

1

2 **Incorporating plant functional diversity effects in ecosystem service**  
3 **assessments**

4

5 Sandra Díaz<sup>\*†</sup>, Sandra Lavorel<sup>‡</sup>, Francesco de Bello<sup>‡</sup>, Fabien Quétier<sup>†,‡</sup>, Karl Grigulis<sup>‡</sup>, and T.  
6 Matthew Robson<sup>¶,‡</sup>

7

8 <sup>\*</sup>IMBIV (CONICET-UNC), Universidad Nacional de Córdoba, Casilla de Correo 495, 5000  
9 Córdoba, Argentina; <sup>‡</sup> Laboratoire d'Ecologie Alpine, UMR 5553 CNRS and Station Alpine  
10 Joseph Fourier, UMS 2925 CNRS, Université Joseph Fourier. BP 53, F-38042 Grenoble,  
11 Cedex 09, France; <sup>¶</sup> Centro de Investigación Forestal (CIFOR), Instituto Nacional de  
12 Investigación y Tecnología Agraria y Alimentaria (INIA), Carretera de La Coruña km 7.5,  
13 Madrid 28040, Spain

14 <sup>†</sup>To whom correspondence should be addressed. E-mail: sdiaz@com.uncor.edu; Fax +54 351  
15 4332104; Phone +54 351 4331097

16

17 Number of text pages: 19

18 Number of figures: 1

19 Number of tables: 1

20 Number of words in the abstract: 244

21 Total number of characters in the paper: 41440 excluding fig. and table; aprox. 47720  
22 including them

23

24 Abbreviations: AGB, ANPP, CWM, EP, ES, FD<sub>veg</sub>, LDMC, LHS, LNC, LTS, NNI, N:P,  
25 Phen, RB, RL, RNC, SANPP, SLA, SRL, VH, WHC

1 **Abstract**

2 Global environmental change and widespread land change affect the sustained provision of a  
3 wide set of ecosystem services. Although modifications in ecosystem services result mostly  
4 from changes in abiotic drivers, they are also modulated by changes in the functional diversity  
5 of biological communities (the value, range and relative abundance of functional traits in a  
6 given ecosystem). Consequently indirect biotic effects introduce uncertainty in our capacity to  
7 predict the consequences of environmental change on ecosystem services. The focus of this  
8 article is on how functional diversity affects ecosystem properties that are directly relevant to  
9 ecosystem services, once the direct effects of environmental conditions have been accounted  
10 for. We propose a systematic way for progressing in understanding effects of land cover  
11 change on these relevant ecosystem properties. Models on links between ecosystem properties  
12 and the local average, range and distribution of plant trait values are numerous, but they have  
13 been scattered in the literature, with varying degrees of empirical support. Here we articulate  
14 them for the first time in a single conceptual and methodological framework that allows  
15 testing them in combination. We illustrate our approach with examples from the literature and  
16 apply the proposed framework to a grassland system in the central French Alps in which  
17 functional diversity, by responding to land change, alters the provision of ecosystem services  
18 important to local stakeholders. We claim that our framework contributes to open a new area  
19 of research at the interface of land change science and fundamental ecology.

20

21 **Keywords:** community weighted mean, diversity, functional divergence, land change, mass  
22 ratio hypothesis, plant functional traits

## 1 **Introduction**

2 Global environmental changes, including land-use and land-cover changes, have considerable  
3 impacts on the ecological properties of ecosystems and thereby on the ecosystem services that  
4 societies derive from them (1). Although links between ecosystem properties (EP) and  
5 ecosystem services (ES) are not always trivial, many ES and their changes can be reasonably  
6 quantified by EP that are routinely measured in ecological studies (2). In this article we will  
7 refer to these collectively as ecosystem properties (EP). Global change effects on EP can be  
8 direct, e.g. through their effects on metabolism and behavior of organisms. Global change  
9 drivers and especially land use can also influence EP indirectly through their impacts on  
10 biodiversity, either through their effects on local biota, or by altering the ability of organisms  
11 to disperse through landscapes. Changes in biodiversity relevant to EP are manifested through  
12 changes in plant functional diversity (FD), i.e. the value, range and relative abundance of plant  
13 functional traits in a given ecosystem (2). Although often subtler than direct effects (3, 4),  
14 these indirect biotic effects remain a major source of uncertainty in predicting the impacts of  
15 global change on ES provision.

16 Conceptual models accounting for links between the functional trait values of local plant  
17 communities on the one hand, and EP on the other hand are scattered in the literature and the  
18 conceptual connections between them are not always clear. For the first time, we articulate the  
19 most important of those models into a small number of logical steps and propose a generic  
20 procedure to reduce uncertainty in the prediction of EP in a land change context (Fig. 1).  
21 Reducing this uncertainty has important theoretical and applied implications. First, although  
22 there is increasing consensus on the fact that plant functional traits strongly affect EP and  
23 resulting ES (5, 6), very little is known about the role of different components of FD, such as  
24 the average and frequency distribution of plant trait values (2, 7). Our generic method allows  
25 to identify cases in which EP can be satisfactorily predicted from different FD components,  
26 and to quantify their relative importance. Second, the reduction of uncertainty will help  
27 identify the ES most vulnerable to biodiversity changes (1, 6, 8, 9).

28

### 29 **Functional Diversity at the interface between global change and ecosystem properties.**

30 FD can be quantified by two main components. First, a community weighted mean value  
31 (hereafter CWM) can be calculated for each trait as the average of trait values in the  
32 community, weighted by the relative abundance of the species carrying each value (10). This  
33 metric represents the expected functional trait value of a random community sample, often

1 understood as the dominant traits in a community. Second, the distribution of trait values  
2 within the community can be expressed through various metrics, among which functional  
3 divergence (hereafter FD<sub>v</sub>) is increasingly used (11). FD can affect ES through its effect on  
4 EP, notably major biogeochemical processes related to carbon, nutrient and water cycling (2,  
5 7), and disturbance regimes (12). All the main candidate mechanisms by which diversity is  
6 expected to act on EP (the selection effect, the niche complementarity effect and the insurance  
7 effect) (6, 8) strongly depend on the functional attributes of local communities that are central  
8 to our procedure (7, 13).

9  
10 **The mass ratio hypothesis: A cornerstone to FD-EP relationships.** The mass ratio  
11 hypothesis (3) states that ecosystem functioning, at a given point in time, is determined to a  
12 large extent by the trait values of the dominant contributors to the plant biomass. According to  
13 this hypothesis, EP should be predictable from the CWM of traits with proven links with  
14 resource capture, usage and release at the individual and ecosystem levels.

15 The mass ratio hypothesis is well supported by both theory and empirical evidence. There  
16 are well-developed conceptual models linking plant and especially leaf traits with EP such as  
17 primary productivity, nutrient cycling, and trophic transfer to herbivores (12, 14-17).  
18 Consistent with these models an important body of literature clearly points to a relatively  
19 small set of plant traits that are strongly and consistently linked to these major EP across  
20 biomes, ecosystems and floras (15, 18). In the case of primary producers, for example, there is  
21 little disagreement in the identification of the key functional traits that are most likely to  
22 account for these EP. A significant amount of evidence for these relationships has been  
23 produced at the level of species for productivity, decomposition, nutrient cycling or suitability  
24 to herbivores (18-22). Direct evidence for the mass ratio at the community level is however  
25 more limited (23-26), although a number of studies that do not directly test the effects of  
26 CWM do suggest that EP are related to the traits of dominant species or functional groups (3,  
27 19, 25, 27-29). Regulating and supporting ES derived from local biogeochemistry therefore  
28 should often depend strongly on CWM and thus on the traits of the most dominant species (2,  
29 6), implying that the distribution (i.e., FD<sub>v</sub>) of plant trait values may only play a secondary  
30 role. Nevertheless, there are a number of situations in which the relationship between CWM  
31 and EP is poor, increasing prediction uncertainty. In such cases other components of  
32 functional diversity, such as FD<sub>v</sub>, might exert relatively strong effects.

## 1 **Results**

### 2 *Reducing uncertainty in six steps*

3 Assuming that within a given land system, the major land cover types could be sampled and  
4 their vegetation described through the relative abundance of species as well as the species-  
5 specific values of key traits (e.g. from plant trait databases), we propose a formal procedure  
6 for (a) identifying the major abiotic and biotic factors that affect EP relevant to ES, and (b)  
7 constructing useful predictive models of these relevant EP (Fig. 1).

8 The procedure is organized in two stages, comprising 6 steps. Stage I uses 4 steps to test  
9 sequentially for the effects of individual sets of factors. It starts by testing abiotic factors as  
10 drivers of EP (Step 1), proceeds with community-aggregated functional properties (CWM;  
11 Step 2), that is, vegetation is simplified into an average trait value that is strongly determined  
12 by the functional trait values of the more abundant species. In Step 3, additional biotic  
13 complexity is taken into account through the variance in the traits of the community (FDvg;  
14 Step 3). Finally, the procedure explores remaining idiosyncratic effects of particular species  
15 (Step 4). As well as proceeding in increasing degree of conceptual complexity, this logic  
16 reflects current knowledge on the most common hierarchy between abiotic and biotic drivers  
17 of EP and ES (2, 4).

18 While taken individually each step in Stage I has already received considerable interest in  
19 the literature, we propose to go further and examine them in combination. Thus, Stage II first  
20 combines all significant variables from Steps 1-4 using a step-wise procedure (Step 5). This  
21 bottom-up approach reflects the choice of being hypothesis-driven in our analysis. Finally,  
22 Step 6 explores the possible discontinuous effects of FD or other variables, thereby accounting  
23 for remaining unexplained variance.

24

### 25 *Stage I: Identifying abiotic and biotic drivers of EP and ES*

26 **Step 1: Direct effects of abiotic factors.** Although the novelty of the procedure proposed here  
27 lies in taking into account indirect biotic effects on EP, abiotic variables often explain a  
28 significant amount of variation in EP. This is especially the case when sampled land cover  
29 types span substantial variations in climate or soil, e.g. driven by topography.

30 The first step in our procedure should thus check for a continuous relationship linking  
31 abiotic factors such as temperature, moisture, or soil chemical quality as independent variables  
32 against EP as a response variable (Fig 1, Step 1). For our approach, this could be seen as an  
33 initial null hypothesis, where biodiversity effects are of no detectable importance to the

1 prediction of EP. The abiotic factor(s) should be measurable at present, but their causes may  
2 be found at present or alternatively be traced back to past conditions or events. There are many  
3 examples of abiotic effects on key EP. Water availability affects litter decomposition (14).  
4 Topography is an important determinant of soil stability (30). Primary productivity and  
5 nutrient cycling are strongly affected by soil fertility and/or water holding capacity (31, 32),  
6 abiotic factors which are in turn affected by land use, including fire regimes (33). Numerous  
7 studies have also demonstrated strong legacies of past land use (e.g. ploughing) or disturbance  
8 regime (e.g. fire) on soils that carry over to current EP and ES. For example, past ploughing  
9 can affect both soil water holding capacity and fertility for decades or centuries after its  
10 discontinuation, and thereby affect EP such as nutrient cycling, primary productivity or litter  
11 decomposition (34-36).

12

13 **Step 2: Effects of Community Functional Properties.** In cases where the variance in EP  
14 cannot be satisfactorily explained by abiotic factors alone, one can assume that FD exerts non-  
15 negligible effects on EP. On that basis, we propose to start the process by testing for a  
16 continuous relationship based on the mass ratio hypothesis (Fig. 1, Step 2). Under Model 2,  
17 the relationship between EP and key plant functional trait CWM should be statistically  
18 significant. It could be accounted for by the CWM of a single trait or by a combination of the  
19 CWM of several traits (i.e. in Step 2  $CWM_i$  could vary from 1 to  $n$ , being  $n$  the number of  
20 traits considered). Both cases conceptually match the mass ratio hypothesis, with the second  
21 alternative putting more emphasis on trait syndromes (22) rather than single traits. Some  
22 examples of CWM strongly influencing EP and ES have been given in the previous section  
23 presenting the mass ratio hypothesis. Other examples include the often dramatic alteration of  
24 EP and ES through changes in CWM due to the expansion of invasive species with functional  
25 traits different from those of the native flora (37). CWM of single traits may be sufficient to  
26 explain the variance in EP. For example specific productivity and litter decomposition have  
27 been explained by single leaf traits (23), and decomposition rate has been explained by leaf  
28 lignin:N ratio or leaf tensile strength (14). However, it is common for multiple traits to affect a  
29 single EP (31). In those cases, the variance in EP is better explained by combining multiple  
30 traits, such as whole-plant and leaf traits, or aboveground and root traits. Here uncertainty in  
31 the prediction of EF from CWM is reduced by the inclusion of one or more traits, but not by  
32 adding information on the distribution of trait values (next step).

33

1 **Step 3: Effects of the distribution of trait values.** In cases where abiotic factors or CWM of  
2 a single or multiple traits do not satisfactorily explain the variance in EP, the effects of the  
3 distribution of trait values (measured for example by FDvg) should be explored (Fig. 1, Step  
4 3). Examples of ecosystem effects attributed to differences in trait values among coexisting  
5 species are common in the literature. They include, for instance, enhanced biomass production  
6 and soil fertility by mixtures of species with and without nitrogen-fixing symbionts (38, 39),  
7 with different leafing phenology (28), different rooting depths (40), or different canopy  
8 heights and degrees of shade tolerance (41). Another example is the alteration of litter  
9 decomposition and thus soil nutrient availability by litter mixing effects associated to the joint  
10 presence of fast-decomposing and slow-decomposing plants (42). Pollination of a particular  
11 species is influenced by the distribution of traits values in the surrounding community (9). In  
12 these cases where the inclusion of FDvg significantly improves the predictive model (Model  
13 3), uncertainty in the prediction of EP can be reduced by the consideration of the distribution  
14 across species of values of one or more plant traits.

15

16 **Step 4: Idiosyncratic effects of particular species.** If EP cannot be satisfactorily explained  
17 by the weighted mean or distribution of the plant traits measured across the different land  
18 cover types, then it is possible that EP is driven by the local abundance of particular plant  
19 species (Fig. 1, Step 4). In other words, EP is associated in a significant and continuous way to  
20 the abundance of particular plant species, although the specific reason why this species is  
21 causing the effect is not obvious to the researcher, and sometimes can only be known *a*  
22 *posteriori*. These effects could be due to functional traits whose links with the EP of interest  
23 are not obvious from first principles or the literature, and thus were not been measured. For  
24 example, biomass production and nutrient retention in the soil of a grassland was best  
25 explained by the colonization ability, rather than by expected traits associated with the nutrient  
26 use strategies among species present within the local community (43). In the absence of data  
27 on colonization ability, the local abundance of certain species could assist in reducing  
28 uncertainty in predicting EP. Idiosyncratic effects could also be due to unknown species  
29 interactions with other plants, animals or micro-organisms (44). Idiosyncratic species effects  
30 can also be examined in an exploratory mode focusing on species that may strongly respond to  
31 environmental change. Combined effects of several species may be tested after individual  
32 effects are demonstrated (19, 27, 31).

33

1 *Stage II: Finding the best predictive model*

2 **Step 5: Combining abiotic factors and FD components.** Individual factors tested in Steps 1-  
3 4 may provide significant models of EP, yet these models might explain only a fraction of the  
4 variance in EP. It is therefore necessary to test various combinations of significant abiotic and  
5 biotic factors, and to retain the final model that explains the largest amount of variance in the  
6 most parsimonious manner (Step 5). This combination may lead to the rejection of some  
7 effects of FD components that are significant when tested individually (i.e. colinearity). In  
8 particular if FD components (CWM and/or FDvg) are significantly correlated with one or  
9 several abiotic factor(s) affecting EP (Step 1), then the explanatory power of the total model  
10 may not be significantly improved by the addition of FD components. In this case one can  
11 conclude that abiotic factors affect EP through changes in FD. However if the explanatory  
12 power of the model is not significantly improved by the addition of FD components, these can  
13 be considered as irrelevant for practical purposes. That is, uncertainty in the prediction of EP  
14 and ES cannot be reduced by additional information on plant traits.

15 There are only few examples in the literature where the effects of abiotic factors and  
16 several FD components have been explored simultaneously. As a notable exception, litter  
17 decomposition is often best explained by a combination of climatic variables and CWM of leaf  
18 traits such as nutrient concentration (14). As a result, the effects of nitrogen addition (e.g. by  
19 atmospheric deposition or through management) often depend on CWM of those leaf traits  
20 (45). Productivity is also the complex outcome of climate, management (e.g. fertilization),  
21 trait values of dominants species, and sometimes various effects of species richness or trait  
22 distribution (25, 28, 29, 38, 39). Most studies however, especially the majority of those  
23 considering effects of species richness on productivity, have not conducted a systematic  
24 analysis of the different components proposed in our model.

25 We suggest building the model with those variables identified in Steps 1–4, using a step-  
26 wise process whereby additional biotic complexity is progressively added to the model until a  
27 satisfactory level of predictive power is reached (Model 5).

28

29 **Step 6: Discontinuous effect of CWM or trait distribution on EF.** In all models discussed  
30 so far, single abiotic factors and/or FD components, or their combinations, helped explain EP.  
31 There can be cases, however, in which none of Steps 1-5 yield a satisfactory model of EP. A  
32 plausible alternative explanation here could be that EP is strongly driven by a biotic or abiotic  
33 factor, but their relationship is discontinuous (Model 6 in Fig 1). For example, in some

1 grasslands soil nitrogen losses depend in a discontinuous way on the C:N ratio of dominant  
2 grasses (46). Flammability of ecosystems also has a strongly discontinuous relationship with  
3 the abundance of flammable species (47). The presence of key species (Step 4) can further  
4 result in discontinuous biotic effects on EP. In order to identify the point of discontinuity  
5 (threshold T in Model 6, Fig. 1), more intensive sampling of the gradient(s) and experimental  
6 and/or modeling approaches are often needed.

7  
8 *Case study: Functional diversity, current and future ecosystem services in subalpine*  
9 *grasslands*

10 We used a previously published data set depicting changes in FD and EP in subalpine  
11 grasslands under different combinations of past and present land use (26, 48, 49). Key  
12 ecosystem services of importance to regional stakeholders, including farmers, other local  
13 residents and tourists, were related to grassland EP (Table 1) (49). The data set was submitted  
14 to the six-step analysis to search for the best model explaining ecosystem service delivery  
15 from abiotic factors and FD components. Results on the significant factors identified via  
16 General Linear Models are presented in Table 1. Below we highlight three cases where  
17 different abiotic or FD factors explain variations in EP relevant to the ES identified in the land  
18 system.

19  
20 **Case 1.** Two EP relevant to fodder production, aboveground net primary productivity (ANPP)  
21 and specific aboveground net primary productivity (SANPP), were best explained by a single  
22 abiotic variable reflecting soil nitrogen fertility, the nitrogen nutrition index (NNI) (Step 1 in  
23 Table 1). Although ANPP was significantly related to the variety of ways in which plants  
24 acquire light, reflected by the distribution within communities of vegetative height  
25 (FDvg\_VH), and of leaf nitrogen content (FDvg\_LNC; marginally significant) (Step 3), these  
26 terms were not retained in the most parsimonious final model (Step 5) because they were no  
27 longer significant after effects of NNI were included. Here, the EP (SANPP) is thus driven by  
28 direct effects of abiotic factors (NNI) and FD components can be ignored in the final model.  
29 Overall, models explained less than 50% of the total variance and were not improved by the  
30 inclusion of idiosyncratic effects such as the abundance of *Festuca paniculata* (Step 4), a  
31 species that sequesters nutrients in large quantities of slowly decomposing litter (26). No  
32 discontinuity was detected by visual inspection of EP-CWM or EP-FDvg graphs (Step 6).

1 Standing green aboveground biomass (AGB) was an extreme case, where no suitable model  
2 could be found across the 5 steps. However, when considering mown fields alone, AGB was  
3 linearly related to mean community leaf nitrogen content (CWM\_LNC), i.e. there was a  
4 discontinuous relationship conditional on current management (Step 6). Hence, fodder  
5 production was largely independent of FD.

6 **Case 2.** Litter accumulation was identified by stakeholders as having a negative effect on a  
7 range of ES including prevention of snow gliding, cultural heritage, and aesthetic value and  
8 provision of habitat for butterflies. In contrast to fodder production, EP associated with litter  
9 accumulation were best explained by CWM of leaf traits (leaf nitrogen and lignin contents;  
10 leaf tensile strength) and CWM of vegetative height in the case of total accumulated litter in  
11 the spring (Step 2). A marginally significant relationship was also found with the distribution  
12 of vegetative height within communities (Step 3), but this term was eliminated from the final  
13 model based on parsimony criteria. Both for standing litter (the pool), and litter  
14 decomposability (the flux), FD components explained a very high proportion of the total  
15 variance. In the case of the ES maintenance of soil fertility, CWM of leaf and root traits  
16 explained a very high proportion of the total variance (Step 2). Hence, services associated by  
17 stakeholders with litter accumulation and soil fertility were strongly related to average  
18 functional properties of the vegetation, providing support for the mass ratio hypothesis.

19 **Case 3.** Finally, sustained fodder production of green fodder through summer, which was  
20 associated with soil water content (SWC) in the summer period, illustrated the case of a  
21 complex model associating both abiotic and functional diversity factors. SWC was explained  
22 by local soil conditions determining water holding capacity and by an additional aboveground  
23 biomass term that accounted for direct biophysical effects of aboveground biomass on soil  
24 evaporation (water conservation) and plant transpiration (water demand). However, as shown  
25 in Case 1, no significant model was found relating aboveground biomass to either local abiotic  
26 conditions or FD components. Effects of community-level averages of leaf area (net positive  
27 effect representing reduction of soil evaporation) and root length (negative effect representing  
28 water uptake) were significant and included in the final model. The latter explained a very  
29 high proportion of the total variance. Hence, the prolonged delivery of green fodder depended  
30 on the combination of local abiotic factors, their effects on aboveground standing biomass,  
31 and average functional properties of the vegetation.

1 **Projecting ES delivery under land change scenarios.** The quantitative models produced can  
2 be applied to make projections of the future delivery of the corresponding ES (49). ES  
3 associated with trait values of the dominant species (Case 2 above) can be projected from the  
4 response of CWM to changes in grassland management (26). At the same time, FD was also  
5 an important component for the prediction of sustained production of green fodder through the  
6 summer, in addition to strong effects of soil water holding capacity. Because historical  
7 ploughing led to soil loss and increased stoniness, thereby decreased WHC, this land-use  
8 legacy will persist in the next decades. Changes in this ES will therefore mostly reflect  
9 management effects on CWM of plant traits. In contrast, future changes in peak fodder  
10 production will be directly driven by changes in fertilization and other practices affecting  
11 fertility (e.g. export of nutrients through mowing), with no detectable FD effects. These may  
12 however be effective over the long term through feedbacks of FD on soil fertility via the  
13 nitrogen cycle (21).

14

## 15 **Discussion**

16 ES are the key conceptual link between social evaluations of ecosystems and their EP. While a  
17 wealth of information is available on land cover change both in the form of current vegetation  
18 maps and as scenario-based projections, few tools exist for translating this information into  
19 relevant indicators of EP or ES provision. Moreover, those studies that do address this  
20 question often do so for individual components of FD or specific EP. Here we propose a way  
21 to address them in combination and assess the relative effects of both abiotic and biotic  
22 factors. Applying the procedure presented here permits a quantitative assessment of the links  
23 between land cover changes and the services provided by affected ecosystems. In this way it  
24 contributes to open a new area of research, at the interface of land change science and  
25 biodiversity research.

26 **Reducing uncertainty in the prediction of ES delivery in response to environmental**  
27 **change.** Our case study illustrates the variety of ways in which EP underlying the delivery of  
28 ES can be related to abiotic factors and different components of FD, and how this knowledge  
29 can be used to project future ES delivery. In the specific example of the subalpine grasslands,  
30 when FD was involved, there was support for the mass ratio hypothesis, as community-level  
31 averages (CWM) rather than the distribution (quantified here by FDvg) of traits ultimately  
32 explained EP. The links between CWM of plant traits and EP are strong and widespread, as

1 shown by theory and accumulating empirical evidence under contrasting ecological and  
2 biogeographical contexts. However, in some cases other components of FD can reduce our  
3 uncertainty in the prediction of EP (2, 8). Finally, as shown in the case study, there are also  
4 cases in which the knowledge of FD does not decrease uncertainty with respect to EP and  
5 abiotic factors are sufficient for practical purposes. Our objective here is therefore to highlight  
6 the fact that the prediction ES from FD is a tractable yet complex task, and that measuring  
7 several components of FD can be useful. In this context, the main strength of our method is to  
8 provide a generic procedure for selecting models and ranking FD components by their  
9 importance to local EP and ES in different land systems.

10 While we have applied the proposed framework to plants for demonstration, we expect it to  
11 be applicable to other organisms and associated ES (e.g. insect diversity and pollination or  
12 crop protection; soil diversity and soil fertility). As a matter of fact, some ES (e.g. pollination,  
13 nutrient cycling) will require the combined consideration of FD across trophic levels (9, 31),  
14 short of which uncertainty in EP can not be reduced from plant FD alone. This should make it  
15 possible to gain a more precise understanding of how much biodiversity needs to be taken into  
16 account in order to predict changes in ES and human well-being under global change  
17 scenarios.

18 It should be noted that, while it can rank different FD components in term of explained  
19 variation in EP and ES, our method is not designed for the critical testing of different  
20 *mechanisms* underlying such FD effects. The mass ratio and idiosyncratic species effect  
21 models have been theoretically linked to the ‘selection’ mechanism, whereas the model that  
22 focuses on FDvg, by stressing the presence of a variety of functional trait values, can be seen  
23 as linked to the ‘niche complementarity effect’ (which also includes facilitation) (6, 7). Rather  
24 than providing a crucial test for these mechanisms, our method explores whether there are  
25 recurrent combinations of abiotic and FD factors that explain EP for different ES, in different  
26 ecosystem types and at different spatial scales.

27 **Practical implications and perspectives.** To link land cover changes to changes in ES, our  
28 procedure requires data on both the relative abundance of species in the different land cover  
29 types under investigation and plant traits of the dominant species. Recording species lists is  
30 often easier than measuring their relative abundance and trait values, yet our approach  
31 provides one more reason for compiling such databases on the basis of the rich yet scattered  
32 information available (50).

1 Assessing the ES consequences of land change also requires its interpretation in terms of  
2 land cover, with corresponding data on abiotic and FD factors. Projections of CWM response  
3 to environmental change are currently well advanced (51), but projections of the responses of  
4 community functional structure (7, 52) and FDvg on the one hand, or projections depicting  
5 discontinuities such as those described in Step 6, on the other hand, are still in their infancy.

6 Adequate societal response to global change requires quantitative assessments of the ES  
7 consequences of land change alternatives (1). In this context, our approach offers an  
8 innovative way to develop quantitative predictive models of land cover change impacts on ES.  
9 By explicitly including FD effects on EP and ES in these models, our procedure also allows  
10 for a formal incorporation of biodiversity as a driving factor in the sensitivity of ES to global  
11 environmental change.

## 12 13 **Methods**

14 **Study site and field measurements.** The Lautaret study site is located in on the south-facing  
15 slopes of Villar d'Arène, central French Alps. The climate is subalpine with a strong  
16 continental influence and the soil is sandy-loam over a calc-shale bedrock. Past and current  
17 land use were analyzed to identify dominant combinations, referred to as 'land use states'. The  
18 five most common land use states were characterized by the presence (terraces) or absence  
19 (traditional grasslands) of past ploughing, and current grassland management: mown and  
20 fertilized terraces, mown but un-fertilized terraces, un-mown and lightly grazed terraces,  
21 mown grasslands, and un-mown and lightly grazed grasslands (26). Fifteen grasslands  
22 representative of the 5 states (3 grasslands per state) were surveyed in June-July 2003 for  
23 floristic composition (species relative abundances), plant functional traits at the population  
24 level, and soil parameters (17)). Community -level averages for root biomass (RB), root length  
25 (RL), specific root length (SRL) and root nitrogen content, stratified by depth, were measured  
26 monthly during 2005 (48). Soil water holding capacity (WHC) was calculated from soil  
27 texture and structural data using the SPAW model (53). Fertility was assessed by the Nitrogen  
28 Nutrition Index (NNI), which quantifies actual nitrogen availability for plant growth through  
29 the dilution of nitrogen in closed canopies (54). Disturbance regimes were quantified using  
30 disturbance date (expressed in degree days), and the percentage of biomass harvested or  
31 alternatively the percentage height loss as measures of disturbance intensity (26).

1 **Ecosystem properties.** Biomass stocks, primary productivity (ANPP and the derived Specific  
2 Aboveground Net Primary Productivity, SANPP) (23), litter accumulation and decomposition  
3 were quantified during the season of 2004 following standardized protocols (23, 26). The leaf  
4 lignin:N ratio and decomposability of litter were determined for samples collected in July  
5 2003 (14). Components of the nitrogen cycle including total nitrogen pools, available nitrates  
6 (estimated with resin bags), and microbial nitrification and denitrification potentials were  
7 quantified throughout the 2004 and 2005 seasons (36). Finally, effects of vegetation on soil  
8 volumetric water content were assessed experimentally by a vegetation removal experiment in  
9 2005 and repeated measurements through the growing season of soil volumetric water content  
10 in vegetated versus un-vegetated plots (48).

11 **Quantification of functional diversity.** Plant functional diversity within each grassland was  
12 quantified using two metrics: CWM trait values calculated using specie's relative abundance  
13 (23), and functional divergence (FDvg) quantified using a modification of Rao's index that  
14 takes into account intra-specific trait variability (52). These two metrics were calculated for:  
15 vegetative height (VH), Specific Leaf Area (SLA), Leaf Dry Matter Content (LDMC), Leaf  
16 Nitrogen Content (LNC), Leaf Nitrogen to Phosphorus ratio (N:P), Leaf tensile strength (LTS)  
17 and flowering phenology (Phen). Root traits and Lignin:N ratio were available only as  
18 aggregated values. Finally we combined SLA, vegetative height and seed mass as a single  
19 functional diversity index representative of species LHS strategies (53) by averaging FDvg  
20 across these three traits.

21 **Statistical analysis.** We tested the relationships between ecosystem properties and functional  
22 diversity using General Linear Models (GenStat 9.0<sup>®</sup>) in the 6 steps of our proposed  
23 procedure. For each of the 6 steps we proceeded preferentially based on expert knowledge  
24 about abiotic factors and traits relevant to the ecosystem property of interest.

25 Step 1: Effects of fertility (represented by NNI), soil water holding capacity (WHC) were  
26 first tested individually, then in combination. Effects of disturbance date or intensity on EP  
27 were tested in (26) but were not significant. We thus chose not to include them in this analysis.

28 Step 2: We used an ascending procedure testing (a) CWM for individual traits and then (b)  
29 combining significant traits.

30 Step 3: We included FDvg of individual traits into previously selected models (significant  
31 terms only), either for traits already significant or additional traits.

1 Step 4: If no significant effects could be found in Steps 2 and 3 we included the abundance  
2 of *Festuca paniculata*, the grass species that strongly dominates un-mown grasslands and is  
3 seen as a successional dead end (26). Our previous analyses highlighted the effects of this  
4 species' abundance on ecosystem properties and services identified by local stakeholders (49).

5 Steps 1-4 were completed sequentially, then in Step 5 all significant terms from Steps 1-4  
6 were combined in a step-wise ascending procedure. The most parsimonious model was  
7 selected using the Akaike criterion.

8 Step 6: If none of the linear models from steps 1-4 (involving functional diversity metrics,  
9 abiotic factors and abundance of *Festuca paniculata*) were satisfactory, we re-inspected data  
10 for possible discontinuities.

### 11 12 13 **Acknowledgements**

14 We thank the organizers of the Missillac Workshop, hosted by the W.A. Beling Family and  
15 funded by the Borchard Foundation, for stimulating discussions that led to this article. Work  
16 was supported by the Inter-American Institute for Global Change Research (IAI) CRN 2015  
17 which is supported by the US National Science Foundation (Grant GEO-0452325), the  
18 European Union RUBICODE Project, CONICET and FONCyT.

### 19 20 **References**

- 21 1. Assessment, M. E. (2005) *Ecosystems and human well-being: Biodiversity synthesis* (World  
22 Resources Institute, Washington (D. C.)), pp. 86.
- 23 2. Diaz, S., Lavorel, S., Chapin, F. S., Tecco, P. A., Gurvich, D. E. & Grigulis, K. (2007) in  
24 *Terrestrial ecosystem in a changing world*, eds Canadell, J., Pataki, D. E. & Pitelka, L.  
25 F. (Springer-Verlag, Berlin), pp. 79-91.
- 26 3. Grime, J. P. (1998) *Journal of Ecology* **86**: 902-910.
- 27 4. Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J. P., Hector, A., Hooper, D. U.,  
28 Huston, M. A., Raffaelli, D., Schmid, B. *et al.* (2001) *Science* **294**: 804-808.
- 29 5. Diaz, S., Fargione, J., Chapin, F. S. & Tilman, D. (2006) *Plos Biology* **4**: 1300-1305.
- 30 6. Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.  
31 H., Lodge, D. M., Loreau, M., Naeem, S. *et al.* (2005) *Ecological Monographs* **75**: 3-  
32 35.
- 33 7. Petchey, O. L. & Gaston, K. J. (2006) *Ecology Letters* **9**: 741-758.
- 34 8. Balvanera, P., Pfisterer, A. B., Buchmann, N., He, J. S., Nakashizuka, T., Raffaelli, D. &  
35 Schmid, B. (2006) *Ecology Letters* **9**: 1146-1156.

- 1 9. Kremen, C., Williams, N. M., Aizen, M. A., Gemmill-Herren, B., LeBuhn, G., Minckley,  
2 R., Packer, L., Potts, S. G., Roulston, T., Steffan-Dewenter, I. *et al.* (2007) *Ecology*  
3 *Letters* **10**: 299-314.
- 4 10. Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E.  
5 (2007) *Oikos* **online early**.
- 6 11. Mason, N. W. H., Mouillot, D., Lee, W. G. & Wilson, J. B. (2005) *Oikos* **111**: 112-118.
- 7 12. Lavorel, S. & Garnier, E. (2002) *Functional Ecology* **16**: 545-556.
- 8 13. Diaz, S. & Cabido, M. (2001) *Trends in Ecology & Evolution* **16**: 646-655.
- 9 14. Aerts, R. (1997) *Oikos* **79**: 439-449.
- 10 15. Bardgett, R. D. & Wardle, D. A. (2003) *Ecology* **84**: 2258-2268.
- 11 16. Chapin, F. S. (2003) *Annals of Botany* **91**: 455-463.
- 12 17. Garnier, E., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Dolezal, J., Eriksson, O.,  
13 Fortunel, C., Freitas, H., Golodets, C. *et al.* (2007) *Annals of Botany* **99**: 967-985.
- 14 18. Diaz, S., Hodgson, J. G., Thompson, K., Cabido, M., Cornelissen, J. H. C., Jalili, A.,  
15 Montserrat-Marti, G., Grime, J. P., Zarrinkamar, F., Asri, Y. *et al.* (2004) *Journal of*  
16 *Vegetation Science* **15**: 295-304.
- 17 19. Bardgett, R. D., Mawdsley, J. L., Edwards, S., Hobbs, P. J., Rodwell, J. S. & Davies, W. J.  
18 (1999) *Functional Ecology* **13**: 650-660.
- 19 20. Coley, P. D. & Barone, J. A. (1996) *Annual Review of Ecology and Systematics* **27**: 305-  
20 335.
- 21 21. Craine, J. M., Tilman, D., Wedin, D., Reich, P., Tjoelker, M. & Knops, J. (2002)  
22 *Functional Ecology* **16**: 563-574.
- 23 22. Grime, J. P. (2001) *Plant strategies, vegetation processes and ecosystem properties* (John  
24 Wiley & Sons, Chichester), pp. 416.
- 25 23. Garnier, E., Cortez, J., Billes, G., Navas, M. L., Roumet, C., Debussche, M., Laurent, G.,  
26 Blanchard, A., Aubry, D., Bellmann, A. *et al.* (2004) *Ecology* **85**: 2630-2637.
- 27 24. Leps, J., Osbornovakosinova, J. & Rejmanek, M. (1982) *Vegetatio* **50**: 53-63.
- 28 25. Polley, H. W., Wilsey, B. J., Derner, J. D., Johnson, H. B. & Sanabria, J. (2006) *Oikos*  
29 **113**: 287-295.
- 30 26. Quetier, F., Thebault, A. & Lavorel, S. (2007) *Ecological Monographs* **77**: 33-52.
- 31 27. Hiremath, A. J. & Ewel, J. J. (2001) *Ecosystems* **4**: 669-682.
- 32 28. Hooper, D. U. (1998) *Ecology* **79**: 704-719.
- 33 29. Vila, M., Vayreda, J., Comas, L., Ibañez, J. J., Mata, T. & Obon, B. (2007) *Ecology*  
34 *Letters* **10**: 241-250.
- 35 30. Tasser, E., Mader, M. & Tappeiner, U. (2003) *Basic and Applied Ecology* **4**: 271-280.
- 36 31. Eviner, V. T. & Chapin, F. S. (2003) *Annual Review of Ecology Evolution and Systematics*  
37 **34**: 455-485.
- 38 32. Personeni, E., Luscher, A. & Loiseau, P. (2005) *Soil Biology & Biochemistry* **37**: 819-827.
- 39 33. Dimitrakopoulos, P. G., Siamantziouras, A. S. D., Galanidis, A., Mprezetou, I. &  
40 Troumbis, A. Y. (2006) *Environmental Management* **37**: 826-839.
- 41 34. Fraterrigo, J. M., Turner, M. G., Pearson, S. M. & Dixon, P. (2005) *Ecological*  
42 *Monographs* **75**: 215-230.
- 43 35. Lawrence, D., Suma, V. & Mogeia, J. P. (2005) *Ecological Applications* **15**: 1952-1967.
- 44 36. Robson, T. M., Lavorel, S., Clement, J. C. & Le Roux, X. (2007) *Soil Biology &*  
45 *Biogeochemistry* **in press**.
- 46 37. Levine, J. M., Vila, M., D'Antonio, C. M., Dukes, J. S., Grigulis, K. & Lavorel, S. (2003)  
47 *Proceedings of the Royal Society of London Series B-Biological Sciences* **270**: 775-  
48 781.

- 1 38. Kirwan, L., Luscher, A., Sebastia, M. T., Finn, J. A., Collins, R. P., Porqueddu, C.,  
2 Helgadottir, A., Baadshaug, O. H., Brophy, C., Coran, C. *et al.* (2007) *Journal of*  
3 *Ecology* **95**.
- 4 39. Spehn, E. M., Scherer-Lorenzen, M., Schmid, B., Hector, A., Caldeira, M. C.,  
5 Dimitrakopoulos, P. G., Finn, J. A., Jumpponen, A., O'Donovan, G., Pereira, J. S. *et*  
6 *al.* (2002) *Oikos* **98**: 205-218.
- 7 40. Dimitrakopoulos, P. G. & Schmid, B. (2004) *Ecology Letters* **7**: 574-583.
- 8 41. Montagnini, F., Cusack, D., Petit, B. & Kanninen, M. (2005) *Journal of Sustainable*  
9 *forestry* **21**: 51-67.
- 10 42. Smith, V. C. & Bradford, M. A. (2003) *Oikos* **102**: 235-242.
- 11 43. Symstad, A. J. & Tilman, D. (2001) *Oikos* **92**: 424-435.
- 12 44. Shachak, M., Jones, C. G. & Granot, Y. (1987) *Science* **236**: 1098-1099.
- 13 45. Knorr, M., Frey, S. D. & Curtis, P. S. (2005) *Ecology* **86**: 3252-3257.
- 14 46. Wedin, D. & Tilman, D. (1996) *Science* **274**: 1720-1723.
- 15 47. Grigulis, K., Lavorel, S., Davies, I. D., Dossantos, A., Lloret, F. & Vila, M. (2005) *Global*  
16 *Change Biology* **11**: 1042-1053.
- 17 48. Gross, N. (2007) *Traits fonctionnels et mécanismes de structuration des prairies*  
18 *subalpines*. PhD Thesis, Université Joseph Fourier, Grenoble, France.
- 19 49. Quetier, F., Lavorel, S., Thuiller, W. & Davies, I. (2007) *Ecological Applications*: in press.
- 20 50. Westoby, M. & Wright, I. J. (2006) *Trends in Ecology & Evolution* **21**: 261-268.
- 21 51. Lavorel, S., Díaz, S., Cornelissen, J. H. C., Garnier, E., Harrison, S. P., McIntyre, S.,  
22 Pausas, J., Pérez-Harguindeguy, N., Roumet, C. & Urcelay, C. (2007) in *Terrestrial*  
23 *ecosystem in a changing world*, eds Canadell, J., Pataki, D. E. & Pitelka, L. F.  
24 (Springer-Verlag, Berlin), pp 171-186.
- 25 52. Leps, J., de Bello, F., Lavorel, S. & Berman, S. (2006) *Preslia* **78**: 481-501.
- 26 53. Saxton, K. E. & Willey, P. H. (2005) in *Mathematical Modeling of Watershed Hydrology*,  
27 eds Singh, V. P. & Frevert, D. (CRC Press LLC), pp.
- 28 54. Duru, M. (1997) *Journal of the Science of Food and Agriculture* **74**: 175-185.
- 29

1 **Legend to Fig. 1**

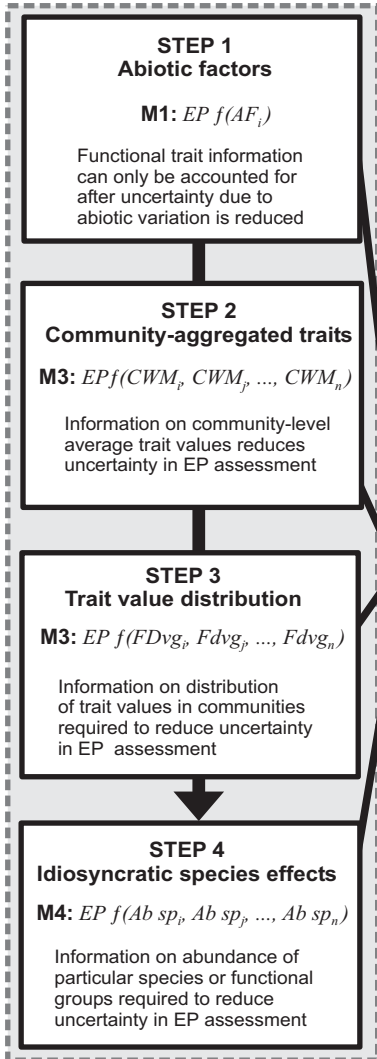
2 Diagrammatic representation of the steps proposed to reduce uncertainty in the prediction of  
3 ecosystem properties (EP) and ecosystem services (ES) on the basis of plant functional  
4 diversity (FD). In Stage I, the models tested at each step (M1-M4) link EP with driving factors  
5 of different nature: abiotic factors ( $AF_i$ ); community-weighted mean of any one functional  
6 trait ( $CWM_i$ ); distribution of values of any one trait present in a community ( $FDvg_i$ ), and  
7 local abundance of any one species present in the community ( $Ab_{sp_i}$ ). At each step,  
8 significant factors are identified and conserved for Stage II. In Stage II, combined models are  
9 built by adding factors from Steps 1 to 4 and conserving those that significantly improve the  
10 model (following a standard criterion, e.g. the Akaike criterion). The process concludes when  
11 further information on FD not necessary to reduce uncertainty in EP prediction.

12

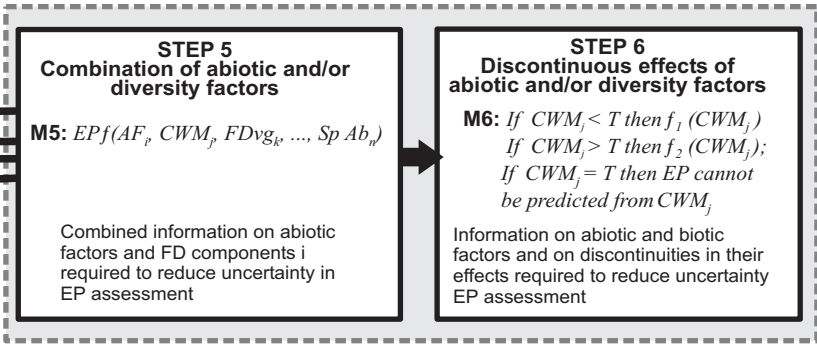
13 **Table 1.** Summary of significant results ( $p < 0.05$ ) for General Linear Models of ecosystem  
14 properties following Steps 1-6 in Fig. 1. Numerical results are presented for Steps 1-3 and  
15 Step 5. Although tested, no significant relationship was found between any of the EP  
16 examined and the abundance of *Festuca paniculata*, hence Step 4 is not presented in the  
17 Table. Ecosystem service categories (1): **P**roduction, **R**egulation, **C**ultural, **S**upporting.  
18 Relevant ecosystem properties were elicited through stakeholder interviews and  
19 complemented by expert scientific knowledge (in italics). - : no significant effect of any  
20 variable tested within the step. Acronyms after CWM\_ and FDvg\_ refer to measured plant  
21 traits. See the Methods section for the full name of each trait and for details on the statistical  
22 methods.

		Stage I: Individual effects of abiotic and biotic factors					Stage II: Combining significant effects into the best predictive model		
		Step 1: Abiotic variables		Step 2: CWM traits		Step 3: Trait distribution		Step 5: Final model	
Ecosystem services	Ecosystem properties	Variable	<i>p</i> -value	Variable	<i>p</i> -value	Variable	<i>p</i> -value	Model	% var.
<b>P:</b> Fodder production	Aboveground net primary production (ANPP)	NNI	0.004	-	-	FDvg_VH FDvg_LNC	0.040 0.091	ANPP = - 0.028 + 0.0014 NNI	44
	<i>Specific aboveground net primary production (SANPP)</i>	NNI	0.045	-	-	-	-	SANPP = - 0.012 + 0.00085 NNI	22
	Standing aboveground biomass (AGB)	-	-	-	-	FDvg_LHS	0.089	No suitable model Nonlinear model depending on past ploughing (Quétier et al. 2007b) (Step 6)	< 15
<b>R:</b> Snow gliding prevention <b>C:</b> Cultural heritage <b>C, S:</b> Habitat for butterflies	Standing litter biomass?? (Litt)	-	-	CWM_VH CWM_LNC CWM_LTS	0.002 0.012 0.046	FDvg_VH	0.10	Litt = 9.4 + 0.35 CWM_VH - 7.54 CWM_LNC - 0.00063 CWM_LTS	75
	Litter decomposability (Decomp)	-	-	CWM_LNC CWM_Lig:N	<.001 <.001	-	-	Decomp = 13.5 + 3.02 CWM_LNC - 0.39 CWM_Lig:N	91
<b>S:</b> Maintenance of soil fertility	<i>Available nitrate</i>	-	-	CWM_LNC CWM_RL	< 0.001 0.044	-	-	NO3 = -25.8 + 21.2 CWM_LNC + 0.0085 CWM_RL	76
	<i>Denitrification potential (Den_P)</i>	-	-	CWM_LNC CWM_RL	0.001 0.034	FDvg_LHS	0.026	Den_P = -59.5 + 80.6 CWM_LNC + 0.042 CWM_RL	67
<b>P:</b> Sustained production of green fodder through the summer	<i>Soil water content (SWC)</i>	WHC AGB	0.003 <.001	CWM_LA CWM_RL	0.043 0.001	-	-	SWC = 2.07 + 1.55 WHC - 1.58 AGB + 0.00083 CWM_LA - 0.0014 CWM_RL	85

**STAGE I**  
Identifying abiotic and biotic factors



**STAGE II**  
Finding the best predictive model



		Stage I: Individual effects of abiotic and biotic factors						Stage II: Combining significant effects into the best predictive model	
		Step 1: Abiotic variables		Step 2: CWM traits		Step 3: Trait distribution		Step 5: Final model	
Ecosystem services	Ecosystem properties	Variable	<i>p-value</i>	Variable	<i>p-value</i>	Variable	<i>p-value</i>	Model	% var.
<b>P:</b> Fodder production	Aboveground net primary production (ANPP)	NNI	0.004	-	-	FDvg_VH FDvg_LNC	0.040 0.091	ANPP = - 0.028 + 0.0014 NNI	44
	<i>Specific aboveground net primary production (SANPP)</i>	NNI	0.045	-	-	-	-	SANPP = - 0.012 + 0.00085 NNI	22
	Standing aboveground biomass (AGB)	-	-	-	-	FDvg_LHS	0.089	No suitable model Nonlinear model depending on past ploughing (Quétier et al. 2007b) (Step 6)	< 15
<b>R:</b> Snow gliding prevention <b>C:</b> Cultural heritage <b>C, S:</b> Habitat for butterflies	Standing litter biomass?? (Litt)	-	-	CWM_VH CWM_LNC CWM_LTS	0.002 0.012 0.046	<i>FDvg_VH</i>	<i>0.10</i>	Litt = 9.4 + 0.35 CWM_VH - 7.54 CWM_LNC - 0.00063 CWM_LTS	75
	Litter decomposability (Decomp)	-	-	CWM_LNC CWM_Lig:N	<.001 <.001	-	-	Decomp = 13.5 + 3.02 CWM_LNC - 0.39 CWM_Lig:N	91
<b>S:</b> Maintenance of soil fertility	<i>Available nitrate</i>	-	-	CWM_LNC CWM_RL	< 0.001 0.044	-	-	NO3 = -25.8 + 21.2 CWM_LNC + 0.0085 CWM_RL	76
	<i>Denitrification potential (Den_P)</i>	-	-	CWM_LNC CWM_RL	0.001 0.034	Fiv_LHS	0.026	Den_P = -59.5 + 80.6 CWM_LNC + 0.042 CWM_RL	67
<b>P:</b> Sustained production of green fodder through the summer	<i>Soil water content (SWC)</i>	WHC AGB	0.003 <.001	CWM_LA CWM_RL	0.043 0.001	-	-	SWC = 2.07 + 1.55 WHC - 1.58 AGB + 0.00083 CWM_LA - 0.0014 CWM_RL	85