversity.

The field experiment is detailed in (Guilpart, Metay, and Gary 2014). Grapevines (*Vitis vinifera* L. cv. Shiraz) were planted in 2002, in rows oriented NW–SE at a density of 3333 stocks per hectare (2.5 m × 1.2 m). Three treatments were designed to create a gradient of soil resources (water and nitrogen): (a) A first treatment was obtained by sowing a mix of annual medics (*Medicago truncatula*, *M. rigidula*, *M. polymorpha*) in the inter-row during autumn 2009 (cover crop treatment hereafter); (b) 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); (c) 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 vinestocks per row and 5 rows) whereas Spontaneous cover treatment composed of 74 vine stocks (37 vinestocks per row and 2 rows).

Depending on the regime of disturbance due to practical operations in the vineyard, weed sampling covers was conducted at several dates during a year, especially before and after treatments and at least two years to record weed communities 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; Tesic, Keller, and Hutton 2007b; King and Berry 2005). 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 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 (AIC; 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 2010) 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 species richness and abundance. We expected that tillage treatment would favor a small number of dominant species (low Shannon indices) whereas vegetation cover will favor 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 (Fig. 3). More precisely, spontaneous treatment showed the highest number of species with an average of 14 species per m<sup>2</sup> observed in all the sampling dates while tillage treatment harbours the lowest number of species and the highest variation across dates (Fig. 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 very abundant (Fig. 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. On the contrary, 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, X. 2010). Weed and cover crop biomass did not vary between the three treatments in April 2010 (Fig. 3c). Spontaneous and cover crop treatments did not

present significant differences during the three dates of measurements, however it is important to notice that cover crop treatment presented a big variability across 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.

Insert Figure 3 here

#### *Hypothesis 2: Functional structure of weed communities responds to management treatments*

The second hypothesis was about species response traits to different management practices: that tillage treatment will favor species with traits corresponding to ruderal strategy (high growth rate, traits favoring resources acquisition), whereas cover crop will favor 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 community-weighted means (CWM; Garnier et al. 2004) and 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 favored species with trait values associated to 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, the highest specific leaf area (SLA) values and late onset of flowering. The opposite pattern was found for species from the cover treatment (Fig. 4). 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 (Laliberté and Tylianakis 2012; Guerrero et al. 2014; Flynn et al. 2009) who showed that the intensification of land use reduced functional diversity and redundancy. We also tested whether tillage treatment (highly disturbed habitat), act as a filter resulting in the convergence of traits within communities whereas plant cover (sown or spontaneous) vegetation will result to less similar species in the communities with large trait variability. We found that spontaneous vegetation treatment showed highest functional richness whereas in tillage treatment functional richness decreased even if species richness increased, thus implying functional convergence (Fig. 4d). Communities in spontaneous vegetation treatment showing high functional divergence, which indicates a high degree of niche differentiation, and thus low resource competition. Thus communities with high functional divergence may have increased ecosystem function, especially improvement of soil fertility and nutrient cycling, as a result of more efficient resource use (N. W. H. Mason et al. 2005).

Insert Figure 4 here

### *Hypothesis 3: Species traits affect ecosystem properties*

We hypothesized that different soil management practices in the vineyards will affect vine growth and performance. Although, spontaneous cover is supposed to have a higher impact on vine yield compared to tillage; it is expected that the effect of the legume cover crop is intermediate after two years, since competition with the vines is compensated by an increase in nitrogen supply and that the presence or the vigor 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<sup>-1</sup> according the density of vines per ha) in spontaneous and tillage treatments versus around 2500 g/ vine (corresponding to 7.5 t grapes ha<sup>-1</sup>) in the cover treatment) (Fig. 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 SLA, which corresponds to resource use). Predawn 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 for tillage and spontaneous treatment respectively) (Fig.5b). Assimilable nitrogen in must was significantly higher at harvest at the tillage treatment (168 mg L<sup>-1</sup> versus 80 mg L<sup>-1</sup> and 105 mg L<sup>-1</sup> for spontaneous and cover treatment respectively). For the latter two, the assimilable nitrogen content in must is below the threshold of 140 mg L<sup>-1</sup> generally considered as nitrogen deficiency threshold (Casalta, Sablayrolles, and Salmon 2013). Cover treatment based on legumes did not show any improvement in vine nitrogen nutrition even if there is a slight increase (Fig. 5c) probably because of the water stress created by the cover crop. In this case, the most limiting factor is water (Fig. 5b).

Lavorel and Grigulis (2012) proposed a framework based on alpine grasslands, differing in their management regime, corresponding to a gradient of management intensity: intensive management practices (like mowing and fertilization), favor species with traits values associated to high resources acquisition (high specific leaf surface for example), and thus 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 (Fig. 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 testing directly the trait-service link and the hypothesis presented in Fig. 1b. This hypothesis should be tested on other ecosystem properties such as decomposition and mineralization as we hypothesize that intensive management practices, like tillage, acting like filter, for species traits favoring high growth rates, rapid nutrient mobilization and then rapid decomposition and mineralization. As a consequence, resources availability is high and vineyard yield increases. Our results did not clearly distinguish tillage treatment and spontaneous vegetation cover. There is a high variability in each treatment, which requires characterizing resources in more details for each community to interpret the results.

Insert Figure 6 here.

## **Conclusion and perspectives**

In conclusion, both spontaneous and tillage treatments appeared acceptable as far as yield was maintained. The advantage of the tillage treatment on one hand was that it seemed efficiently able to limit weed growth (see biomass data in Fig. 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 tradeoff for the winegrowers between improving soil properties, limiting mechanical work and maintaining vine production. This case study was the first demonstration of a direct relationship between functional traits and ecosystem services in perennial crop systems. This result confirms our initial hypothesis that the functional characterization of communities' responses to different management practices is a key issue to the management of inter-row communities, as traits with certain functional properties (e.g., ability to fix N<sub>2</sub>) can be chosen in order to select or promote spontaneous species with those traits.

In this paper, we introduced a trait-based framework to assess vineyard inter-row soil management. As demonstrated in our case study, this framework has the potential to improve the understanding of weed community assembly and allow an adaptation of different soil management practices. According to this framework, it is essential to:

- (i) Characterize different management practices as disturbance and resource gradients in order to identify which traits may respond to these gradients;
- (ii) Quantify resources availability and disturbance intensity; this will inform on which factors determine the abundance and species richness. For associated diversity, it is important to take the periodicity of disturbance turnover into account;
- (iii) Identify and measure traits that are closely related to functions and processes across the gradients (response traits) as different functional traits are important for different services and ecosystem processes (see Table 3);
- (iv) Measure the processes and services;
- (v) Compare the diversity and ecosystem function(s)/service(s) of different management practices;
- (vi) Test the linkages between traits and services (effect traits) and propose quantitative relationships. These relationships would make it possible to use traits to scale from individual plants and the communities they form to the ecosystem level function.

Given the results obtained, different “ideotypes”, i.e. species with required traits, providing several services, could be proposed considering both grapegrower’s objectives. The choice of those “ideotypes” will contribute to design more sustainable grapevine systems. More precisely based on Table 3 we propose species with:

- 516 (i) High specific leaf area and low dry matter content as well as N fixing species  
517 which will improve soil fertility and nutrient cycling;
- 518 (ii) High root density in order to support water regulation;
- 519 (iii) Rosette and herbaceous species with high growth rate which will support soil  
520 stability.
- 521  
522

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