Multiple ecosystem services in smallholder agriculture

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Submitted in partial fulfillment of the requirements for the degree of
Doctor of Philosophy
in the Graduate School of Arts and Sciences

COLUMBIA UNIVERSITY

2012
ABSTRACT

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Recent research into the ecological origins and social implications of ecosystem services, the benefits ecosystems provide to society, is predicated on the downward trends observed for many services. Current work increasingly emphasizes how interactions among ecosystem services (synergies and trade-offs) affect the delivery of multiple services, from soil fertility at field scales to watershed-scale hydrological function, to global climate regulation. Meanwhile, research on the relationship between biodiversity and ecosystem functioning has identified substantive linkages between the biodiversity of ecosystems and the services they provide, provoking interest in aligning biodiversity conservation with the sustained delivery of ecosystem services. To better understand the delivery of multiple ecosystem services relevant to smallholder farmer livelihoods in the tropics, the production of wood and livestock forage and the structure and fertility of soils were examined in grazed and improved fallows in western Kenya. The objectives were to investigate fine-scale interactions among ecosystem services, and the potential of fallow plant diversity to enhance levels of multiple services simultaneously, i.e., ecosystem service multi-functionality. To examine influences of fallow vegetation and management on soil structure and fertility, the biomass and functional traits (green tissue N, lignins, polyphenols, lignins+polyphenols) of fallow plants and the condition of soils were quantified. Positive associations of tissue content of lignins+polyphenols with soil organic carbon (SOC) and steady infiltration rates indicated a role of recalcitrant carbon compounds in slowing SOC turnover and supporting soil structural development, while grazed fallows had lower infiltration than improved fallows, likely a result of livestock trampling and soil compaction. To investigate whether woody overstory plants and fallow management generate interactions between the production of wood and livestock forage, the relationships of overstory biomass, overstory diversity as a proxy for niche complementarity, grazing
intensity, and soil conditions with the biomass and quality (crude protein:lignin) of forage species were studied. Overstory competition in densely planted improved fallows resulted in an apparent trade-off with forage biomass, however in grazed fallows overstory and forage biomass were positively associated, likely due to negative effects of grazing on both; in addition, reduced forage quality and biomass of quality forage species were attributable to selective grazing. Finally, to assess whether plant diversity enhances joint levels of multiple ecosystem services, two indices of ecosystem multi-functionality were designed for four ecosystem functions: wood biomass, forage biomass, soil base cations, and infiltration. Evidence for positive effects of diversity on multi-functionality was clearer in grazed fallows, while in improved fallows environmental favorability appeared more influential. The difference in the diversity-multi-functionality relationship among fallow types appeared related to contrasting management, disturbance, species composition, and the productivity of vegetation and soils. The results suggest that plant diversity and site productivity can enhance multiple ecosystem services in smallholder fallows, yet diversity effects may vary with management, species composition, and site conditions.
# Table of Contents

**Chapter 1: Ecology, management, and multiple ecosystem services in smallholder agriculture**

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abstract</td>
<td>1</td>
</tr>
<tr>
<td>Ecosystem services and questions of ecological complexity</td>
<td>2</td>
</tr>
<tr>
<td>Ecosystems and their services</td>
<td>4</td>
</tr>
<tr>
<td>Ecosystem multi-functionality and ecosystem services</td>
<td>14</td>
</tr>
<tr>
<td>A framework for multiple ecosystem services in smallholder agriculture</td>
<td>19</td>
</tr>
<tr>
<td>Conclusions</td>
<td>31</td>
</tr>
<tr>
<td>Tables and Figures</td>
<td>35</td>
</tr>
</tbody>
</table>

**Chapter 2: Vegetation mediation of land use effects on soil organic carbon and soil infiltration capacity**

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abstract</td>
<td>37</td>
</tr>
<tr>
<td>Introduction</td>
<td>38</td>
</tr>
<tr>
<td>Methods</td>
<td>43</td>
</tr>
<tr>
<td>Results</td>
<td>48</td>
</tr>
<tr>
<td>Discussion</td>
<td>50</td>
</tr>
<tr>
<td>Tables and Figures</td>
<td>58</td>
</tr>
</tbody>
</table>

**Chapter 3: Effects of trees and large shrubs on livestock forage in smallholder fallows**

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abstract</td>
<td>64</td>
</tr>
<tr>
<td>Introduction</td>
<td>65</td>
</tr>
<tr>
<td>Methods</td>
<td>71</td>
</tr>
<tr>
<td>Results</td>
<td>78</td>
</tr>
</tbody>
</table>
List of Tables and Figures

Chapter 1

Box 1.1. Conceptual framework: Multiple ecosystem services in smallholder agroecosystems 35

Figure 1.1. Direct ecological interactions among ecosystem services important to smallholder farmers 36

Chapter 2

Table 2.1. Description of model variables and summary statistics 58

Table 2.2. Comparison of full models with ‘best’ models selected by AICc 59

Table 2.3. Model coefficients and results for multi-model inference conducted by model averaging 60

Figure 2.1. Variation in soil organic carbon and steady infiltration rates with fallow type 61

Figure 2.2. Relationships of soil organic carbon with attributes of fallow vegetation and soil sand content 62

Figure 2.3. Relationships of steady infiltration rates with attributes of fallow vegetation and soil sand content 63

Chapter 3

Table 3.1. Definitions of forage variables and their significance to the ecosystem service of forage production 92

Table 3.2. Description of forage, overstory, and environmental variables 93

Table 3.3. Effects of overstory interactions and environmental conditions on forage variables in grazed fallows 94
Table 3.4. Effects of overstory interactions and environmental conditions on forage variables in improved fallows

Figure 3.1. Relationships of total forage biomass with overstory biomass and diversity, and environmental conditions

Figure 3.2. Relationships of quality forage biomass with overstory biomass and diversity, and environmental conditions

Figure 3.3. Relationships of forage quality with overstory biomass and diversity, and environmental conditions

Chapter 4

Table 4.1. Focal ecosystem services and summary statistics for ecosystem functions serving as ecosystem service indicators in smallholder fallows

Table 4.2. Summary statistics for indicators of fallow ecosystem service multi-functionality, and for plant diversity and environmental variables serving as linear predictors of multi-functionality

Table 4.3a. Grazed fallows: Results from linear models predicting ecosystem service multi-functionality using plant diversity and environmental variables

Table 4.3b. Improved fallows: Results from linear models predicting ecosystem service multi-functionality using plant diversity and environmental variables

Figure 4.1. Correlations among ecosystem functions

Figure 4.2. Fallow type and the proportion of ecosystem functions above 25, 50, and 75% of respective function maxima

Figure 4.3. Relationships of plant diversity and environmental variables with the proportion of ecosystem functions above half-maximum
Figure 4.4. Relationships of plant diversity and environmental variables with mean percentage excess above mean ecosystem function values

Figure 4.5. Grazed fallows: Relationship of fallow plant functional diversity with the proportion of functions above half-maximum within grazing intensity groups

Figure 4.6. Grazed fallows: Relationship of fallow plant functional diversity with percentage excess above mean function values with grazing intensity groups

Figure 4.7. Incidence of jointness for pairs of ecosystem functions above 50% of function maxima, and above mean function values

Figure 4.8. Distributions of ecosystem functions in grazed fallows

Figure 4.9. Distributions of ecosystem functions in improved fallows

Figure 4.10. Correlations between fallow plant functional diversity and ecosystem functions

Figure 4.11. Correlations between fallow plant species richness and ecosystem functions

Appendix A

Table A1. Derivation of biovolume-biomass conversion factors for herbaceous species

Table A2. Derivation of biovolume-biomass conversion factors for subshrub species

Table A3. Derivation of biovolume-biomass conversion factors for shrub species

Table A4. Derivation of biovolume-biomass conversion factors for tree species
Acknowledgements

I would like to thank first and foremost my advisor, Shahid Naeem, for the fantastic opportunities afforded under his mentorship, and for the resources that made my work possible. I am particularly indebted to him for his high standards and his belief in the unlimited power of the individual, essential elements of the privilege of seeking one’s own unique path. The Naeem lab provided a wealth of assistance, feedback, camaraderie, and ever-stimulating discussions.

I am most grateful to my committee: Maria Uriarte changed forever my view of science, Kevin Griffin is among the wisest and most supportive professors I have known, and I thank Cheryl Palm and Markus Walsh for supporting my work with the Millennium Villages Project, for deepening my respect for the complexities of soils and agroecosystems, and for being lovely and generous people. I would also like to single out the instrumental support of Eleanor Sterling.

The TransLinks project, led by David Wilkie and J. Carter Ingram, and the United States Agency for International Development (USAID) provided essential funding support. This work was made possible by USAID under the TransLinks Leader with Associates Cooperative Agreement No. EPP-A-00-06-00014-00 to The Wildlife Conservation Society.

Sauri MVP director Patrick Mutuo was a critical support in field work as well as to conceptual development, Victor Omollo, Chris Ekise, Herine Okoth, Steve Okulo, Carlos Onyalo, and George Baison provided field assistance, and Keith Shepherd and Elvis Weullow of ICRAF-Nairobi assisted with soil analyses.

I am finally eternally indebted to my parents, to my brothers, and to Sheri Richardson for their unconditional encouragement and support, and to Sean Smukler, Charles Huang, Marko Pecarevic, Ferdie Yau, Leo Douglas, Saifedean Ammous, Heather Wyllie, Kifle Bantayehu, Sean Mount, and Ryan Thomforde among the friends and colleagues too numerous to list.
I dedicate this work to my parents, whose ardent encouragement, unwavering confidence, and steadfast support are among the most precious gifts I have been so fortunate to receive.
Chapter 1: Ecology, management, and multiple ecosystem services in smallholder agriculture

Abstract

Synergies and trade-offs among ecosystem services have important implications for the overall supply of services. Taking such interactions among services into account can improve natural resource management. Here, the focus is on smallholder agricultural systems and how sets of multiple ecosystem services are influenced by ecosystem service interactions. A conceptual framework is presented for the production of sets of multiple ecosystem services, based on how ecological factors and management affect interactions among services. It is argued that understanding such interactions is as important as understanding the influences of species, other ecosystem service providers (ESPs), the diversity of ESPs, and other ecological factors on the delivery of ecosystem services. Without information on interactions among services, it will be more difficult to understand the implications for human well-being when management alters the structure and function of a managed ecosystem. The framework is also useful in explaining the formation of feedback loops among ecosystem services arising from temporally-mediated synergies and trade-offs. The overall degree of complementarity apparent among species (or other ESPs), and their contributions to ecosystem service delivery, should increase when complementarities among services are considered in addition to complementarities specific to individual services. As a greater number of ecosystem services are considered, complementary effects of ESPs on multiple ecosystem services should be expected to increase the cumulative
benefits accruing from ESPs and the diversity of ESPs. Since ESPs and biodiversity can have complex effects on ecosystem services, their cumulative contributions to delivery of services may be more difficult to replace than managers may expect. Management decisions that excessively discount returns to the abundance and diversity of certain ESPs could impede progress toward achieving management goals comprising multiple ecosystem services.

**Ecosystem services and questions of ecological complexity**

Land management typically alters the structure and function of ecosystems to maximize the production of specific goods (Rodriguez et al. 2006). Marketable goods such as agricultural commodities provide consistent returns on investments, and as a result agricultural systems now predominate among the terrestrial ecosystems of the planet (Vitousek et al. 1997). Although specialization accomplishes its goal of increasing the short-term supply of agricultural goods, agriculture frequently degrades other benefits provided by ecosystems (Foley et al. 2005, Kareiva et al. 2007)—from soil quality within fields to regulation of the global climate. While there is increasing recognition of the important roles that agriculture plays in economic development and poverty reduction (Sanchez et al. 2007, IRDB 2008, Kiers et al. 2008), the amount of cultivated land in developing countries is expected to expand by up to 12% by 2050 if current trends continue (Bruinsma 2009), and sustainable agricultural systems are greatly needed. Better understanding of how ecological factors and management practices regulate agroecosystem functioning may ultimately improve decision-making by farmers and policy-makers, and allow
humanity to more fully realize the potential benefits of land management while minimizing costs and risks.

Ecosystem services are of tremendous value to society, as they provide a ‘missing link’ between the natural capital of ecosystems—their capacity to produce valuable goods and services—and the financial and physical capital that society derives from ecological systems. Natural and managed ecosystems provide a wide range of benefits to humanity, termed ecosystem services (MA 2003). Market values exist almost exclusively for provisioning services such as crops, wood, livestock, and other agricultural commodities. Ecosystem services that play supporting and regulating roles—such as productivity, water regulation, climate regulation, soil formation, and nutrient cycling—rarely have markets. As a consequence, the costs of their degradation do not appear in the ledgers of producers until provisioning services begin to decline.

Ecosystem services are regulated ecologically by a wide array of biotic factors within local and regional abiotic filters. Ecosystem service providers (ESPs) are the subsets of the biota responsible for production of an ecosystem service (Kremen 2005). In most ecosystems, services are linked together by ecological interactions among their respective ESPs. As a result, production of one ecosystem service often affects the magnitudes of other services (Bennett et al. 2009, Carpenter et al. 2009). In agroecosystems for example, crop production, nutrient cycling, and the maintenance of soil fertility and structure are intimately intertwined. The existence of ecosystem service interactions implies that where management goals encompass the production of multiple ecosystem services, achieving these goals depends on the conditionality of services upon one another.

The goal of maximizing production of provisioning services typically shifts the identity of ESPs that produce ecosystem services, and results in the simplification of managed ecosystems.
Land managers usually select species and varieties of crops and trees capable of rapid production. The organisms providing supporting and regulating services such as soil formation and nutrient cycling may also change dramatically as land use intensity increases. Soil tillage, fertilization, and other common management practices create ecological conditions that differ greatly from the pre-agriculture state of the ecosystem, favoring soil organisms that can survive and grow under intensified management regimes (Beare et al. 1997, Giller et al. 1997).

Simplification and intensification of agroecosystems typically reduces the diversity of species, and can restrict variation in the functional traits of organisms (Swift et al. 2004), potentially affecting the capacity to supply ecosystem services.

The goal of this review is to contribute to understanding of ecosystem service delivery in tropical smallholder agricultural systems. The specific objective is to expand conceptual understanding of the delivery of multiple ecosystem services in these systems. An overview is provided on the biophysical regulation—i.e., regulation by ecological factors and management—of ecosystem services, and the reasons for the current expansion of inquiry from single to multiple ecosystem services. A framework is then presented to conceptually integrate interactions among services into ecosystem service delivery in smallholder systems.

**Ecosystems and their services**

Ecosystem processes are transfers and transformations (i.e., fluxes) of energy and matter between pools (i.e., stocks) in an ecosystem. Key terrestrial ecosystem processes include net primary productivity (NPP), decomposition, the movement and cycling of carbon, water,
nutrients, and energy, and trophic interactions (e.g., predation, herbivory). Ecosystem services are the benefits provided by ecosystems to society (MA 2003), while costs are termed ecosystem disservices (Zhang et al. 2007). Any ecosystem service can be viewed as the outcome of a set of key ecosystem processes. The term ecosystem function can refer to an ecosystem process, an ecosystem property (e.g., stability, resistance to invasions), or an ecosystem service. Since some processes and properties are also services, all three terms may refer to precisely the same ecological phenomenon. NPP is an ecosystem process of fundamental significance in all ecosystems. Since soil-based services and provisioning services depend on NPP, NPP is a supporting ecosystem service (MA 2003).

Ecosystem processes and dynamics are constrained by ecosystem state factors, which determine the overall state of the ecosystem relative to other possible states. Key state factors include environmental conditions such as soil physical characteristics, topography and climate, and biotic factors such as the composition of ecological communities (Amundson and Jenny 1997). Because ecological conditions differ among ecosystem states, rates of ecosystem processes vary accordingly, likely influencing the supply of ecosystem services (Walker and Meyers 2004). While in some cases ecosystem states may have discontinuous boundaries, in practice discrete states are difficult to establish, and variation among states may best be viewed as continuous.

Abiotic regulation plays two main roles in regulating ecosystem services. First, the possible range of magnitudes for a terrestrial ecosystem process is constrained by abiotic factors that vary over regional spatial scales, and over long time periods, e.g. decades. For example, higher rainfall typically leads tropical forested regions to have much higher annual net primary productivity (ANPP) than tropical grassland regions, and thus have greater C inputs to the ecosystem. Vast differences among such systems in rates of decomposition and nutrient cycling may further
amplify differences in NPP. Regional differences also largely determine the potential of the system to produce agricultural commodities. Some abiotic factors such as climatic regimes and soil texture are ‘slow’ ecosystem variables, requiring long periods to change, while others such as rainfall vary seasonally. Second, variation in abiotic conditions influences ecosystem processes at finer scales, but are further modulated through fine-scale biotic effects. For example, in a field of an annual crop, ‘fast’ abiotic factors such as soil water balance and temperature are partly the result of regional and local climate. Soil water balance and temperature may exhibit fine-scale influence of abiotic factors such as topographical position, and fine-scale biotic factors, such as the presence and arrangement of trees in and around the crop, which can alter the microclimate of the field (Lott et al. 2003, Muthuri et al. 2005).

Ecosystem service providers (ESPs) are the subsets or components of the biota that are directly responsible for specific roles in the production, or supply, of an ecosystem service (Kremen 2005). The ESPs for provisioning ecosystem services are easy to identify—i.e., a field of a crop for crop production, a stand of trees for wood production, and so on. ESPs for NPP are also fairly clear, namely plant populations or plant communities, depending on the spatial scale and the degree of spatial heterogeneity in the ecosystem. Identification of ESPs for supporting and regulating services is generally more complicated. Diverse assemblages of soil microbes and soil macro- and micro-fauna together bear responsibility for soil formation and the maintenance of soil fertility and structure, although the roles of groups of soil organisms differ greatly (Beare et al. 1997). Ecological regulation of some services, such as nutrient cycling and carbon sequestration, is highly complex; plants and soil organisms are the primary subsets of the biota controlling long-term carbon storage, but identifying the precise role of each and every species would be logistically intractable. ESPs can include genes, individual organisms, populations,
stands of trees, species, communities, habitats, and ecosystems, and can be defined over spatial scales ranging from a gram of soil up to whole regions of the planet. Thus, ESPs exist at every level of biological and spatial hierarchy.

Populations of organisms and biotic communities influence ecosystem processes and services through the functional traits of organisms. Functional traits include those determining the influences of populations and communities on the ecosystem (effect traits), and traits mediating responses of populations and communities (response traits) to changing environmental conditions (Díaz and Cabido 2001, Naeem and Wright 2003, Suding et al. 2008). The effect of the population of an ESP on an ecosystem service is due primarily to the size of the ESP population, and the distribution of functional trait values among individuals in the population.

Plant life history strategies provide a perspective for conceptualizing plant species effects on ecosystem processes. Across biomes and major taxonomic groups, plant functional traits frequently exhibit a trade-off between traits that enable rapid growth, and traits that provide protection from herbivory or adverse conditions and thereby promote conservation of resources the plant has obtained (Grime 1979, Aerts and Chapin 2000, Wright et al. 2004). Plants capable of a high relative growth rate (RGR; growth rate relative to biomass) tend to produce nutrient-rich tissues more palatable to herbivores, while species with low RGR tend to have unpalatable tissues, due to low nutrient content and production of structural and defensive compounds such as lignins and phenolics. Faster-growing species are often suited to fertile or productive habitats; in contrast, many species from less fertile habitats grow slowly because they allocate resources to protection of tissues with structural and chemical defenses (Lambers and Poorter 1992, Cornelissen et al. 1999). Rapid growth furthermore enables recolonization and an avoidance response to disturbance, while species that conserve resources can often tolerate disturbances
(McIntyre et al. 1999, Lavorel and Garnier 2002). Thus, adaptation of plant species to habitats differing in fertility or disturbance regime can generate a trade-off between growth and defense that significantly determines growth rates, along with a variety of traits associated with growth rates.

Though it may seem that faster growth rates should increase annual productivity, the relationship between the two is variable. Growth rates and annual NPP (ANPP) can be positively related—for example, ANPP of deciduous trees exceeds that of conifers in temperate zones (Pan et al. 2006). However, the converse is often true. In spite of lower RGR, trees can contribute the vast majority of ANPP in ecosystems where both trees and herbaceous species are abundant (Caylor et al. 2004); some of this effect can be attributed to the effective difference in the length of the growing season for woody versus herbaceous species. Species with rapid growth traits do in fact sustain higher instantaneous productivity and specific annual NPP (SANPP; ANPP relative to starting biomass) but may cause ANPP to be lower (Garnier et al. 2004).

NPP increases the quantity of litter inputs to soils, which in turn increases rates of soil processes, while plant tissue chemistry and the quality of litter inputs further modulate the functioning of soil subsystems (Wardle 2002, Wardle et al. 2004). Litter quality refers to a suite of plant traits that determine the susceptibility of organic residues to decomposition by soil organisms and modification by physical and chemical processes (Cadisch and Giller 1997, Bronick and Lal 2005). Three important litter quality traits are N content (or C:N ratio), lignin content, and phenolic content (Cadisch and Giller 1997), each of which influences the activity of soil organisms. High quality litters with low C:N (i.e., high N content) tend to have high content of labile C compounds that support rapid microbial breakdown and decomposition, and mineralization of C and nutrients in litter (Gentile et al. 2009). In contrast, low quality litters
decompose slowly, such that C and nutrients are mineralized over a long time period, due to high C:N or high content of recalcitrant C compounds (Vanlauwe et al. 2005) that resist microbial breakdown (de Boer et al. 2005). Litters high in recalcitrant forms of C such as lignins and polyphenols can contribute significantly to formation of long-lived soil C pools such as humus (Zech et al. 1997).

Soil organic carbon (SOC), robust soil structure, and soil hydraulic properties are important regulators of plant growth, and key indicators of soil quality in agricultural systems (Arshad and Martin 2002). Cycling of C and N through ecosystems tends to be coupled, and agricultural management affects the degree to which soil C and N are maintained, increased (Blair et al. 2006b), or together decline during degradation (Mosier 1998), especially over long time-scales. SOC enhances the bioavailability of soil nutrients and increases nutrient retention in soils by providing cation exchange capacity (Bell et al. 1998) and binding nutrients in soil organic matter (SOM), the recalcitrance of which determines the time-scale of nutrient release (Barrios et al. 1997, Vanlauwe et al. 2005). High soil infiltration rates for a given soil texture are indicative of robustly structured soils that are less vulnerable to runoff and soil erosion and have greater water storage capacity (Seobi et al. 2005). Soil infiltration capacity responds to changes in soil aggregation, bulk density, and porosity (Salako and Kirchhof 2003) and channels created by plant roots (van Noordwijk et al. 1991). For these reasons, planting of trees tends to improve soil hydraulic properties (Siriri et al. 2006, Ilstedt et al. 2007), and the often relatively high recalcitrance of their litter may play a role as well. By inducing aggregation of soil particles and reducing soil bulk density (Martens 2000), SOM improves soil structure, and increases infiltration and water retention (Seobi et al. 2005). Soil hydraulic functions can be performed by both labile (Blair et al. 2006a) and recalcitrant (Martens 2000) SOM fractions, though probably over
different time-scales. Labile SOM fractions and their physical effects are more responsive to
changes in inputs and soil disturbance, while the effects of recalcitrant forms are probably more
lasting (Bronick and Lal 2005) on account of longer residence times.

When multiple plant species are present, interactions among litters during decomposition
generate non-linear and idiosyncratic effects on soil processes. Mixing litters of different quality
results in positive effects of mineralization of nutrients in superior quality litters on breakdown of
poorer quality litters, as well as negative effects of inferior quality litters on superior litters
through immobilization of nutrients. Litter mixing effects are often non-additive (e.g., Dijkstra et
al. 2009, Meier and Bowman 2010), but may be additive if positive and negative effects
neutralize one another (Hoorens et al. 2010).

As for populations, influences of biotic communities on ecosystem processes are mediated
by functional traits. Numerically dominant species typically have the strongest influence on
ecosystem processes among the species in a community (e.g., Garnier et al. 2004, Díaz et al.
2007a) due to their proportionally greater abundance, an effect termed the mass ratio hypothesis
(Grime 1998). Accordingly, the stronger the dominance in a plant community, the more
consequential are the traits of dominant species. Greater evenness should rather equalize effects
of various species on ecosystem process rates (Hillebrand et al. 2008), at least over fine spatial
scales such as plant neighborhoods and habitats. Trait values can be aggregated to account for
mass ratio effects, usually by taking mean trait values of species in a community, weighted by the
abundance of each species in the community (Garnier et al. 2004, Ackerly and Cornwell 2007).
Functional composition is the primary means by which plant communities influence ecosystem
processes and dynamics. In some cases, the effects of a few dominant species may sufficiently
represent the influence of the entire plant community (Garnier et al. 2004).
After the effects of dominant species and mass ratio effects, the functional diversity (FD) of biotic communities often explains additional variation in ecosystem process rates. FD refers the degree of variation or divergence in functional traits within a biotic community or an assemblage of species (Díaz and Cabido 2001, Petchey and Gaston 2002), a potentially important mediator of community influences on ecosystem dynamics (e.g., Díaz et al. 2007a, Schumacher and Roscher 2009). When species have different, or complementary, niches the values of their traits that influence particular ecosystem processes are likely to diverge. Because FD reflects dissimilarity among the species in a community, FD can be considered a measure of niche complementarity (Mason et al. 2005, Petchey and Gaston 2006). In practice, the traits and methodology used to calculate FD can alter its estimation (Petchey and Gaston 2009).

Organismal traits should be selected with care to reflect functional effects and responses relevant to the ecosystem functions or perturbations of interest, and to avoid collinearities among traits and other undesirable statistical properties. Species with complementary niches and complementary effects on an ecosystem process have low redundancy with respect to that process (Walker 1992), and the loss of functionally unique species will affect the ecosystem process more strongly than the disappearance of species similar to others present.

In recent decades a growing body of evidence, mostly from manipulative experiments, has demonstrated that the diversity of species in ecological communities can significantly influence ecosystem processes and properties. Experimental manipulations of plant species and functional group diversity, predominately in grasslands, demonstrate that effects of biodiversity on ecosystem functions such as biomass production and nutrient retention are typically positive and tend to saturate at high species richness (Hooper et al. 2005, Balvanera 2006, Cardinale et al. 2006). Diversity effects on productivity have been documented in several terrestrial ecosystems,
including grasslands (Tilman et al. 2001, Spehn et al. 2005), shrublands (Troumbis and Memtsas 2000) and forests (Erskine et al. 2006, Vila et al. 2007). The two most widely acknowledged mechanisms responsible are complementarity effects and sampling or ‘selection’ effects. Sampling effects arise from the higher probability of a species efficacious for a particular function being represented when species richness is higher. Complementarity effects occur through niche partitioning among species. Complementary niches among species can reduce competition, increasing the efficiency of resource capture and utilization by the community. For example, a grass and a forb grown in mixture may compete less intensely with one another than with their conspecifics. If the forb is leguminous, the grass may additionally be facilitated by soil N fixed by the legume. Consequently, productivity, utilization of soil nutrients, and rates of other ecosystem processes commonly increase. In grassland plant communities, complementarity effects may be the predominant mechanism responsible for biodiversity effects on productivity (Cardinale et al. 2007).

When a biotic community is exposed to a perturbation, the overall importance of functional trait diversity depends on whether the traits that make species vulnerable to the perturbation (response traits) are the same traits determining species effects on ecosystem functioning (effect traits). When species with stronger effects are also more vulnerable, the likely result is a decline in ecosystem function that is greater than expected with random loss of species (Suding et al. 2008). For instance, larger bee species can be more effective pollinators, yet are more prone to extinction, causing a disproportionate decline in pollination at low species richness (Larsen et al. 2005). If timber extraction favors tree species of high wood density, aboveground carbon storage should decline rapidly with species loss (Bunker et al. 2005). Hence, a key goal in current BEF research is to distinguish functional traits mediating the distribution and abundance
of organisms, including responses to perturbations and global change drivers, from functional traits determining the effects of organisms on ecosystem processes (Díaz et al. 2006, Hillebrand and Matthiessen 2009).

Ecologists have made great strides in linking ecological regulatory factors, ecosystem processes and properties, and ecosystem service delivery. Yet ecosystem services are at once ecological, economic and social, and are best understood when these spheres are linked at appropriate spatial, temporal, and institutional or social scales. Greater insight into ecosystem services is possible if the ecosystem origins of services are linked with their ecological and social fates to form the ecosystem supply chain: from production of services to their accrual to beneficiaries. The disciplinary specificity of ecological and economic work has restricted synthesis of knowledge across these disciplines, and understanding of the delivery of ecosystem services is ultimately constrained by scientific understanding of the regulation of ecosystem services by ecological factors and management approaches (NRC 2005).

The delivery of an ecosystem service generally does not occur in isolation from other services. Rather, most exhibit causal or correlative relationships with other services (Bennett et al. 2009, Power 2010). In addition, ecological forces regulating services may influence more than one service simultaneously, may mediate interactions among services, or both (Bennett et al. 2009). For example, biodiversity is not merely a property of ecosystems, but is also a potential regulatory factor that remains poorly understood in relation to most ecosystem services. Conservation strategies tend to be based on either primarily intrinsic and cultural values of biodiversity (e.g. Redford and Adams 2009), or these values together with use values (Naidoo et al. 2008, Sutherland et al. 2009). Biodiversity relationships with ecosystem services could eventually be leveraged to inform conservation efforts, by reducing risks of under- or over-
estimating the utility of biodiversity to local and regional stakeholders. However, relationships of biodiversity with multiple ecosystem functions appear to differ from relationships with single functions (Hector and Bagchi 2007). Elucidating joint regulation of multiple ecosystem services should help to clarify the roles of ecological regulatory factors, from abiotic factors to species and other ESPs, in contributing to human well-being.

Ecosystem multi-functionality and ecosystem services

To date, much research on ecosystem services has been over brief temporal extents, and focused on single services (Foley et al. 2005, Carpenter et al. 2009), while studies on multiple services at landscape scales have not accounted for direct interactions among ecosystem services (Bennett et al. 2009). Management and policy formulation typically utilize coarse information (Antle and Valdiva 2006), at times qualitative or anecdotal. Case studies on individual services, usually restricted in spatial and temporal resolution and conducted in regions that have seen much research effort, produce limited generalizable knowledge (Carpenter et al. 2009). Enhancing understanding of the regulation of multiple ecosystem services should facilitate progress toward the ultimate goal of managing ecosystems to satisfy the multiple demands that people make of ecosystems.

Valuation always fails to capture the full value of ecosystems to society, largely because many ecosystem benefits are difficult to quantify (NRC 2005). Studies of multiple ecosystem services that incorporate interactions with other services should more fully account for the value of ecosystem services, and the contributions of ESPs and other ecological factors to the value of
ecosystem services. Research priorities are increasingly expanding from regulation and valuation of single ecosystem services, toward the simultaneous consideration of multiple services (Bennett et al. 2009, Carpenter et al. 2009).

The primary rationale for research on multiple ecosystem services is that ecosystem services are known to interact. Ecosystem service interactions refer to the ecological (Bennett et al. 2009, Power 2010) and economic (Wossink and Swinton 2007) trade-offs and synergies among services. A synergy occurs when the supply of one service increases with the supply of another service (Bennett et al. 2009). That is, the ‘ecological production functions’ (Polasky 2008) of two services are considered to be complementary in the sense of ecological economics (Wossink and Swinton 2007), such that production of one or both enhances production of the other, or their rates of production are positively correlated. In a trade-off, the supply rate of a service declines when the supply of another increases (i.e., the production functions are competitive, or their rates of production are negatively correlated). Synergies, trade-offs and feedbacks between ecosystem services can affect the magnitude of each service produced, and can thereby alter the outcomes of management decisions. Ecosystem ‘multi-functionality’ refers to the ability of an ecosystem to support multiple ecosystem functions at a specified level of each function (sensu Hector and Bagchi 2007). Achieving greater ecosystem multi-functionality in terms of multiple ecosystem services is likely to benefit from consideration of potential interactions among services.

Ecosystem service interactions can occur in the same place at the same time, or can be mediated by spatial and temporal exchanges in energy and materials. Spatial exchanges occur between the locations where two ecosystem services are produced, while temporal exchanges occur between points in time. As spatiotemporal scales increase, synergies and trade-offs between magnitudes of ecosystem services can intensify or diminish. Different rates of underlying
ecosystem processes and lags in timing between service production and accrual to beneficiaries (or ‘consumption’) can generate interactions leading to outcomes ranging from detrimental (e.g., field-scale soil degradation, and global climate warming) to ameliorative (field-scale soil quality improvement, and global climate stabilization) in their effects. Spatial patterns in land cover and land use types, including the degree of landscape heterogeneity, patch sizes, and inter-patch distances significantly affect interactions between ecosystem services produced in different parts of a landscape (van Noordwijk 2002, Barbier et al. 2008).

Landscape models simulate the magnitudes of multiple ecosystem services based on land use or cover types (Chan 2006, Groot et al. 2007, Nelson et al. 2009). Modeling multiple services based on spatial concordance within landscape units is useful, yet accounting for interactions among services would improve understanding of the delivery of multiple services (Bennett et al. 2009). Spatial interactions in the landscape, temporal exchanges within landscape units, and fine-scale ecological and social complexity in terms of abiotic conditions, community composition, management practices, and institutional characteristics all appear to be sources of non-linearities in ecosystem service delivery (Bennett et al. 2009, Carpenter et al. 2009).

Understanding of multiple ecosystem service delivery has benefitted perhaps most greatly from empirically driven investigations of the effects of land use change on sets of ecosystem services. These studies provide clear evidence for synergies and trade-offs. A meta-analysis of hundreds of agricultural development projects in developing countries found that these projects improved ecosystem service outcomes by encouraging the use of soil conservation measures, agroforestry, small-scale water harvesting, and integration of crop and livestock production (Pretty et al. 2006). Crop production increased, along with soil quality, carbon sequestration, and water availability. Together with a global model of terrestrial carbon sequestration potential
(Smith et al. 2008), these data support claims that targeted agricultural management can increase crop yields without diminishing other important ecosystem services (Cassman et al. 2003, Sanchez et al. 2007, Swinton et al. 2007).

In contrast, van Noordwijk et al. (2008) documented persistent trade-offs between carbon sequestration and land uses that local livelihoods rely on in rural Indonesia. The study used a spatially and temporally explicit model (van Noordwijk 2002) to simulate rotations of forests and crops, and found that a restricted solution space makes win-win scenarios improbable. This and other temporally and spatially explicit models (Barbier et al. 2008) effectively illustrate how land use and land cover change can generate landscape-wide synergies and trade-offs among services over relevant time-scales.

Over long time periods, trade-offs and synergies among ecosystem services can generate feedback loops that mediate social and ecological transitions. For example, unplanned agricultural intensification leads to a trade-off between crop production and soil quality, which results in degraded soils and low crop yields (Enfors and Gordon 2007). In the opposite direction, sustainable agricultural intensification can create synergies leading to soil improvement and greater agricultural production (Pretty et al. 2006).

Bennett et al. (2009) introduced a typology for characterizing ecosystem service relationships. The typology categorizes relationships among services according to two types of underlying mechanisms: whether common drivers influence pairs of services, and whether the pair of services themselves interact. In their typology, a shared driver may affect two services in the same direction, leading to a correlative synergy, or alternatively, a shared driver may enhance one service while impairing another, generating a correlative trade-off. However, ecosystem services may share common regulatory factors unrelated to environmental change, such as soil
types and topography, which cannot be meaningfully considered drivers; the terms ‘ecological factor’ and ‘management practice’ enable greater generality and are preferable to ‘driver’. Interactions among ecosystem services may result in causal trade-offs and synergies between services, in which one service directly affects another (unidirectional interaction), or two services affect one another (bidirectional).

The main value of the Bennett et al. typology is that when different types of mechanisms produce observed relationships among ecosystem services, potential leverage points for managing multiple services may differ. When there is no causal interaction between services, an observed correlation may be attributable to a third factor, e.g., an ecological factor or land management practice, and management that addresses the causal third factor could be sufficient to mitigate a trade-off or exploit a synergy. In contrast, when ecosystem services interact through causal linkages, management addressing the services themselves will likely be necessary to successfully minimize trade-offs and maximize synergies.

The growing literature on multiple ecosystem services provides little guidance to answer a variety of important questions pertaining to the needs of resource-limited smallholder farmers, whose livelihoods depend on ecosystem services. For example, how greatly does an ecosystem service, such as the wood produced in a given year, affect field-scale production of commodities over the next five years? Or, what ecological factors and management practices are key in determining the interactions of wood production with soil-based services and hence crop production over a five-year time horizon? What proportion of the economic value of a crop can be attributed to indirect effects of the trees harvested five years ago? What ecological dynamics must be accounted for to estimate the total economic value, in terms of wood produced as well as indirect effects on commodities later produced in the field, that can be attributed to one of
several tree species grown in mixture? How do the ecological effects and economic value of the trees diminish as years pass since their harvest? Did tree species richness or functional diversity improve wood production or soil quality, and if so, what economic value is attributable to a unit of tree diversity? What characteristics and behavior unique to smallholder agroecosystems influence joint levels of multiple ecosystem services? What management techniques most efficiently prevent soil degradation or enable soil rehabilitation by reducing trade-offs or enhancing synergies among services? Documenting important interactions affecting levels of multiple ecosystem services is one step toward using ecological and interdisciplinary research to answer these and other questions relevant to smallholder agriculture.

Improved understanding of the regulation of multiple ecosystem services has potential to enable more effective decision-making on the part of farmers, businesses, communities, and policy-makers seeking to achieve multiple management goals. Identifying and quantifying ecosystem service interactions may reduce the risk of unanticipated trade-offs, and enable fuller realization of opportunities provided by underutilized synergies. To improve understanding of the delivery of multiple ecosystem services, a framework is presented to conceptually integrate important ecosystem service interactions into the regulation of ecosystem services in tropical smallholder agroecosystems.

A framework for multiple ecosystem services in smallholder agriculture

A conceptual framework accounting for effects of ecosystem service interactions helps to disentangle the influences of multiple regulatory factors on sets of multiple ecosystem services.
The framework developed here is specific to smallholder agricultural systems in rural areas of developing countries, and draws its inspiration from smallholder systems in Sub-Saharan Africa. Understanding ecosystem service dynamics in smallholder farms is well worthwhile; among other reasons, land degradation and subsequent clearing of new agricultural land remains a predominant cause of deforestation in Sub-Saharan Africa, and agriculture is a significant driver of deforestation elsewhere in the tropics (Lambin et al. 2003).

Smallholder agricultural systems in the tropics have several characteristics making them well-suited to inquiry on multiple ecosystem services, and interactions among services. Smallholder farms tend to be more multi-functional (Altieri 1999) than commercial agriculture, with plants ranging from annual and perennial crops to livestock forages, to tree-crops, to trees for timber and construction material. Ecosystem services other than crop production, such as wood and livestock production, can be important subsistence needs and may be used to mitigate climatic risks (Enfors and Gordon 2007). Smallholder farmers are often unable to purchase external inputs, requiring the use of organic inputs and periodic land use rotations to maintain soil fertility, and leading to spatiotemporal exchanges in energy and materials. They often utilize trees that improve soil quality while also producing wood (Ståhl et al. 2002) or tree-crops (Schroth et al. 2002), as well as perennial crops that may restore soil fertility following annual crops (Fermont et al. 2008). Each of these characteristics increases the potential for synergies and trade-offs among ecosystem services in smallholder agriculture.

The integrated nature of services in smallholder agroecosystems is most evident in the tendency of smallholders to produce multiple agricultural commodities, and in the centrality of NPP, soil formation, and nutrient cycling in linking together the ecosystem services most important to farming households. Significantly, the high degree of integration and interaction
among ecosystem services in smallholder systems enables all regulatory influences on ecosystem services to be viewed purely in terms of the interactions among services. The ecology of some smallholder agroecosystems has been characterized fairly well, providing opportunities for making explicit linkages among services. Since the relevant spatial units are relatively small (e.g., plant neighborhoods, fields/patches/stands, farms) and smallholder farms often fall under private ownership, management has clear linkages with the production and accrual of the benefits from ecosystem services at the farm or household scale.

Types of ecosystem service interactions

The framework proposed here seeks to embody the multi-functionality and potential for ecosystem service interactions in smallholder systems. Ecological production functions are partitioned into a series of ‘interaction functions’ that account for the influences of ecology and management on ecosystem services over a given time period. For brevity, the framework presented here encompasses a set of services limited to those most frequently relevant to the sustained capacity for agricultural production: crop production, wood production, annual net primary productivity (ANPP), soil formation, and nutrient cycling in soils. The framework could extend to include other services accruing at or below the farm scale, such as pollination, pest and disease regulation, and carbon sequestration, with minimal modification. To incorporate public goods and ecosystem services requiring large areas to characterize production of the service would require expansion. Rather than scaling downward from above, the framework allows for understanding of ecosystem service delivery within smallholder ownership boundaries, and provides a foundation for building upward to dynamics at landscape or regional scales.
Here, relationships among ecosystem services are treated as ‘direct’ interactions, ‘opportunity’ interactions, and ‘indirect’ interactions (Box 1.1). In a ‘direct’ interaction the ESPs for one service directly alters production of another service (Figure 1.1). ‘Opportunity’ interactions result purely from trade-offs in allocating parts of the farm to various land uses. ‘Indirect’ interactions occur when the supply rates of two services are positively or negatively correlated, due to both services being influenced by a third factor, particularly ecological factors and management practices that affect both services.

In a ‘direct interaction,’ the ESPs providing one service have a direct and unequivocal influence on the ESPs providing a second service. Direct interactions may be mediated not only by relatively ‘fast’ ecosystem variables, detectable over within-season time-scales, but also ‘slow’ ecosystem variables operating over multiple years or longer time periods. Direct interactions among the services considered here include, among others, the positive influences of soil formation and nutrient cycling in soils on ANPP, and the reciprocal effect of ANPP on soil processes (Box 1.1, Figure 1.1). Such interactions can occur through a variety of mechanisms; for example, trees may improve soil fertility and structure not just directly via litter inputs, but also through additional benefits such as providing arbuscular mycorrhizal inoculum and supporting populations of beneficial soil organisms. The direct interaction of ANPP with the production of crops and wood is a special case, as the ESPs for the two services are the same plants; the amounts of harvestable crops and wood produced depends on the NPP of crops and trees, as well as the relative allocation of photosynthate in these plants to harvestable tissues. Note that the usage of ‘direct’ here is much broader than ‘direct interactions’ among species in community ecology.
‘Opportunity’ interactions are trade-offs mediated by land allocation. These interactions reflect the reciprocal opportunity costs inherent in allocating land to any given land use or ecosystem service (Antle and Valdiva 2006), which necessarily comes at the expense of alternative land uses and ecosystem services derived therein. Land devoted to soil fertility and soil nutrient cycling includes fallows not managed to produce wood, and rotational cover crops. Opportunity interactions involve land allocated to all ecosystem services except for ANPP, which farmers do not explicitly manage for. For ANPP, opportunity interactions are simply a function of the amounts of land allocated to production of crops, wood, and soil fertility and nutrient cycling.

In an ‘indirect’ interaction, two ecosystem services have correlated supply rates due to the influence of a third, shared regulatory factor that affects the ESPs of both services (Box 1.1). Two subtypes of indirect interactions are considered here, namely management practices applied within fields that affect the service currently being produced as well as production of services under the subsequent land use, and regulatory ecological factors that two services share in common. The subtypes are respectively termed ‘management-mediated’ interactions and ‘indirect ecological’ interactions. A variety of management practices can affect multiple ecosystem services, such as soil tillage which negatively affects soil structure, and is thus likely to affect the capacity of soils to support plant growth and NPP, as well as the production of commodities. Abiotic ecological factors such as temperature and precipitation, and biotic factors such as the prior NPP of a field, affect soil processes as well as ANPP and production of crops and wood in a given year. Thus, any apparent trade-off or synergy among services such as these may be entirely the product of a separate underlying mechanism in the agroecosystem, unrelated to any direct interaction among the ESPs of the services. The functioning of agroecosystems centers on the responses of the vegetation and soil subsystems to management, which
subsequently determine the potential to produce ecosystem services. Indirect interactions may
result from correlated responses to shared drivers of environmental change, including global
drivers of change in climate, plant nutrient use, land use, disease, and biological invasions (Nelson
et al. 2006). However, a variety of ecological factors may influence a given pair of services, many
of which cannot be meaningfully considered drivers of environmental change.

The high degree of integration and interaction among ecosystem services in smallholder
systems enables all regulatory influences on ecosystem services to be viewed purely in terms of
the interactions among services. In the framework proposed herein, a profile $P$ of ecosystem
services is a vector of the supply rates $S$ for each ecosystem service $i$ derived by a smallholder
farmer or household from their land. The interaction functions $D_i$, $O_i$, $M_i$, and $E_i$ portray
significant ecosystem service interactions that underlie the production of ecosystem service $i$.
Interaction functions $D_i$, $O_i$, $M_i$, and $E_i$ refer to, respectively: direct, opportunity, indirect
management-mediated, and indirect ecological interactions. The profile $P$ is given by the
cumulative influence of ecosystem service interactions,

$$P = (S_1, \ldots, S_n) = (D_1, \ldots, D_n) + (O_1, \ldots, O_n) + (M_1, \ldots, M_n) + (E_1, \ldots, E_n).$$

To restrict the framework to the most fundamental interactions between on-farm
ecosystem services, it is assumed (somewhat unrealistically) that crops and trees do not interact
directly. Such interactions are known to occur via modification of microclimate, soil erosion
control, pest and disease regulation, and tree-crop competition. Inclusion of these effects would
enable consideration of spatial interactions among ecosystem services, as well as tree intercrops
and multi-strata agroforestry systems. Here, however, the focus is on the most common and
significant interactions among services that regulate the sustained capacity for agricultural
production in smallholder agroecosystems, which operate to a great extent through temporally-
mediated interactions among services.

The ecology and management of multi-functional smallholder agriculture

A key objective of the proposed framework is to illustrate how ESPs may affect more than
one ecosystem service over time, through the interactions among services. ESPs in smallholder
systems influence multiple services through a combination of direct and indirect linkages. For
example, the ANPP of trees in a field directly influences soil formation and nutrient cycling
through the amount and quality of litter deposited. If a crop is grown at the next time interval,
the effect of tree ANPP on soils will indirectly influence crop ANPP, and crop production. At a
third time interval, the initial tree ANPP will likely retain a diminished influence on soil
conditions, directly as well as through the indirect effect on crop ANPP. Starting with a crop field
instead, crop ANPP would similarly affect soil functioning (more positively so with retention of
crop residues), and crop ANPP will likewise indirectly influence ANPP and commodity
production at the next time interval, and so on. In this way, any ecosystem service supplied by a
field at a given point in time sequentially affects future supply rates of ecosystem services in that
field, the effect diminishing to some degree over time.

In addition to direct and indirect ecological interactions among services, management
affects the delivery of ecosystem services in current and future time intervals. Effects of
management practices on soil quality result in propagation of their influence through time,
largely by altering exchanges of energy and materials between above- and belowground
subsystems. The reciprocal opportunity costs of allocating fields to one land use versus another
affect the amount of area in which ecosystem services are supplied at various rates. They furthermore alter the potential of indirect effects of ecological factors and management practices to influence future delivery of ecosystem services, depending on what specific plants and management practices are employed in various land use types. Management appears to be crucial to ecosystem service interactions, especially since it can alter feedbacks controlling agricultural production capacity. In smallholder systems the use of reduced tillage, soil conservation structures, and targeted fertilization can slow erosion and improve crop yields, stimulating further investment in maintaining productive soils (Gordon and Enfors 2008). Greater wood production is an additional benefit where resource-conserving management approaches involve agroforestry, and other services such as water regulation may also improve. From a global perspective, the same feedbacks affect the capacity of agroecosystems to sequester carbon in soils and vegetation (Smith et al. 2008). This synergy may eventually yield local benefits as well (Unruh 2008), to the extent that payments for carbon sequestration can feasibly reach resource-poor farmers.

Despite their importance, the mechanisms by which many soil organisms provide ecosystem services in soils are not well understood, nor are responses of soil communities to management. Although their roles in agroecosystems are difficult to quantify, soil communities have incontrovertible value to agricultural production. Soil macrofauna such as earthworms can act as ecosystem engineers by mixing soil layers and promoting soil aggregation, and are affected by inputs of organic resources as well as soil disturbance (Swift et al. 2004). Soil macrofauna and microbes improve the uptake and use efficiency of nutrients and water by crops and provide resistance to disease and drought (Brussaard et al. 2007). Most crop species have arbuscular mycorrhizal (AM) fungal symbionts, yet soil tillage and other common management practices are
detrimental to AM fungi (Gosling et al. 2006). In addition, fertilization can shift interactions of plants with root-associated AM fungi and rhizobia from being symbiotic to parasitic (Kiers et al. 2002). Beneficial soil microbes can be managed directly through inoculation with AM fungi (Munyanziza et al. 1997), and rhizobia in legumes (Onduru et al. 2008). Because soil communities are difficult to manipulate directly, effective approaches will probably depend on targeted combinations of inputs and management practices such as reduced soil tillage and cover crops that favor desirable soil fauna (Brussaard et al. 2007). Since soil communities provide important services in agriculture, and often respond to management and soil inputs, better understanding of their roles and responses in agriculture is likely to help shift interactions away from trade-offs and toward synergies.

At a given point in time, the net benefits of prior land use are embodied in the value of current agricultural production. Ecosystem service valuation cannot completely account for many benefits provided by ecosystems (NRC 2005), leading to chronic underestimation. Valuation using the framework as a guiding structure should partition the final market values of multiple services among the contributions of ESPs, the diversity of ESPs, and other ecological factors. Failing to partition multiple influences of ecological variables on ecosystem services would lead to the ecological equivalent of counting intermediate consumption, the value of goods and services used up during production (Matero and Saastamoinen 2007), in national or environmental accounting. In agricultural systems, the costs of previous land uses may be manifested as degradation and lower production, while favorable soil conditions and agricultural production capacity derive benefits from effective past management. If valuation does not consider legacies of effective prior land management as components of the value of current
production, the result is to underestimate the total value attributable to ESPs and other ecological
factors in earlier years, that contributed indirectly to production in the current year.

For example, trees often have higher NPP and benefit soil formation and the cycling and
retention of nutrients, and when a plot of trees is converted, crop production is also likely to
benefit. Unfortunately, trees often decline early in the process of agricultural intensification
(Gibbons et al. 2008). The remaining woody plants can be a pivotal component of functional
diversity in agricultural landscapes dominated by crops, grasses and other herbaceous plants, and
may contribute to counteracting land degradation and rehabilitation of degraded soils. If the
value of the trees in a field are assessed solely on the basis of wood production in a single
rotation, we effectively ignore their value to other services. Doing so underestimates
complementarities of trees with ESPs providing other services at later time points, and the
cumulative contribution of trees to the value of agricultural output of the field over several years.

The biodiversity of ESPs—e.g., species, functional, and habitat diversity—is likely to
affect delivery of multiple ecosystem services. The diversity of a given group of organisms can
potentially influence any ecological or management interaction in the agroecosystem, whether
directly or indirectly. Recent studies based on grassland biodiversity manipulation experiments in
Europe (Hector and Bagchi 2007, Gamfeldt et al. 2008) and North America (Zavaleta et al. 2010)
have found that plant species richness increased the ability of plant communities to support
multiple ecosystem functions. Several possible mechanisms may explain influences of biodiversity
on multiple functions.

Plant species complementarities among ecosystem functions are one mechanism that may
link biodiversity with multiple functions. Although similar species are commonly redundant in
their effects on a particular ecosystem function, a pair of species redundant for one function may
possess traits making them more distinct from one another (i.e., less redundant) in their effects on another function (Hector and Bagchi 2007). Functional uniqueness of species among ecosystem functions, and consequently greater cumulative complementarity among the species in a community, may improve ecosystem multi-functionality. For example, crops produce edible carbohydrate in large quantities, but cannot supply wood or sequester carbon in plant tissues; while most tree biomass is inedible they produce wood and sequester carbon. On an annual basis, NPP of trees is higher than for crops, and they generate greater quantities of litter. Litter inputs from both crops and trees improve soil fertility, yet trees are often more beneficial to soil structure and soil hydraulic properties (Ilstedt et al. 2007). More labile C substrates such as annual crop residues can increase soil respiration, and annual cropping systems can further increase soil respiration due to low vegetation cover at the soil surface, soil tillage (La Scala et al. 2006), and erosion (Lal 1996), often leading to SOC losses (West and Post 2002). More labile inputs of crop residues decompose and provide soil hydrological function more quickly than more recalcitrant inputs such as the litter of many tree species, while the effects of recalcitrant inputs are likely to be more lasting (Bronick and Lal 2005). Thus, plant functional traits in conjunction with management practices can lead to divergent effects of crops and trees on different ecosystem services provided by soil subsystems, over different time-scales.

Another mechanism may arise from ‘multi-functional’ species capable of contributing effectively to more than one ecosystem service simultaneously. Two species of ‘multi-purpose’ trees commonly used in agroforestry systems, *Sesbania sesban* (L.) Merr. and *Calliandra calothyrsus* Meissn., serve as good examples. *Sesbania* is highly productive compared to other agroforestry trees, and both species are capable of fixing over 50% of their N content from the atmosphere, and preventing NO$_3^-$ leaching losses (Ståhl et al. 2002). *Calliandra* has high content of polyphenols
in tissues both above- and belowground (Lehmann et al. 1998), and may be effective for building long-lived soil C pools, with possible further benefits for the structure and hydraulic properties of soils. Some perennial crops are multi-functional, including cassava (*Manihot esculenta* Crantz), which may restore soil fertility following annual crops (Fermont et al. 2008). Various cultivars of banana and plantain (*Musa* spp.) are eaten as fruits or as a staple carbohydrate in parts of East Africa, probably conserve soils compared to annual cropping systems, can serve as a canopy for coffee (Oduol and Aluma 1990) and provide habitat for birds and bats (Harvey and González Villalobos 2007) that may regulate insect pests. Multi-functional species may possess unique combinations of functional traits, or their abundance may increase probabilistically with species richness.

Finally, species may influence ecosystem functions indirectly. Plant species may benefit other species through facilitation or indirect positive interactions, including trophic interactions. For instance, a plant species redundant with others for a particular function may benefit a species that is functionally unique for that function. Species unique among an assemblage in providing litter or microhabitats that suit ecosystem engineers (Jones et al. 1994, Anderson 1995) such as earthworms, termites, and other soil macrofauna may indirectly enhance the performance of other species.

Thus the diversity of soil biota may also contribute to observed effects of plant diversity. The diversity of soil organisms is linked to plant functional traits (Wardle et al. 2003, Tedersoo et al. 2006) and can increase with plant diversity (Spehn et al. 2000, Stephan et al. 2000). Though poorly understood, soil macrofauna can have strong effects, and very different effects, on soil processes in agroecosystems (Beare et al. 1997). Different plant species that support different macrofauna can increase ecosystem process rates in soils and litter in mixed assemblages (van
Eekeren et al. 2009). Effects of plant species on communities of soil organisms could generate positive feedbacks on the performance of the plant community by improving the fertility and structure of soils. The diversity of soil organisms can influence soil processes (van der Heijden et al. 1998, Gessner et al. 2010), and strong interactive effects of functionally differentiated soil macrofauna on decomposition and microbial activity been demonstrated experimentally (Heemsbergen et al. 2004). Nonetheless, the implications of the diversity of soil organisms for soil processes are poorly understood (Hättenschwiler et al. 2005, Brussaard et al. 2007) and remains a rich area for future work.

Conclusions

Accounting for the contributions of ESPs, the diversity of ESPs, and other ecological factors to multiple ecosystem services will ultimately enable more complete recognition of their full roles in agroecosystem functioning and sustained agricultural production, and thus their contributions to human well-being. In many systems, including smallholder agroecosystems, temporally-mediated ecosystem service interactions can affect the overall state of the ecosystem, and thus the potential benefits provided. However, interactions occurring over long time scales are more difficult to detect. The studies that provide the greatest insight into delivery of multiple services either employ dynamic or time-step models, or use data reflecting patterns and processes operating over annual or greater time scales. Long temporal extents are key to feedback loops and the social and ecological transitions they can generate.
Interactions and feedbacks among ecosystem services increase the cumulative values attributable to ecological factors responsible for the delivery of ecosystem services in agriculture. Further research on ecological regulation of ecosystem services and responses of regulatory factors to management will provide a basis for establishing useful ecological production functions for non-provisioning ecosystem services in agricultural systems. Because resource-poor farmers have little recourse to external investments and depend on supporting and regulating ecosystem services, smallholder agricultural systems should be prioritized for research on multiple ecosystem services.

Slowly changing ecosystem variables and time-lags in the effects of ecological factors are inherent in the functioning of agroecosystems and remain a major challenge in designing effective management. Viewing agriculture from a perspective of multiple ecosystem services assists in understanding feedback loops in agricultural systems, especially those affecting agricultural production capacity in smallholder systems. Management techniques that replace nutrients lost through harvest, and reduce erosion and leaching losses of nutrients, can shift deleterious trade-offs that cause land degradation into promising synergies and agroecosystem restoration. Positive feedbacks may alternately threaten or improve local livelihoods, depending on the extent to which management generates trade-offs versus synergies between provisioning services and supporting and regulating services.

Much work remains ahead in investigating long term effects of the variety of management practices employed worldwide on the sets of multiple ecosystem services provided by the agroecosystems of the planet. Clearly, differences in management can alter ecosystem service interactions. The next step is to more precisely identify the mechanisms that enable changes in management to alter service interactions. Despite significant progress in quantifying
effects of plant functional traits on soil processes and properties, the effects of soil inputs vary across management regimes and with environmental conditions. Combinations of inputs and management regimes may be identified that effectively improve crop production together with other important ecosystem services such retention of soil nutrients, field-scale soil hydrological functioning, and water regulation at larger scales. Soil communities remain an enigmatic component of agroecosystems, especially soil microbes. More precise quantification of the fundamental roles of soil communities in agricultural systems, and how soil communities respond to management practices and soil inputs, may improve synergies among multiple services in agriculture. Technological advancement in molecular characterization of microbial communities and detection of enzymatic activity may well revolutionize agricultural soil science by elucidating the aboveground consequences of soil microbial activity.

It is important to consider that since ecosystem service values depend on fluctuating market prices, variation in the ecological supply of an ecosystem service is unlikely to be linearly related to variation in the value of the service. Ultimately, ecosystem service magnitudes are primarily a concern of the ecologist. When economic values are applied to service magnitudes, they become tender for conversation with a farmer or an economist. Even when ecological evidence exists for an interaction among ecosystem services, in all but the clearest of cases valuation will be required to assess whether or not the interaction in fact also generates a trade-off or synergy in terms of the values accruing to beneficiaries. The role of the ecologist is to ensure that market prices account for the behavior of ecosystems as accurately as possible, so that fewer benefits and costs are hidden, and ecosystem management can take them into consideration. As our ability improves in detecting multiple influences of ecological factors on ecosystem services, we should expect an increase in the values attributable to ESPs, biodiversity,
and ecological factors in general that benefit human well-being by providing valuable ecosystem services.
**Box 1.1. Conceptual framework: Multiple ecosystem services in smallholder agroecosystems.**

The framework illustrates interactions among crop production (CP), wood production (WP), annual net primary productivity (ANPP), and soil formation and nutrient cycling in soils (SFNC). A profile \( P \) of ecosystem services is a vector of the supply rates \( S \) for each ecosystem service \( i \) demanded by a smallholder farmer or household, and is given by the cumulative influences of interactions among ecosystem services:

\[
P = (S_1, \ldots, S_n) = (D_1, \ldots, D_n) + (O_1, \ldots, O_n) + (M_1, \ldots, M_n) + (E_1, \ldots, E_n),
\]

where \( D_i \) = Direct ecological interaction function for ecosystem service \( i \), \( O_i \) = Opportunity interaction function, \( M_i \) = Indirect management-mediated interaction function, and \( E_i \) = Indirect ecological interaction function.

**Direct ecological interactions:**

<table>
<thead>
<tr>
<th>Ecosystem service</th>
<th>Interaction function</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crop production (CP)</td>
<td>( D_{CP} = f(SFNC, ANPP_{Crop}) )</td>
</tr>
<tr>
<td>Wood production (WP)</td>
<td>( D_{WP} = f(SFNC, ANPP_{Tree}) )</td>
</tr>
<tr>
<td>Productivity (ANPP)</td>
<td>( D_{ANPP} = f(SFNC) )</td>
</tr>
<tr>
<td>Soil formation/nutrient cycling in soils (SFNC)</td>
<td>( D_{SFNC} = f(ANPP_{Crop}, ANPP_{Tree}, ANPP_{Fallow}, Soil respiration, Nutrient depletion) )</td>
</tr>
</tbody>
</table>

**Opportunity interactions:**

<table>
<thead>
<tr>
<th>Ecosystem service</th>
<th>Interaction function</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crop production (CP)</td>
<td>( O_{CP} = f(Area_{CP}, Area_{WP}, Area_{SFNC}) )</td>
</tr>
<tr>
<td>Wood production (WP)</td>
<td>( O_{WP} = f(Area_{CP}, Area_{WP}, Area_{SFNC}) )</td>
</tr>
<tr>
<td>Productivity (ANPP)</td>
<td>( O_{ANPP} = f(Area_{CP}, Area_{WP}, Area_{SFNC}) )</td>
</tr>
<tr>
<td>Soil formation/nutrient cycling in soils (SFNC)</td>
<td>( O_{SFNC} = f(Area_{CP}, Area_{WP}, Area_{SFNC}) )</td>
</tr>
</tbody>
</table>

**Indirect management-mediated interactions:**

<table>
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<tr>
<th>Ecosystem service</th>
<th>Interaction function</th>
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<tr>
<td>Crop production (CP)</td>
<td>( M_{CP} = f(Soil tillage, Fertilization, Soil conservation measures, Woodlot duration, Fallow duration) )</td>
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<td>Wood production (WP)</td>
<td>( M_{WP} = f(Soil tillage, Fertilization, Soil conservation measures, Woodlot duration, Fallow duration) )</td>
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<td>Productivity (ANPP)</td>
<td>( M_{ANPP} = f(Soil tillage, Fertilization, Soil conservation measures, Woodlot duration, Fallow duration) )</td>
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<tr>
<td>Soil formation/nutrient cycling in soils (SFNC)</td>
<td>( M_{SFNC} = f(Soil tillage, Fertilization, Soil conservation measures, Woodlot duration, Fallow duration) )</td>
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**Indirect ecological interactions:**

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<tr>
<td>Crop production (CP)</td>
<td>( E_{CP} = f(Temperature, Precipitation, Soil respiration, Nutrient depletion, ANPP_{tree}, ANPP_{Fallow}) )</td>
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<tr>
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<td>( E_{WP} = f(Temperature, Precipitation, Soil respiration, Nutrient depletion, ANPP_{Crop}, ANPP_{Fallow}) )</td>
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Figure 1.1. Direct ecological interactions among ecosystem services important to smallholder farmers. Crop production, wood production, annual net primary productivity (ANPP), and soil formation and nutrient cycling in soils (SFNC) interact directly with one another in smallholder agroecosystems. Here, SFNC is represented as dimensionless, however it reflects annual relative changes in important elements of soil quality (e.g., SOC, stocks of various chemical forms of N and other nutrients, soil infiltration capacity, soil aggregation). Removal of nutrients in harvested plant tissues, leaching, and erosion account for most nutrient depletion. Among other factors, labile C substrates such as crop residues can increase soil respiration compared to more recalcitrant litters. Allocation refers to allocation of photosynthate within individual plants.
Chapter 2: Vegetation mediation of land use effects on soil organic carbon and soil infiltration capacity

Abstract

A primary goal of fallows in tropical smallholder agriculture is to improve the fertility and structure of soils to achieve a higher subsequent crop yield. The effectiveness of fallows for improving soil quality is likely to vary with abiotic factors, the composition of fallow vegetation, whether fallows are grazed with livestock, and land use history. Soil organic carbon (SOC) and soil infiltration capacity are key indicators of soil quality in agricultural systems, and are significantly affected by attributes of fallow vegetation, especially the quantity and quality of above- and belowground plant litter inputs. To assess whether the characteristics of fallow vegetation mediate effects of fallow type on SOC and infiltration capacity, a study was conducted in fallow fields of smallholder farms in Siaya District, western Kenya. In 23 grazed fallows and 23 improved fallows, stem diameter of trees and cover and height of shrub and herb species were measured and used to estimate biomass. Near infrared spectroscopy was used to predict soil properties (SOC and sand content), and steady infiltration rates were estimated from asymptotic regression of ring infiltrometer data. SOC and infiltration rates were hypothesized to decline with grazing due to trampling and biomass removal by livestock, to increase with standing green biomass due to potentially greater litter input quantity, and to increase with green tissue contents of N and lignins+polyphenols (LPP) due to contrasting effects of vegetation associated with litter input quality (N content is associated with biological nitrogen fixation and biomass production;
LPP reduces SOM turnover). Model comparison via AICc and model averaging for generalized linear models demonstrated that green tissue LPP content was the only attribute of vegetation with apparent positive influence on both SOC and steady infiltration rates. Infiltration was lower in grazed than in improved fallows, but SOC did not vary among the two fallow types, suggesting an effect of livestock trampling. SOC was positively associated with sand content, likely due to less intensive past cropping of sandier fallows, while infiltration exhibited a non-linear pattern in relation to sand content. Positive effects of vegetation with high recalcitrant C content (LPP) on SOC and infiltration may be attributable to slower SOM turnover, build-up of long-lived SOC pools, and improvement of soil structure, thus enhancing soil infiltration capacity. However, litter input quality could not be definitively separated from input quantity. The results suggest that in smallholder agroecosystems, the functional traits of fallow species may be a reliable indicator of how substantially a fallow with a particular vegetation composition will support ecosystem services provided by soil organic matter.

**Introduction**

In rural areas throughout Sub-Saharan Africa, the historically predominant approach to replenishing soil fertility was to leave fields in spontaneous fallows of natural vegetation that regenerates after cultivation. With rapid population growth, farmers throughout the global tropics have been forced to leave progressively little land out of cultivation, and consequently soil degradation and declining soil fertility have become widespread (Mosier 1998). Research into practical means of maintaining soil productivity and rehabilitating degraded soils has identified
strategies of integrating cropping with production of woody and herbaceous perennials, usually N-fixing leguminous species. The effectiveness of fallows planted with woody leguminous species, often referred to as improved fallows, for improving crop yields has been debated, yet a meta-analysis demonstrated that several approaches involving the addition of leguminous species to fallows increased maize yields (Sileshi et al. 2008). Rural development projects have found that improved fallows and other ways of integrating woody legumes with crops hold promise for improving crop yields while also producing much-needed fuelwood (Pretty et al. 2006, Sanchez et al. 2007).

In western Kenya, social and economic constraints on agricultural management begin with the high population density in the region, and at the household scale frequently include large family sizes, periodic hunger, and limited land, capital, market access, and off-farm income (Mutuo et al. 2007). Households typically allocate fields with more productive soils to nutrient-demanding annual crops, continuously or nearly so. Fast-maturing improved fallows are sometimes planted in these fields to help maintain soil fertility. Less productive areas are typically allocated to less pressing needs: extensive grazing and wood production in natural fallows, woodlots (esp. *Eucalyptus* spp.), and production of thatch (especially *Andropogon gayanus*). Such fields are cropped infrequently, and these land use types often persist for long periods of time, perhaps because rehabilitation could require costly investments of fertilizer, improved fallow seeds, labor, etc. Some fields may be left in grazing partly because livestock, especially cattle, are rarely sold as they confer social status and an economic buffer in leaner times.

The constraints facing farmers induce them to produce goods in every field, including those not being cropped. Thus, fallows are rarely the natural fallows historically common in African agriculture, often termed ‘bush’ or ‘long’ fallows, left to undergo natural succession.
Fallows common in western Kenya include improved fallows, as well as extensive fallows, often referred to as ‘natural’ fallows, which are variably composed of native plants, weeds, and invasive and naturalized exotics. Improved fallows are typically ungrazed and produce significant quantities of wood, while extensive fallows provide variable quantities of wood and forage for grazing livestock. Differences in fallow land use and management are likely to affect soil quality, in conjunction with associated differences in the frequency and duration of fallow and crop rotations. As a result, the management of fallows on smallholder farms involves potential trade-offs and synergies among ecosystem services provided during periods of fallow, as well as with subsequent provision of other ecosystem services. In this study, the focus is on the provisioning services of production of wood and forage, and the supporting service of soil formation.

After climatic and edaphic factors, the quantity and quality of litter inputs are among the predominant ecological factors that regulate the functioning of soil subsystems (Wardle 2002, Wardle et al. 2004). Net primary productivity (NPP) largely determines the amounts of organic inputs to soils, while the quality of these materials significantly controls rates of transformation by soil organisms and modification by physical and chemical processes (Cadisch and Giller 1997, Bronick and Lal 2005). Soil organisms process organic inputs, breaking them down into simpler forms, and in the process improve the fertility and structure of soils.

Litter quality is a suite of plant traits that determine the susceptibility of organic residues to decomposition. Three important and widely studied elements of litter quality are N content (or C:N ratio), lignin content, and phenolic content (Cadisch and Giller 1997). Litters of different qualities vary in their palatability to herbivores, as well as the capacity to support the activity of soil organisms. High quality litters with low C:N (i.e., high N content) tend to have high content of labile C compounds that support rapid microbial breakdown and decomposition, and
mineralization of C and nutrients in litter (Gentile et al. 2009). In contrast, lower quality litters decompose more slowly, such that C and nutrients are mineralized over a longer time period, due to high C:N or a high proportion of recalcitrant C compounds (Vanlauwe et al. 2005) resistant to microbial breakdown (de Boer et al. 2005). Recalcitrant forms of C such as lignins and polyphenols are known to be involved in the formation of humus and other long-lived soil C pools (Zech et al. 1997).

Soil organic carbon (SOC) affects soil processes important for plant growth, and is therefore an important indicator of soil quality in agricultural systems (Arshad and Martin 2002). Cycling of C and N through ecosystems tends to be coupled. In agroecosystems, agricultural management affects the degree to which soil C and N are maintained, increased (Blair et al. 2006b), or together decline during degradation (Mosier 1998), especially over long time-scales. SOC enhances the bioavailability of soil nutrients and increases nutrient retention in soils by providing cation exchange capacity (Bell et al. 1998) and binding nutrients in soil organic matter (SOM), the recalcitrance of which determines the time-scale of nutrient release (Barrios et al. 1997, Vanlauwe et al. 2005).

Soil infiltration capacity, the ability of water to enter the soil surface, is a similarly useful indicator of soil quality in agricultural systems (Arshad and Martin 2002). Infiltration rates are high when soil porosity is high and bulk density is low, and are expected to be higher for soils of a sandy texture (Siriri et al. 2006). High infiltration rates for a given soil texture are indicative of robustly structured soils that experience less runoff and soil erosion, and often have greater water storage capacity (Seobi et al. 2005). Since infiltration is responsive to changes in soil aggregation, bulk density, and porosity, it is sensitive to physical soil disturbance (Salako and Kirchhof 2003, Siriri et al. 2006) and channels created by plant roots (van Noordwijk et al. 1991). By altering soil
structure through inducing aggregation of soil particles and reducing soil bulk density (Martens 2000), SOM increases infiltration capacity and water retention (Seobi et al. 2005). Soil hydraulic functions can be performed by both labile (Blair et al. 2006a) and recalcitrant (Martens 2000) SOM fractions, probably over different time-scales. Labile SOM fractions and their physical effects are more responsive to changes in inputs and soil disturbance, while the effects of recalcitrant forms are probably more lasting (Bronick and Lal 2005), on account of longer residence times.

In western Kenya and elsewhere in the humid tropics, land use factors relevant to soil quality include grazing, fallow type (here, improved versus extensive grazed fallows), and the frequency and duration of fallow and crop rotations. In the study area, improved fallows are more productive, with leguminous species that fix N and produce N-rich litter. Livestock grazing may influence SOC stocks by reducing litter inputs and altering plant functional traits and thus litter quality. Grazing may furthermore reduce infiltration rates due to trampling by livestock and soil compaction. As such, improved fallows might be expected to have greater SOC stocks and infiltration rates than grazed fallows. However, influences of land use on soils were expected to vary according to how edaphic conditions, especially soil texture, may influence agricultural management regimes.

The objective of this study was to assess whether the characteristics of fallow vegetation mediate effects of fallow type on SOC and soil infiltration capacity. SOC and infiltration rates were hypothesized a priori to be lower in grazed than in improved fallows, on account of consumption and removal of biomass by grazing livestock and, for infiltration rates, trampling by livestock. SOC and infiltration rates were furthermore hypothesized a priori to increase with: A) standing green biomass, due to greater biomass production and potentially higher litter inputs; B)
green tissue N content, due to its association with biological nitrogen fixation and greater biomass production by legumes; and C) green tissue content of lignins and polyphenols, on account of recalcitrant C compounds possibly reducing SOM turnover.

Methods

Study systems. The Millennium Villages Project (MVP) is an evidence-based approach to alleviating extreme rural poverty in sites throughout Sub-Saharan Africa, in which agricultural development plays a strategic role (Sanchez et al. 2007). The data for this study were collected in 2008-2009 in the Sauri MVP site in Siaya District, western Kenya.

Sauri MVP has a humid tropical climate with two rainfall peaks and potential cropping seasons yearly, and elevation ranges from 1,300 to 1,470 m. The clayey, well drained Oxisols and Ultisols are soil orders representative of soils common in Sub-Saharan Africa. The landscape in Sauri is a shifting agricultural matrix primarily composed of maize and other annual crops, with lower landscape cover of woodlots, land dedicated to grazing, and fallow fields. Land use in the area cycles between periods of annual crops, and periods of fallow intended to regenerate soil fertility and to provide wood products, green manures from foliage of woody plants, and forage for livestock, among other goods. High population density, high cropping frequency and inadequate fertilization having led to degradation since the early 20th century (Scherr 1995), and soils in the area are relatively depleted of N and C. However, Sauri agroecosystems may currently be undergoing long-term rehabilitation.
**Fallow type.** ‘Improved’ fallows of fast-growing leguminous trees are promoted by MVP to improve soil fertility and fuelwood. They are usually planted with *Téphrosia candida* DC, and less commonly with *Crotalaria paulina* Schrank, *Calliandra calothyrsus* Meissn. or other exotics, and are not grazed with livestock. Grazed fallows, often considered ‘natural’ or ‘weed’ fallows, are less common, and contain a variety of species, most of which are native. The most common trees in grazed fallows are the native *Markhamia lutea* (Benth.) K. Schum., *Sesbania sesban* (L.) Merr., and the exotic *Psidium guajava* L. Most grazed fallows combine production of wood and green manures with livestock grazing, although heavily grazed fallows do not produce wood.

**Data collection.** Fallow fields identified for sampling ranged from 0.02 to 0.25 ha in area, with a mean size of approximately 0.1 ha. Data were collected from 18 grazed and 21 improved fallows. Data were collected using a slight adaptation of the Land Degradation Surveillance Framework (LDSF; Walsh and Vagen 2006), modified for field-scale sampling. LDSF involves characterization of vegetation structure (diameter at breast height (DBH) and height of trees, tree and shrub stem density, and vegetation cover), soil conditions (soil properties, soil infiltration capacity, rock cover and erosion), and FAO-standard land use/cover. Soils were sampled at depths of 1-20 cm (topsoil) and 20-50 cm (subsoil).

The LDSF protocol was reproduced at the scale of a single 100 m² plot located randomly in the interior of each fallow. Two 2 m² subplots were established within each 100 m² sample plot, one in the center, and one randomly located tangent to the plot edge. Soil samples were collected and soil infiltration capacity measured in both subplots. Biovolume (m³) of each plant species was characterized by visually estimating cover and average height. Cover was scored as the mid-point of cover classes on a 5-point scale: 1-4, 4-15, 15-40, 40-65, and > 65 m².
intensity was recorded by visually estimating cover for evidence of grazing—bite marks, trampling, feces, and hair—on the same 5-point scale.

**Standing biomass—large woody stems.** For all woody stems $\geq 2.5$ cm DBH, aboveground standing biomass (t ha$^{-1}$) was estimated by using DBH measurements to calculate whole-tree biomass ($Y$) by the general allometric equation, $Y = e^{-2.134 + 2.53 \ln DBH}$ for humid regions (Ponce-Hernandez 2004). To estimate belowground biomass, aboveground biomass estimates were multiplied by the mean of values from the literature for root-to-shoot ratio (RSR) of tree species common in the study site (Appendix A). Above- and belowground biomass estimates were summed to estimate total standing biomass.

**Standing biomass—small woody stems and herbaceous species.** For all woody plants $< 2.5$ cm DBH and all non-woody species, cover estimates were multiplied by average height to estimate biovolume by species, then multiplied by a conversion factor to estimate aboveground biomass (Appendix A). To estimate belowground biomass, aboveground biomass estimates were multiplied by the mean of values from the literature for RSR of species common in the study site (Appendix A). Above- and belowground biomass estimates were summed to estimate total standing biomass.

**Standing green biomass.** To obtain estimates of standing green biomass, the same procedure was used as for standing (total) biomass, except using conversion factors that reflect aboveground biomass for leaves and young green twigs (Appendix A).

**Soil infiltration capacity.** Infiltration was measured with ring infiltrometers 20 cm in diameter over approximately 2.5 hours, or until steady state had clearly been reached. Soil infiltration capacity was quantified as steady infiltration rates (mm hour$^{-1}$), the lower asymptote approached by infiltration rate over time, and the mean was taken for the 2 nested subplots. Each $\sim 2.5$ hr
measure was modeled as a random effect in a non-linear mixed effects model of the Horton equation (Horton 1940), via asymptotic regression using the nlmern function in the lme4 package (Bates and Maechler 2010) in R (R Development Core Team 2008).

**Soil chemistry.** Soil organic carbon (SOC), soil base cations, and soil sand content were quantified by means of near infrared reflectance spectroscopy (NIRS; Shepherd and Walsh 2002, Shepherd and Walsh 2007), which utilized extensive soil libraries developed for the study site and the region to predict values of soil properties. Predictions were made by using linear mixed effects models to predict SOC, base cations, and sand from the principal components (PCs) of first-derivative NIR spectral reflectance in the 700 to 2500 nm range. Topsoil and subsoil were modeled as random effects. Cross-validation based on an independent sample set demonstrated that model fits in terms of $r^2$ were: 0.91 for SOC; 0.92 for Mg; 0.70 for Ca; 0.88 for K; and 0.92 for sand. Estimates of Mg, Ca, and K were summed to estimate base cations. For estimates of SOC, base cations, and sand contents the mean was taken for the 2 nested subplots.

**Plant trait data.** Samples of leaves and young green twigs were collected from a subset of study plots, and NIRS was used to predict content of N, lignins and polyphenols for the most abundant species. Dry green tissue samples—leaves for herbaceous species, and leaves combined with young green twigs for woody species. Predictions were made by using partial least squares regression models to model N, lignin, and total soluble polyphenol from PCs of first-derivative NIR spectral reflectance in the 1250 to 2500 nm range. Cross-validation based on an independent sample set demonstrated model fits in terms of $r^2$ were: 0.98 for N; 0.73 for lignin; and 0.86 for polyphenol. Mean trait values were calculated by species. For species not collected in study plots, mean trait values by species were obtained from the Organic Resource Database (Palm et al. 2001).
Community-weighted trait means. Community-weighted mean (CWM) green tissue contents of N, lignins, polyphenols, and lignins+polyphenols, were calculated for each plot. CWMs were calculated with Equation 1 (Ackerly and Cornwell 2007) from species mean trait values, weighted upon species abundance in terms of standing green biomass, as

\[ p_j = \frac{\sum_{i=1}^{S} a_{ij} t_i}{\sum_{i=1}^{S} a_{ij}} \]  

where \( p_j \) is the abundance-weighted mean for trait \( t \) in plot \( j \), \( t_i \) is the value of trait \( t \) for species \( i \), \( a_{ij} \) is the abundance of species \( i \) in plot \( j \), and \( S \) is the total number of species present. Trait values were log-transformed prior to calculation of CWMs.

Statistical analysis. Effects of vegetation, soils, and land use variables (Table 2.1) on SOC and infiltration rates were modeled using generalized linear models (GLMs) implemented with an identity link function for the Gamma distribution in R, and were subjected to model comparison on the basis of AICc, the Akaike Information Criterion corrected for small sample sizes (Burnham and Anderson 2002). Multi-model inference was conducted using the AICcmodavg package (Mazerolle 2011) in R, by model averaging to derive parameter coefficients from the full set of candidate models nested in the full models (Table 2.2). For model averaging of main effects, where an independent variable was also present in an interaction term, the model was excluded from averaging of the main effect parameter.
Results

Soil organic carbon

Land use and edaphic factors. Soil sand content (Sand) was not a significant predictor of SOC in ‘near-best’ models; however, in the AICc ‘best’ model, the effect of Sand was positive and marginally significant (Table 2.3). Fallow type (FT) did not affect SOC (Figure 2.1), and the 95% CIs for the parameters Sand and FT overlapped zero (Table 2.3). With the possible exception of standing green biomass (Biomass), the lack of evidence for interactions of independent variables with FT implies that ecological regulation of SOC stocks did not differ greatly among improved and grazed fallows.

Biomass. Biomass was not a significant predictor of SOC stocks (Figure 2.2) in ‘near-best’ models (though Biomass was significant at $P < 0.05$ in lower-ranked models), and the 95% CI overlapped zero (Table 2.3). In one of the ‘near-best’ models, the Biomass X FT interaction was significant ($P < 0.05$), and the 95% CI was entirely positive (Table 2.3). Biomass production is a source of greater litterfall and root exudates, which could explain a possible FT-dependent effect of Biomass on SOC (Figure 2.2).

Plant traits. The ‘best’ model for SOC stocks from model selection on the basis of AICc was comprised of green tissue content of lignins+polyphenols (LPP), Sand, and FT (Table 2.2). Each of the 9 ‘near-best’ models of SOC—defined as those with $\Delta$AICc < 4 and AICc evidence ratio < 10— included LPP as a parameter, and always as a significant predictor. The 95% confidence interval (CI) for LPP parameter estimates from model averaging was wholly positive (Table 2.3), demonstrating consistent effects of LPP on SOC (Figure 2.2), in models with and without Sand. Recalcitrant C compounds such as lignins and polyphenols decompose slowly,
which may enhance build-up or maintenance of SOC. The effect of LPP did not vary among grazed and improved fallows (Table 2.3; Figure 2.2). In contrast, there was no evidence that green tissue N content influenced SOC stocks (Table 2.3; Figure 2.2).

Steady infiltration rates

Land use and edaphic factors. In a univariate model that was among the ‘near-best’ set, steady infiltration rates differed significantly \((P < 0.05)\) between improved and grazed fallows, although the 95\% CI for FT overlapped zero (Table 2.3). Infiltration rates were significantly higher in improved fallows (Figure 2.1; \(P < 0.05\)), probably because livestock trampling compacted soils in grazed fallows. Despite the apparent effects of FT on infiltration rates, there was no evidence for interactions of any independent variable with FT.

Sand was not a significant predictor of steady infiltration rates, and the 95\% CI overlapped zero (Table 2.3). Sand did not influence infiltration consistently, although some patterns may hint at Sand effects. In improved fallows, infiltration rates and Sand were positively correlated; in grazed fallows, infiltration rates were associated with sand content in a complex, non-linear pattern (Figure 2.3). In grazed fallows, both the highest and lowest rates of infiltration were observed with higher sand content, while rates varied widely on less sandy soils. However, no Sand X FT interaction was detected.

Biomass. Though present in some ‘near-best’ models, there was no evidence that Biomass influenced infiltration rates (Table 2.3; Figure 2.3). Unlike for SOC, there was no evidence for any Biomass X FT interaction (Table 2.3).

Plant traits. The ‘best’ model for steady infiltration rates was comprised of LPP and FT (Table 2.2). LPP was a parameter in 10 of the 15 ‘near-best’ models, and the effect of LPP was
always significant. The 95% CI for the LPP parameter from model averaging was wholly positive (Table 2.3), demonstrating that LPP was a consistent predictor of infiltration rates (Figure 2.3). By increasing build-up or maintenance of SOC, slowly decomposing C compounds such as lignins and polyphenols may enhance infiltration rates.

Green tissue N content was not a significant predictor of infiltration rates (Figure 2.3) in models that included LPP, and the 95% CI for the N parameter overlapped zero (Table 2.3). However, N content was a significant predictor of SOC in one ‘near-best’ model (N + FT + N:FT; \( P < 0.05 \) for main effect of N, other terms insignificant). Although this model cannot be dismissed on the basis of AICc alone, the effect of N may be suspect since it was not consistent, and because the model has a parameter in addition (K = 5) to the ‘best’ model (K = 4). The model fit was also somewhat poorer (linear regression of observed and predicted values, intercept = 88.09; slope = 0.59; \( R^2 = 0.098 \)) than the ‘best’ model.

Discussion

SOC stocks and infiltration rates were influenced similarly by attributes of vegetation, yet influenced differently by land use and edaphic factors. Green tissue LPP content was the attribute of vegetation that best explained both SOC stocks and steady infiltration rates. With respect to the evidence presented here, influences of land use (i.e., improved vs. grazed fallows) on soil properties (i.e, SOC, infiltration) were significantly mediated by vegetation. Determining the precise mechanisms underlying these findings is not possible without more logistically intensive methodology, but the results point to possible mechanisms worth investigating.
Soil organic carbon

Greater stocks of SOC in fallows with higher green tissue LPP content indicate that SOC benefits from vegetation with lower litter quality. Higher SOC in fallow soils of higher sand content may be related to a lower intensity of past land use, perhaps over long time periods.

Land use and edaphic factors. The expected relationship for SOC with soil sand content is a decline; here an increase in SOC with sand content was observed, contradicting this expectation. What created this deviation from the expected pattern? The answer appears to lie in the significance of soil texture in these agricultural systems.

The soil texture of a farm or field can shape management decisions—e.g., which crops to plant, where to plant them, how often, and what inputs to use. In Western Kenya, high population density, small farm size, and the pressures of poverty and hunger to cultivate land intensively and to produce goods even in unproductive fields (e.g., by grazing livestock or producing thatch), mean that land use decisions are critical to long term sustainability of farming in the region. Over long time periods—e.g., decades—avoidance of cultivation may have its strongest effects on soil properties, especially SOC given its ‘slow’ behavior as an ecosystem variable. In this study, improved fallows tended to be located on slightly less sandy soils, which are more inherently productive. As such, higher SOC stocks might be expected in improved fallows. However, over the long term, these more fertile fields have likely been cropped at higher frequency, which should diminish their ability to retain SOC. Neither improved nor natural fallows differed in SOC from nearby maize fields (data not presented), despite improved fallows and maize fields tending to be located on slightly less sandy soils. In this study system, there is
scarcely another mechanism that could explain higher SOC in sandier soils, although rooting patterns might have had a role.

Biomass. Higher SOC in fallows with greater standing green biomass could suggest that potentially greater litter inputs to soils may have benefitted SOC. This result would point to the essential role of primary production of biomass and litter deposition in buildup of SOC. Improved fallows had greater biomass but since they are likely tilled and cropped more frequently, retention of SOC may be lower. In grazed fallows lower biomass is probably due to a combination of an absence of tree planting, grazing, and selection of less productive fields for grazing.

Plant traits. SOC stocks benefitted most consistently from greater representation in the plant community of species with high green tissue content of lignins and polyphenols. Through litterfall and other mechanisms, vegetation with higher content of recalcitrant C sources may have slowed microbial attack and decomposition, resulting in higher SOC stocks where vegetation was of low litter quality. However, with these data, litter input quality could not be definitively separated from litter input quantity.

Across biomes and broad phylogenetic groups, production of structural and defensive compounds such as lignins and polyphenols in plant tissues are often associated with a lower relative growth rate (RGR; biomass growth increment relative to starting biomass) (Silla and Escudero 2004, Poorter et al. 2006). Residues containing high content of recalcitrant C compounds require longer periods of time for decomposition and incorporation into soil food webs to occur (Martens 2000), likely resulting in more lasting benefits to soil fertility and structure (Bronick and Lal 2005). LPP content did not vary among fallow types, and was effectively invariant along the gradient in soil texture.
In contrast, litter quality in terms green tissue N content did not appear to influence SOC. In these systems, the tissue N content of the plant community largely reflects the relative abundance of legumes. This result suggests that higher litter N (or low C:N), through its associations with biological nitrogen fixation and greater biomass production on the part of legumes, may not improve SOC. One explanation is that litter N accelerated decomposition, increasing microbial respiration and release of SOC to the atmosphere. Measurements of N content from green tissues did not account for N reabsorbed during senescence, which may have been over 40% of green N content (Ndufa et al. 2009).

Steady infiltration rates

Higher steady infiltration rates in fallows with higher green tissue LPP content indicate that, like SOC, soil infiltration capacity benefits from vegetation with lower litter quality. Lower infiltration rates in grazed fallows are probably related to trampling by livestock.

Land use and edaphic factors. Grazed fallows had reduced steady infiltration rates, possibly a result of trampling under the hooves of livestock and subsequently compacted soils. Soil compaction reduces soil porosity and increases bulk density, conditions that impair infiltration capacity (Salako and Kirchhof 2003, Siriri et al. 2006).

Soil sand content may have influenced infiltration, but any such effects were complex and variable. First, recall that SOC and sand were positively correlated, both of which should increase infiltration rates. When planted with trees, sandy soils have higher infiltration rates due to larger inter-particle spaces and lower bulk density (Siriri et al. 2006). In improved fallows, infiltration was positively correlated with sand content, as might be expected (i.e., due to sand and/or SOC). In grazed fallows, however, both the highest and lowest rates of infiltration were
observed on sandier soils, while rates were closer to the mean in less sandy fields. It is not known whether infiltration rates in grazed fallows correspond to the duration or intensity of grazing, which could not be verified, yet sandier soils might have been more sensitive to trampling and compaction. Finally, grazed fallows tended to be sandier and older than improved fallows, meaning that sandy fields are probably more prone to be exposed to soil compaction, and often so for several years. Thus, sand content may influence infiltration through the direct effect of texture, but also through management effects in terms how often a field is cropped, whether and how much it is grazed during periods of fallow, and the sensitivity of soils to livestock trampling.

**Biomass.** There was no evidence for effects of biomass on infiltration rates. It is not clear to what extent variation in biomass removal (i.e., from grazing and coppicing of woody stems). In grazed fallows, standing biomass may be particularly irrelevant to infiltration; alternatively, detection of biomass effects may have been impeded by strong effects of grazing on both standing biomass (e.g., from consumption and shifting the plant community toward herbaceous dominance) and infiltration (e.g., from soil compaction). If primary productivity influences infiltration, detection of this effect would require a more detailed methodological approach.

**Plant traits.** Infiltration rates increased most consistently from greater representation in the plant community of species with high green tissue content of lignins and polyphenols. As for SOC, this result provides support for vegetation of lower litter quality slowing decomposition or otherwise maintaining stocks of SOC, and thus benefitting soil structure and increasing infiltration capacity. The relationship of LPP on infiltration rates was weaker than that of LPP with SOC, suggesting that physical disturbance (e.g., grazing, past cultivation) and perhaps other mechanisms influenced infiltration rates, in addition to effects on infiltration capacity occurring via change in SOC.
Infiltration did not appear to be influenced by N content of vegetation, indicating that higher N (or C:N) and associated N-fixation and greater biomass production did not improve infiltration. Vegetation N content could have increased SOC turnover. Measuring N content in unsenesced tissues and strong effects of land use on infiltration rates may have also reduced the ability to detect an N content effect.

**Synthesis**

The results provide evidence that vegetation with higher recalcitrant C content significantly benefits SOC stocks and soil infiltration capacity, two of the foremost indicators of soil productivity in agricultural systems, in two types of fallows. This finding is significant since there has been substantial debate among agricultural scientists as to the effectiveness of fallows in improving soil conditions in smallholder farming systems (Sileshi et al. 2008), and whether input quality affects long-term SOM dynamics (Gentile et al. 2011). The results suggest that in smallholder agroecosystems, the functional traits of fallow species may be a reliable indicator of how substantially a fallow of a particular vegetation composition will support ecosystem services provided by soil organic matter.

That the two soil properties were best explained by LPP should result, in part, from infiltration capacity not being independent of SOC. The relationship between SOC and steady infiltration rates was roughly similar in improved ($r = 0.407$) and grazed fallows ($r = 0.358$). One of the main ways that vegetation influences infiltration capacity is by depositing litter above- and below-ground that becomes incorporated into soil organic matter (Blair et al. 2006a). The degree to which litter inputs of a certain quantity improve aggregation of soil particles and soil structure—and thus infiltration—can be enhanced with the proportion of recalcitrant C compounds
entering the soil subsystem (Martens 2000). Recalcitrant C may be playing important roles here as source matter for long-lived SOC pools, in the formation and binding together of stable soil aggregates, and in providing for robust soil structure. Consequently, vegetation with high recalcitrant C content may have slowed SOC turnover, building up long-lived pools of SOC, and improved soil structure, enhancing soil infiltration capacity. Nonetheless, litter input quality could not be definitively separated from litter input quantity.

Relationships of biomass with soil properties were consistently weaker than relationships with content of recalcitrant C compounds, which could suggest that the quality of litter produced by fallow vegetation was more influential than the quantity of standing vegetation biomass. Sampling was conducted around the time of peak annual biomass, although methodology may have affected measurement of potential litter input quantity. Long growing seasons and removal of biomass make quantification of NPP difficult (Fahey and Knapp 2007). The humid tropical climate, periodic wood harvests, and ongoing livestock grazing render standing biomass insufficient as an indicator of NPP in these systems.

Differences between SOC and infiltration capacity in their response to agroecosystem variables may be affected by how rapidly each soil property changes. Physical disturbance to soils, such as cultivation, compaction, termite burrowing, plant root penetration, may cause infiltration capacity to be less closely coupled to attributes of vegetation than is SOC. Each soil property was more strongly associated with different agroecosystem variables, that likely operate over different temporal scales—SOC with sand content, and infiltration rates with grazing. Infiltration capacity may have declined relatively quickly in the presence of grazing, whereas there was no evidence of grazing effects on SOC. SOC is known to be a ‘slow’ ecosystem variable requiring long periods of time for observable change. Although infiltration capacity should likewise increase slowly as
SOC stocks and soil structure improve, infiltration may be a ‘faster’ variable in agricultural systems when declining. The positive effect of sand content on SOC suggests that SOC may be more strongly influenced by past cropping intensity, perhaps over long time periods, than is infiltration.
Tables and Figures

*Table 2.1.* Description of model variables and summary statistics. GLM distributions used for response variables, and transformations applied to independent variables prior to GLM analysis are included.

<table>
<thead>
<tr>
<th>Dependent variables</th>
<th>Abbrev.</th>
<th>Units</th>
<th>Distr.</th>
<th>Fallow type</th>
<th>n</th>
<th>Mean</th>
<th>SD</th>
<th>SEM</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soil organic carbon</td>
<td>SOC</td>
<td>%</td>
<td>Gamma</td>
<td>All</td>
<td>46</td>
<td>1.527</td>
<td>0.337</td>
<td>0.050</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Grazed</td>
<td>23</td>
<td>1.543</td>
<td>0.350</td>
<td>0.073</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Improved</td>
<td>23</td>
<td>1.510</td>
<td>0.331</td>
<td>0.069</td>
</tr>
<tr>
<td>Steady infiltration rate</td>
<td>SIR</td>
<td>mm hr⁻¹</td>
<td>Gamma</td>
<td>All</td>
<td>44</td>
<td>306.3</td>
<td>174.8</td>
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<td></td>
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<td></td>
<td>Grazed</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>Improved</td>
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<td>362.5</td>
<td>144.2</td>
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<table>
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<tr>
<th>Independent variables</th>
<th>Abbrev.</th>
<th>Units</th>
<th>Transf.</th>
<th>Fallow type</th>
<th>n</th>
<th>Mean</th>
<th>SD</th>
<th>SEM</th>
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</thead>
<tbody>
<tr>
<td>Green tissue lignin + polyphenol content CWM</td>
<td>LPP</td>
<td>log(%)</td>
<td>arcsine square root</td>
<td>All</td>
<td>46</td>
<td>3.895</td>
<td>0.283</td>
<td>0.042</td>
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<td></td>
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<td></td>
<td>Grazed</td>
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<td>3.834</td>
<td>0.358</td>
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<td></td>
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<td>Improved</td>
<td>23</td>
<td>3.936</td>
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<td>0.037</td>
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<tr>
<td>Green tissue nitrogen content CWM</td>
<td>N</td>
<td>log(%)</td>
<td>arcsine square root</td>
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<td>1.252</td>
<td>0.134</td>
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<td></td>
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<td></td>
<td></td>
<td>Grazed</td>
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<td>1.149</td>
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<td>0.022</td>
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<td>Improved</td>
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<td>1.355</td>
<td>0.058</td>
<td>0.012</td>
</tr>
<tr>
<td>Standing green biomass</td>
<td>Biomass</td>
<td>t ha⁻¹</td>
<td>square root</td>
<td>All</td>
<td>46</td>
<td>7.895</td>
<td>3.941</td>
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<td>4.775</td>
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<td>Improved</td>
<td>23</td>
<td>11.016</td>
<td>2.081</td>
<td>0.434</td>
</tr>
<tr>
<td>Soil sand content</td>
<td>Sand</td>
<td>%</td>
<td>arcsine square root</td>
<td>All</td>
<td>46</td>
<td>15.330</td>
<td>4.848</td>
<td>0.715</td>
</tr>
<tr>
<td></td>
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<td></td>
<td>Grazed</td>
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<td>17.260</td>
<td>5.289</td>
<td>1.103</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Improved</td>
<td>23</td>
<td>13.401</td>
<td>3.510</td>
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</tr>
<tr>
<td>Fallow type</td>
<td>FT</td>
<td>NA</td>
<td>NA</td>
<td>All</td>
<td>46</td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td>Grazed</td>
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<td></td>
<td>Improved</td>
<td>23</td>
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</tbody>
</table>
Table 2.2. Comparison of full models with ‘best’ models selected by AICc. Results for evaluation of AICc ‘best’ models are from linear regressions of observed values upon values predicted by the model.

### A. Soil organic carbon (SOC)

<table>
<thead>
<tr>
<th>Model</th>
<th>Model structure</th>
<th>K</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>Evidence ratio</th>
<th>Intercept</th>
<th>Slope</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>‘Best’</td>
<td>LPP + Sand + FT</td>
<td>5</td>
<td>22.60</td>
<td>0</td>
<td>0.2562</td>
<td>1</td>
<td>0.03</td>
<td>0.98</td>
</tr>
<tr>
<td>Full</td>
<td>LPP + N + Biomass + Sand + FT + LPP:FT + N:FT + Biomass:FT + Sand:FT</td>
<td>11</td>
<td>32.76</td>
<td>10.16</td>
<td>0.0016</td>
<td>160.83</td>
<td>0.82</td>
<td>0.107</td>
</tr>
</tbody>
</table>

### B. Steady infiltration rate (SIR)

<table>
<thead>
<tr>
<th>Model</th>
<th>Model structure</th>
<th>K</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>Evidence ratio</th>
<th>Intercept</th>
<th>Slope</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>‘Best’</td>
<td>LPP + FT</td>
<td>4</td>
<td>535.24</td>
<td>0</td>
<td>0.1593</td>
<td>56.78</td>
<td>0.82</td>
<td>0.107</td>
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</table>
Table 2.3. Model coefficients and results for multi-model inference conducted by model averaging.

Model averaging included parameter coefficients among all candidate models (for main effects, models with interactions were excluded). Significance levels for t statistic in GLMs: * = \( P < 0.05 \); ** < 0.01; *** < 0.001; **** < 0.0001; ms = \( P < 0.1 \).

A. Soil organic carbon (SOC)

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</thead>
<tbody>
<tr>
<td>‘Best’</td>
<td>1.539</td>
<td>0.352</td>
<td>—</td>
<td>—</td>
<td>0.166</td>
<td>-0.023</td>
<td>—</td>
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<td></td>
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<td>****</td>
<td>***</td>
</tr>
<tr>
<td>Full</td>
<td>1.479</td>
<td>0.411</td>
<td>0.278</td>
<td>-0.424</td>
<td>0.170</td>
<td>0.019</td>
<td>0.161</td>
<td>-0.760</td>
<td>0.860</td>
<td>-0.089</td>
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Model averaging:

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</thead>
<tbody>
<tr>
<td>Estimate</td>
<td>1.541</td>
<td>0.378</td>
<td>-0.137</td>
<td>0.080</td>
<td>0.166</td>
<td>-0.044</td>
<td>0.110</td>
<td>-0.346</td>
<td>0.746</td>
<td>-0.004</td>
</tr>
<tr>
<td>95% C.I. Upper</td>
<td>1.696</td>
<td>0.576</td>
<td>0.126</td>
<td>0.427</td>
<td>0.348</td>
<td>0.192</td>
<td>0.541</td>
<td>0.329</td>
<td>1.397</td>
<td>0.380</td>
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<tr>
<td>95% C.I. Lower</td>
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<td>0.180</td>
<td>-0.400</td>
<td>-0.266</td>
<td>-0.016</td>
<td>-0.280</td>
<td>-0.320</td>
<td>-1.020</td>
<td>0.095</td>
<td>-0.388</td>
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</table>

B. Steady infiltration rate (SIR)

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</thead>
<tbody>
<tr>
<td>‘Best’</td>
<td>276.50</td>
<td>119.88</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>89.94</td>
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<td></td>
<td></td>
<td></td>
<td>****</td>
<td>*</td>
</tr>
<tr>
<td>Full</td>
<td>274.41</td>
<td>150.15</td>
<td>574.95</td>
<td>-549.42</td>
<td>49.13</td>
<td>156.86</td>
<td>-23.08</td>
<td>-824.72</td>
<td>638.54</td>
<td>14.49</td>
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</table>

Model averaging:

<table>
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</thead>
<tbody>
<tr>
<td>Estimate</td>
<td>299.3</td>
<td>113.5</td>
<td>76.7</td>
<td>106.0</td>
<td>-27.6</td>
<td>73.1</td>
<td>-34.5</td>
<td>-362.4</td>
<td>81.5</td>
<td>130.8</td>
</tr>
<tr>
<td>95% C.I. Upper</td>
<td>405.8</td>
<td>207.8</td>
<td>224.0</td>
<td>275.8</td>
<td>70.9</td>
<td>249.8</td>
<td>200.9</td>
<td>87.9</td>
<td>531.6</td>
<td>401.6</td>
</tr>
<tr>
<td>95% C.I. Lower</td>
<td>192.8</td>
<td>19.2</td>
<td>-70.6</td>
<td>-63.8</td>
<td>-126.1</td>
<td>-103.5</td>
<td>-269.8</td>
<td>-812.7</td>
<td>-368.7</td>
<td>-140.0</td>
</tr>
</tbody>
</table>
Figure 2.1. Variation in SOC and steady infiltration rates with fallow type.
Figure 2.2. Relationships of SOC with attributes of fallow vegetation and soil sand content. Curves are plotted for variables significant in bivariate GLMs, i.e., comprised of the x-axis variable and fallow type, with no interaction term.
Figure 2.3. Relationships of steady infiltration rates with attributes of fallow vegetation and soil sand content. Curves are plotted for variables significant in bivariate GLMs.
Chapter 3: Effects of trees and large shrubs on livestock forage in smallholder fallows

Abstract

Interactions among ecosystem services are increasingly perceived as important to the delivery of ecosystem services. Positive and negative interactions among ecosystem services, termed synergies and trade-offs, arise through ecological interactions among ecosystem service providers (ESPs), or through correlated influences of other factors on both services. In agroforestry systems, net interactions among trees and plants growing underneath are the outcome of the combined competitive and facilitative effects of the overstory. Trees can compete severely with the understory for light and soil resources, yet trees can benefit plants growing nearby through improved soil conditions. To investigate whether and how the overstory may interact with forage species growing beneath, thereby leading to ecosystem service interactions, the biomass of wood and livestock forage were examined in smallholder fallows in Siaya District, western Kenya. In 18 grazed fallows and 21 improved fallows, stem diameter of trees and cover and height of shrub and herb species were used to estimate biomass, and near infrared spectroscopy was used to predict soil properties (organic carbon, base cations, and sand content). The objectives were to test whether trees and large shrubs may reduce the biomass and quality of forage species growing beneath through competition, and whether niche complementarity among woody overstory species may exacerbate competition with forage species, or alternatively, may ameliorate competition with or enhance facilitation of forage species. In improved fallows, forage biomass
declined with the biomass of trees and shrubs, providing evidence for competitive suppression of forage species and a trade-off between wood and forage production. The biomass of higher quality forage species in grazed fallows was positively associated with overstory biomass, likely due to correlated negative responses to grazing, indicating an indirect wood-forage synergy. Overstory niche complementarity, quantified in terms of the taxonomic and functional diversity of trees and shrubs, did not appear to influence forage species positively or negatively in either fallow type. Management differences in terms of the presence and intensity of grazing and the planting of fallows with woody legumes appear largely responsible for the different relationships between overstory and forage species among fallow types.

**Introduction**

Land management typically alters ecosystem structure and function to increase the production of specific goods such as agricultural commodities (Rodriguez et al. 2006). At global scales, increasingly specialized land management has increased the supply of crops and other provisioning ecosystem services (MA 2003), yet degrades other other benefits provided by agroecosystems (Foley et al. 2005, Kareiva et al. 2007)—from soil quality within fields to regulation of the global climate.

Ecosystem services are regulated ecologically by a wide array of biotic factors within local and regional abiotic filters. Ecosystem service providers (ESPs) are the subsets of the biota responsible for production of an ecosystem service (Kremen 2005). In most ecosystems, services are linked together by ecological interactions among their respective ESPs. As a result,
production of one ecosystem service often affects the magnitudes of other services (Bennett et al. 2009, Carpenter et al. 2009).

Ecosystem service interactions are the trade-offs and synergies among services (Bennett et al. 2009, Power 2010). In a trade-off, the supply of one service declines when the supply of another increases, while a synergy occurs when the supply rates for two services increase together (Wossink and Swinton 2007). Interactions may arise when one service influences another directly, or when their supply rates are correlated (Bennett et al. 2009).

Despite significant research effort, most work on multiple ecosystem services has been conducted at landscape or greater scales that are mis-matched with ecological interactions occurring over finer scales, leaving significant gaps in knowledge on interactions among services (Bennett et al. 2009). Some relationships between ecosystem services have been little studied in smallholder systems in the humid tropics, including the potential of wood production to affect the production of forage for livestock in the same field.

In tree intercrops and multi-strata agroforestry systems, effects of trees on crops growing beneath them are thought to be the net outcome of competition with crops for light and soil resources, and simultaneous facilitation of crops by improving soil conditions (Kho 2008). Trees are capable of competing severely with nearby plants for light, soil nutrients, and water—including crops, for which water competition is most apparent in drier regions (Ong et al. 2002), and livestock forages (Dupraz and Newman 1997). Yet the crop component of tree intercropping systems can derive significant benefits from inputs of nutrients and C from tree litter (Ong et al. 2002). Trees may similarly exert a combination of competitive and facilitative effects on forage species growing beneath them in the humid tropics.
In fallow fields in smallholder farms of western Kenya, wood is produced by the overstory of trees and large shrubs, while forage for livestock is produced by plants growing in the predominately herbaceous understory beneath. That is, different ecosystem services are provided by different vegetative strata in fallows in the area. Interactions of trees and shrubs with forage species may affect the quantity and quality of forage biomass in the fallow. Trees and shrubs are likely to compete for light and soil resources to some degree with forage species growing beneath them, reducing the abundance of forage species and forage production. Constraining the light and nutrients available to the understory might also shift species composition toward forage species more tolerant of stress from low resource availability, especially shaded conditions. Plants able to tolerate more stressful conditions tend to have a more conservative life history strategy emphasizing conservation of limited resources at the expense of rapid growth. Slow-growing, stress-tolerant species typically have lower tissue nutrient content and higher content of defensive compounds (Ackerly and Cornwell 2007, Poorter 2009), traits that reduce the quality of plant tissues as forage for livestock. At the same time, trees and shrubs may facilitate growth of forage species by improving soil conditions, which could encourage growth of forage species, and perhaps especially forage species of higher quality. Thus, interactions between the provisioning ecosystem services of wood production and forage production may arise via positive and negative interactions of plants producing wood with those producing forage.

In fallows managed for simultaneous production of wood and forage, forage species in the understory are likely to face competition from trees and shrubs (Dupraz and Newman 1997), but the intensity of competition may vary widely. Competitive and facilitative effects of trees on forage species could vary with the composition and densities of fallow species, and interactions
might shift away from competition and toward facilitation where abiotic stressors (Callaway et al. 2002, Brooker et al. 2008) and disturbance (Graff et al. 2007) are more prevalent.

Higher niche complementarity among overstory trees and large shrubs, quantified in terms of functional trait diversity, could potentially exert both positive and negative effects on forage species growing below the overstory. To the extent that complementarity increases the efficiency with which trees and shrubs capture and utilization of soil N (Oelmann et al. 2007), other nutrients, light, and water, competitive suppression could become more intense.

Alternatively, complementarity among the niches of trees and shrubs could reduce the intensity of competition, or even generate facilitation of forage species. Modification of belowground interactions between large woody plants and forage species is perhaps the most likely mechanism by which tree and shrub diversity could enhance facilitation of forage species, but functional diversity among large woody plants could influence forage productivity positively in several ways.

Complementarity among woody overstory plants may positively affect belowground interactions with forage species through two primary means. First, the degree to which forage growth is limited by any particular soil resource—especially nutrients and water—may be reduced by greater variation in strategies of large woody plants for acquisition of soil resources (requirements, depths, chemical forms taken up), and by greater variation in litter content of nutrients. Second, tree and shrub species with different functional traits such as leaf and root chemistry (Zech et al. 1997, Vanlauwe et al. 2005, Gentile et al. 2009) could positively influence contrasting elements of soil fertility and soil structure. Greater variation in the quality of above- and belowground tissues deposited should generate a broader range of rates at which nutrients in litter and soil organic matter are mineralized and made available to forage species. Higher quality
litters with lower C:N and more labile C compounds that support greater microbial activity and more rapid mineralization of litter N (Gentile et al. 2009) and other nutrients may provide nutrients more rapidly in forms available for uptake by forage species. Meanwhile, C and nutrients in lower quality litters are mineralized more slowly (Vanlauwe et al. 2005), largely due to higher content of recalcitrant C compounds. Recalcitrant C substrates may improve build-up of long-lived soil C pools (Zech et al. 1997), which over longer time periods should benefit growth of forage species. Finally, faster mineralization of nutrients from higher quality litters in combination with slower mineralization from lower quality litters could have a stabilizing effect on nutrient availability (Kimetu et al. 2008), potentially supporting more consistent growth of forage species.

Forage species could also benefit from trophic interactions induced by trees and shrubs. For example, trees and shrubs might reduce mortality by facilitating escape from natural enemies of forage species, including diseases and seed predators, i.e. Janzen-Connell effects (Janzen 1970, Connell 1971). Unpalatable species commonly protect palatable species from grazers (Graff et al. 2007, Smit et al. 2007). Woody species with spiny stems (e.g., Lantana camara L.) and leaves (e.g., Acanthus pubescens (Thomson ex Oliv.) Engl.) can protect undergrowth from livestock grazing in the study area (Sircely, pers. obs.). Tree and shrub species producing large quantities of nutrient-rich litter could also attract or enhance the activity of soil macrofauna such as earthworms that are drawn by of high quality litters (van Eekeren et al. 2009). In a fallow dominated by grasses with high C:N, N-rich tree litter could have significant facilitative effects on forage species by supporting beneficial soil organisms.

Niche complementarity can be quantified by means of methods for describing dissimilarity in functional traits among species. Functional diversity (FD) refers the degree of
variation or divergence in functional traits within a biotic community or an assemblage of species (Díaz and Cabido 2001, Petchey and Gaston 2002). When species have different, or complementary, niches the values of their traits that influence particular ecosystem processes are likely to be divergent. Because FD reflects dissimilarity among the species in a community, FD can be considered a measure of niche complementarity (Mason et al. 2005, Petchey and Gaston 2006) superior to species richness. However, no published study to date has addressed whether diversity or niche complementarity among woody overstory plants may affect interactions with the understory.

The goals of this study were to investigate the existence of possible trade-offs and synergies between the ecosystem services of wood production and livestock forage production in smallholder fallows, and to assess how management and environmental factors relate to any ecosystem service interactions. Three specific hypotheses were tested. First, greater biomass of trees and shrubs suppresses the growth of forage species through competition for light and soil resources, reducing the overall quantity of forage biomass, the biomass of higher quality forage species, and the overall quality of forage biomass. Second, by increasing utilization of light and soil resources, niche complementarity among trees and large shrubs exacerbates competition with forage species, reducing overall forage biomass, biomass of higher quality forage species, and overall forage quality. Finally, and in contrast to the second hypothesis, niche complementarity among trees and large shrubs, primarily by improving soil conditions, partially ameliorates competition with or results in facilitation of forage species, increasing overall forage biomass, biomass of higher quality forage species, and overall forage quality.
Methods

Study systems. The Millennium Villages Project (MVP) is an evidence-based approach to alleviating extreme rural poverty in sites throughout Sub-Saharan Africa, in which agricultural development plays a strategic role (Sanchez et al. 2007). The data for this study were collected in 2008-2009 in the Sauri MVP site in Siaya District, western Kenya.

Sauri MVP has a humid tropical climate with two rainfall peaks and potential cropping seasons yearly, and elevation ranges from 1,300 to 1,470 m. The clayey, well drained Oxisols and Ultisols are soil orders representative of soils common in Sub-Saharan Africa. The landscape in Sauri is a shifting agricultural matrix primarily composed of maize and other annual crops, with lower landscape cover of woodlots, land dedicated to grazing, and fallow fields. Land use in the area cycles between periods of annual crops, and periods of fallow intended to regenerate soil fertility and to provide wood products, green manures from foliage of woody plants, and forage for livestock, among other goods. High population density, high cropping frequency and inadequate fertilization having led to degradation since the early 20th century (Scherr 1995), and soils in the area are relatively depleted of N and C. However, Sauri agroecosystems may currently be undergoing long-term rehabilitation.

Fallow type. ‘Improved’ fallows of fast-growing leguminous trees are promoted by MVP to improve soil fertility and fuelwood. They are usually planted with *Tephrosia candida* DC, and less commonly with *Crotalaria paulina* Schrank, *Calliandra calothyrsus* Meissn. or other exotics, and are not grazed with livestock. Grazed fallows, often considered ‘natural’ or ‘weed’ fallows, are less common, and contain a variety of species, most of which are native. The most common trees in grazed fallows are the native *Markhamia lutea* (Benth.) K. Schum., *Sesbania sesban* (L.) Merr., and
the exotic *Psidium guajava* L. Most grazed fallows combine production of wood and green manures with livestock grazing, although heavily grazed fallows do not produce wood.

*Data collection.* Fallow fields identified for sampling ranged from 0.02 to 0.25 ha in area, with a mean size of approximately 0.1 ha. Data were collected from 18 grazed and 21 improved fallows. Data were collected using a slight adaptation of the Land Degradation Surveillance Framework (LDSF; Walsh and Vagen 2006), modified for field-scale sampling. LDSF involves characterization of vegetation structure (diameter at breast height (DBH) and height of trees, tree and shrub stem density, and vegetation cover), soil conditions (soil properties, soil infiltration capacity, rock cover and erosion), and FAO-standard land use/cover. Soils were sampled at depths of 1-20 cm (topsoil) and 20-50 cm (subsoil).

The LDSF protocol was reproduced at the scale of a single 100 m$^2$ plot located randomly in the interior of each fallow. Two 2 m$^2$ subplots were established within each 100 m$^2$ sample plot, one in the center, and one randomly located tangent to the plot edge. Soil samples were collected and soil infiltration capacity measured in both subplots. Biovolume (m$^3$) of each plant species was characterized by visually estimating cover and average height. Cover was scored as the mid-point of cover classes on a 5-point scale: 1-4, 4-15, 15-40, 40-65, and > 65 m$^2$. Grazing intensity was recorded by visually estimating cover for evidence of grazing—bite marks, trampling, feces, and hair—on the same 5-point scale.

*Standing biomass—large woody stems.* For all woody stems $\geq 2.5$ cm DBH, aboveground standing biomass (t ha$^{-1}$) was estimated by using DBH measurements to calculate whole-tree biomass ($Y$) by the general allometric equation, $Y = e^{(-2.134 + 2.53 \ln DBH)}$ for humid regions (Ponce-Hernandez 2004). To estimate belowground biomass, aboveground biomass estimates were multiplied by the mean of values from the literature for root-to-shoot ratio (RSR) of tree species.
common in the study site (Appendix A). Above- and belowground biomass estimates were summed to estimate total standing biomass.

**Standing biomass**—small woody stems and herbaceous species. For all woody plants < 2.5 cm DBH and all non-woody species, cover estimates were multiplied by average height to estimate biovolume by species, then multiplied by a conversion factor to estimate aboveground biomass (Appendix A). To estimate belowground biomass, aboveground biomass estimates were multiplied by the mean of values from the literature for RSR of species common in the study site (Appendix A). Above- and belowground biomass estimates were summed to estimate total standing biomass.

**Standing green biomass.** To obtain estimates of standing green biomass, the same procedure was used as for standing (total) biomass, except using conversion factors that reflect aboveground biomass for leaves and young green twigs (Appendix A).

**Soil infiltration capacity.** Infiltration was measured with ring infiltrometers 20 cm in diameter over approximately 2.5 hours, or until steady state had clearly been reached. Soil infiltration capacity was quantified as steady infiltration rates (mm hour$^{-1}$), the lower asymptote approached by infiltration rate over time, and the mean was taken for the 2 nested subplots. Each ~2.5 hr measure was modeled as a random effect in a non-linear mixed effects model of the Horton equation (Horton 1940), via asymptotic regression using the nlmer function in the lme4 package (Bates and Maechler 2010) in R (R Development Core Team 2008).

**Soil chemistry.** Soil organic carbon (SOC), soil base cations, and soil sand content were quantified by means of near infrared reflectance spectroscopy (NIRS; Shepherd and Walsh 2002, Shepherd and Walsh 2007), which utilized extensive soil libraries developed for the study site and the region to predict values of soil properties. Predictions were made by using linear mixed effects
models to predict SOC, base cations, and sand from the principal components (PCs) of first-derivative NIR spectral reflectance in the 700 to 2500 nm range. Topsoil and subsoil were modeled as random effects. Cross-validation based on an independent sample set demonstrated that model fits in terms of \( r^2 \) were: 0.91 for SOC; 0.92 for Mg; 0.70 for Ca; 0.88 for K; and 0.92 for sand. Estimates of Mg, Ca, and K were summed to estimate base cations. For estimates of SOC, base cations, and sand contents the mean was taken for the 2 nested subplots.

*Plant trait data.* Samples of leaves and young green twigs were collected from a subset of study plots, and NIRS was used to predict content of N, lignins and polyphenols for the most abundant species. Dry green tissue samples—leaves for herbaceous species, and leaves combined with young green twigs for woody species. Predictions were made by using partial least squares regression models to model N, lignin, and total soluble polyphenol from PCs of first-derivative NIR spectral reflectance in the 1250 to 2500 nm range. Cross-validation based on an independent sample set demonstrated model fits in terms of \( r^2 \) were: 0.98 for N; 0.73 for lignin; and 0.86 for polyphenol. Mean trait values were calculated by species. For species not collected in study plots, mean trait values by species were obtained from the Organic Resource Database (Palm et al. 2001).

*Forage quality.* The community-weighted mean (CWM) of forage quality among all forage species present, was calculated as the ratio of two plant functional traits, measured from at the species level: estimated green tissue content of crude protein (CP) (i.e., green tissue N x 6.25) and lignin (Genin and Quiroz 1993). The CWM for CP : lignin was calculated with Equation 1 (Ackerly and Cornwell 2007) from species mean trait values, weighted upon species abundance in terms of standing green biomass, as
where $p_j$ is the abundance-weighted mean for trait $t$ in plot $j$, $t_i$ is the value of trait $t$ for species $i$, $a_{ij}$ is the abundance of species $i$ in plot $j$, and $S$ is the total number of species present. Trait values were log-transformed prior to CWM calculation. Forage quality is the abundance-weighted mean of CP : lignin quality among all forage species present, and indicates the overall quality of forage biomass. Table 3.1 summarizes the definitions of forage quality and biomass variables, and their significance to the ecosystem service of forage production.

Forage biomass variables. ‘Total forage biomass’ is the summed total (above- + belowground) biomass of all herbaceous species, and all woody species $< 0.7$ average height. Thus, total forage biomass reflects the overall abundance of forage species and potential standing forage biomass (see Table 3.1).

‘Quality forage biomass’ is the summed green biomass of higher quality forage species, i.e. those species with CP : lignin $\geq 0.8$ (see Forage quality above). For the ecosystem service of forage production, the ecosystem service providers (ESPs; Kremen 2005) were taken to be the forage species producing forage of higher quality, i.e. those species useful for feeding livestock. The green tissue CP : lignin ratio of $\geq 0.8$ approximates the upper limit of the lowest quartile of CP : lignin values among species in the sample, and all species in the sample known to be used for feeding livestock (Dear et al. 2012) had CP : lignin $> 0.8$ (Sircely, pers. obs.), while all species not known to be used as forage had CP : lignin $< 0.8$. Forage species with lower CP relative to lignin content should be of little use as feed for livestock, as lignin reduces the ability of livestock to digest and absorb nutrients. Thus, quality forage biomass reflects the edible biomass of higher
quality forage species, and is indicative of the actual amount of biomass useful as livestock forage (see Table 3.1).

*Tree and large shrub biomass.* For the ecosystem service of wood production, the ESPs were taken to be the species of trees and large shrubs that were sufficiently large in a plot to serve as fuelwood for cooking. Biomass of trees and large shrubs includes individual stems ≥ 2.5 cm DBH, and all woody species with average height ≥ 0.7 m. With few exceptions, woody species of smaller stature provide insignificant quantities of useful wood. Total (above- + belowground) biomass of trees and large shrubs was used to represent the abundance of the ESPs for wood production.

*Functional diversity.* Functional diversity (FD) was used as a proxy for niche complementarity among fallow trees and shrubs (Petchey and Gaston 2002). Because FD reflects dissimilarity among the species in a community, FD can be considered an indicator of niche complementarity (Mason et al. 2005, Petchey and Gaston 2006). FD was calculated as the summed branch length of dendrograms generated by UPGMA average linkage clustering of Euclidean multivariate distances among species in terms of three functional traits: green tissue contents of N, lignins, and polyphenols. Trait values were log-transformed prior to FD calculation, and re-scaled to a mean and standard deviation of 1. FD calculations were robust to the traits selected; upon inclusion of maximum height, RSR, lignins+polyphenols, growth form, and woodiness, FD estimates were highly correlated with one another. As such, the conservative set of three traits was selected. In the study system, green tissue contents of N, lignins, and polyphenols may be associated with rates of production and accumulation of biomass, biological nitrogen fixation, plant species effects on soil processes, competitive and facilitative species interactions, and responses to grazing. Thus, this limited set of traits contains significant information on the niches
of plants present in a fallow, and FD provides an estimate of niche complementarity in terms of aspects of the niches of large woody plants directly and indirectly related to these traits. Although species richness is likely a less effective indicator of niche complementarity, it was included for comparison with FD.

**Statistical analysis.** Functional diversity of trees and shrubs cannot be calculated where they are absent, nor for an overstory monoculture; in such cases, FD is undefined and not zero. As such, models with FD were limited to a subset of fields, and had fewer replicates (Table 3.2). Given that sample size was not uniform, linear models were used to test the proposed hypotheses rather than, for instance, maximum likelihood model selection. The primary explanatory variables of interest were the biomass and diversity of trees and shrubs, which were postulated to influence interactions between the overstory and forage species. In addition, possible influences of environmental conditions on forage variables were considered, including soil conditions and grazing intensity. Preliminary inspection of bivariate relationships between environmental conditions and forage variables indicated that soil organic carbon (SOC) and soil base cations were the most likely to have influenced forage variables, and were included in linear models. Soil infiltration capacity appeared unlikely to have influenced forage variables and was correlated with SOC, significantly in improved fallows (d.f. = 19; \( r = 0.446; \ P = 0.043 \)) and insignificantly in grazed fallows (d.f. = 16; \( r = 0.301; \ P > 0.1 \)), and was thus not considered in statistical analyses.

To test the hypotheses proposed as plausibly characterizing overstory interactions with forage species, each bivariate relationship was examined among the 3 forage variables (total forage biomass; quality forage biomass; forage quality), with each of the 2 measures of tree and shrub diversity (species richness; functional diversity), and each environmental variables (SOC; soil base cations; grazing intensity in grazed fallows only). Bivariate relationships were analyzed
with linear regressions implemented within fallow types (grazed and improved). To improve normality, forage biomass variables were square root-transformed; biomass and species richness of trees and shrubs were log-transformed. SOC, base cations, and grazing intensity were arcsine square root-transformed to address their proportional characteristics.

Only linear models with a single main effect were considered, on account of the modest sample size and thus limited statistical power, and additionally because in some cases models with two main effects, inclusion of an interaction term would be appropriate, further restricting power. Grazed and improved fallows were separated for analysis since the ecological factors and mechanisms influencing forage variables were suspected to differ substantially between the two fallow types. Most saliently, it was suspected that livestock grazing intensity might be influential in grazed fallows, while the improved fallows in the study sample were not exposed to grazing. Alternative approaches could have included conducting regressions among the two fallow types, and testing for significant interactions or quadratic terms indicating divergent behavior among fallow types. These alternatives were considered less meaningful, since the primary goal was testing for the existence of overstory-forage interactions and the sources of these interactions, rather than characterizing differences in interactions among fallow types.

**Results**

Forage biomass was significantly higher in grazed than improved fallows, for both total forage biomass (ANOVA, d.f. = 37; \( F = 6.76; \ P = 0.013 \)) and quality forage biomass (d.f. = 37; \( F = 4.87; \ P = 0.034 \)). Forage quality did not differ (d.f. = 37; \( F = 0.02; \ P = 0.879 \)) among fallow
types (see Table 3.1 for definitions of the three forage response variables and their significance to the ecosystem service of forage production).

Tree and shrub biomass was significantly lower in grazed than in improved fallows (ANOVA, d.f. = 37; $F = 99.53; P < 0.0001$), while there was no difference among fallow types in the diversity of trees and large shrubs, in terms of species richness (d.f. = 37; $F = 0.27; P = 0.610$) or FD (d.f. = 20; $F = 1.01; P = 0.326$). SOC did not differ among fallow types (d.f. = 37; $F = 0.18; P = 0.676$), and soil base cations were marginally significantly higher in improved than in grazed fallows (d.f. = 37; $F = 3.84; P = 0.058$).

**Grazed fallows**

In grazed fallows, total forage biomass displayed a marginally significant (i.e., $0.05 < P < 0.1$) increase with the biomass of trees and shrubs (Table 3.3; Figure 3.1), while quality forage biomass increased significantly with tree and shrub biomass (Table 3.3; Figure 3.2). Forage quality was not associated with overstory biomass (Table 3.3; Figure 3.3) in grazed fallows.

Taxonomic (species richness) and functional diversity (FD) of trees and shrubs, indicators of the degree of niche differentiation among woody overstory species, were not associated, positively or negatively, with total forage biomass, quality forage biomass, or forage quality (Table 3.3; Figures 3.1–3.3) in grazed fallows.

Total forage biomass was not significantly associated with environmental conditions, namely SOC, soil content of base cations, or grazing intensity (Table 3.3; Figure 3.1). In contrast, both quality forage biomass (Table 3.3; Figure 3.2) and forage quality (Table 3.3; Figure 3.3) declined significantly with grazing intensity, as did tree and shrub biomass (d.f. = 16; $r = -0.473; P$
In grazed fallows, neither SOC nor soil base cations was associated with quality forage biomass (Table 3.3; Figure 3.2) or forage quality (Table 3.3; Figure 3.3).

With the exception of grazing intensity, trends in quality forage biomass were similar to those for total forage biomass, in accordance with the close correlation (d.f. = 16; $r = 0.809; P < 0.0001$) between the two forage biomass variables. Forage quality did not correlate with total forage biomass (d.f. = 16; $r = 0.022; P = 0.930$) in grazed fallows, but exhibited a marginally significant positive correlation with quality forage biomass (d.f. = 16; $r = 0.427; P = 0.077$).

**Improved fallows**

In improved fallows, total forage biomass declined significantly as the biomass of trees and shrubs increased (Table 3.4; Figure 3.1), and quality forage biomass exhibited a similar decline with overstory biomass (Table 3.4; Figure 3.2). In contrast, forage quality was not associated with tree and shrub biomass (Table 3.4; Figure 3.3) in improved fallows.

As for grazed fallows, in improved fallows, indicators of niche differentiation among trees and large shrubs—species richness and FD—did not appear to positively or negatively influence total forage biomass, quality forage biomass, or forage quality (Table 3.4; Figures 3.1–3.3).

Neither of the environmental variables examined, SOC and soil content of base cations, were associated with total forage biomass (Table 3.4; Figure 3.1), quality forage biomass (Table 3.4; Figure 3.2), or forage quality (Table 3.4; Figure 3.3) in improved fallows.

In improved fallows, trends in total forage biomass resembled those for quality forage biomass even more closely than in grazed fallows, as the two forage biomass variables were very tightly correlated (d.f. = 19; $r = 0.925; P < 0.0001$). Forage quality did not correlate with total
forage biomass (d.f. = 19; \( r = 0.042; P = 0.856 \)), and unlike in grazed fallows, forage quality was uncorrelated with quality forage biomass as well (d.f. = 19; \( r = 0.186; P = 0.421 \)).

**Discussion**

Forage variables exhibited contrasting relationships with overstory biomass and environmental conditions among fallow types, while in both grazed and improved fallows substantive relationships of forage variables with overstory niche complementarity were similarly absent. Forage biomass variables were positively related to the biomass of trees and large shrubs in grazed fallows, while in improved fallows, both forage biomass variables declined with overstory biomass, providing evidence of competitive suppression of forage species. Niche complementarity among overstory species, as indicated by taxonomic and functional diversity, did not appear to influence forage variables in either fallow type, positively or negatively, suggesting that niche differentiation did not alter interactions of the overstory with forage species. Quality forage biomass and forage quality declined with grazing intensity, an effect specific to grazed fallows, while environmental conditions did not appear to influence forage variables in improved fallows. Thus, improved fallows appeared prone to a trade-off between the production of wood and livestock forage production, while such a trade-off was unlikely in grazed fallows.

*Overstory-forage relationships in grazed fallows*

In grazed fallows, total and quality forage biomass were positively related to tree and shrub biomass, contradicting the hypothesis that overstory competition suppresses the growth of
forage species in general and species of higher forage quality. Overstory biomass did not influence forage quality, which together with the positive relationship with quality forage biomass, indicated there were no more negative overstory effects for higher quality forage species arising from their potentially lower tolerance of stress from shade or low soil resource availability. That the relationships of forage biomass variables with overstory biomass were positive could suggest the contrary to competition, that trees and shrubs could have potentially facilitated forage species. Large woody plants could have facilitated forages by improving soil conditions, and unpalatable woody plants may have provided protection from grazers; the latter effect can be observed in the study site (Sircely, pers. obs.). The positive relationship of overstory biomass with quality forage biomass was stronger than that with total forage biomass, indicating that if facilitation did occur, species of higher quality benefitted more greatly, which suggests either facilitation of palatable species by unpalatable (Graff et al. 2007, Smit et al. 2007) woody species, or higher quality species responding to improvement in soil conditions. However, the negative relationships of forage biomass variables and overstory biomass with grazing intensity cast the possibility of overstory facilitation of forage species into doubt.

Overstory species richness and FD did not have any apparent influence on forage variables, indicating that niche complementarity among tree and large shrub species did not alter overstory interactions with forage species in the understory of grazed fallows. Niche complementarity can increase the efficiency with which a plant community utilizes available resources, resulting, for example, in the drawdown of N in soil solution (Oelmann et al. 2007). Alternatively, niche differentiation among tree and shrub species could, for example, improve conditions for the growth of forage species due to contrasting benefits of overstory species for soil conditions, and or reduce the likelihood of any particular soil resource limiting the growth of
forage species, and thereby improving the availability of soil resources to forage species. There was no evidence for negative effects of overstory diversity on forage variables, indicating that overstory niche complementarity did not enhance the intensity of competition by enabling trees and large shrubs to more completely capture available light and soil resources. Meanwhile, the absence of positive effects of diversity on forage variables indicated that niche complementarity among overstory species did not facilitate the growth of forage species in grazed fallows.

The significant declines in quality forage biomass and forage quality under heavier grazing suggest that livestock grazing disproportionately focused forage species of higher quality. This assessment is also consistent with the failure of total forage biomass to respond to grazing intensity. Declining forage quality at higher grazing intensity indicates that selective grazing on higher quality forage species shifted understory species composition to favor less palatable species. Effects of grazing on palatability vary widely, especially in humid regions that lack a long history of grazing, for which a general pattern of response is difficult to characterize (Díaz et al. 2007b).

Grazing often reduces the abundance of forbs and increases the abundance of species less palatable on account of, for example, low specific leaf area and low leaf N content (Graff et al. 2007, Quétier et al. 2007, Smit et al. 2007), traits respectively associated with leaf toughness and low protein content. Negative responses of palatability to grazing tend to hold in regions with a dry climate or a long history of grazing (Díaz et al. 2007b). Positive palatability responses among grasses in humid and sub-humid regions can occur through an overcompensatory growth response (McNaughton 1983, Augustine and McNaughton 2006), in which growth rates rise dramatically following grazing. The probable advantage of overcompensation is to grow taller and avoid further consumption, although the more rapid growth partly results from fast-growing species exploiting a flush of newly available light and soil resources (Herms and Mattson 1992,
Augustine and McNaughton 2006). Because quality forage biomass declined at higher grazing intensity, the results could suggest that overcompensatory growth probably did not occur, which is consistent with a negative effect of grazing on palatability, i.e., forage quality. However, the standing biomass of forage species is not a reliable indicator of their productivity in these humid tropical systems, and variation in palatability here reflects the species composition of the plant community, not responses in the palatability of individual species to grazing.

In contrast, SOC and soil base cations did not have any apparent influence on forage variables, indicating that grazing effects were stronger than other environmental influences on forage biomass and quality in grazed fallows. The lack of significant effects of SOC and base cations on total or quality forage biomass moreover suggest that positive associations of forage biomass variables with overstory biomass did not arise from common responses to higher soil fertility.

There was evidence that both the overstory and forage species responded negatively to increasing grazing pressure. The reduction of quality forage biomass and forage quality indicated significant negative effects of selective grazing on higher quality forage species that paralleled the decline in overstory biomass at higher grazing intensity. These parallel negative relationships with grazing intensity strongly suggest that the increase in quality forage biomass with overstory biomass, and the marginally significant association of overstory biomass with total forage biomass, are probably correlative in nature. Since the positive relationships of forage biomass variables with overstory biomass most likely reflect correlated negative responses to increasing grazing exposure, these relationships probably did not result from the woody overstory facilitating forage species.
Overstory-forage relationships in improved fallows

In improved fallows, trees and large shrubs reduced the biomass of forage species underneath, probably through competition for light, soil nutrients, water, or some combination thereof. Observed effects of overstory biomass on total forage biomass and quality forage biomass were comparable and provide evidence that the overstory competitively suppressed forage species in general as well as higher quality forage species. Thus, overstory competition apparently reduced the abundance of forage species (total forage biomass) and the level of useful forage biomass (quality forage biomass) as well.

Trees and large shrubs did not appear to suppress higher quality forage species more strongly than species producing lower quality forage. Forage species of higher quality may be less tolerant of stress from shade or low soil resource availability resulting from overstory competition. Higher N content and lower lignin content in green tissues are associated with higher growth rates and less conservative life history strategies, meaning that species with these traits are likely better suited to habitats with greater availability of light and soil resources (Ackerly and Cornwell 2007, Poorter 2009) in which rapid growth is more advantageous than conservation of limited resources. However, since total forage biomass and quality forage biomass had similar relationships with the biomass of trees and large shrubs, and since overstory biomass did not affect forage quality, forage species of higher quality did not appear to experience disproportionately greater effects of overstory competition.

In improved, as in grazed fallows, hypotheses proposing that overstory niche complementarity may affect forage species through increasing the intensity of competition, or alternatively ameliorating competition or enhancing facilitation, once again did not find support. Species richness and FD of trees and large shrubs did not affect forage variables negatively,
suggesting that competition was no more intense where overstory niche complementarity was higher on account of more complete resource utilization. The alternative was also unsupported, that niche differentiation among overstory species might ameliorate overstory competition or enhance facilitation, as the absence of positive overstory diversity effects on forage variables suggest.

The two environmental variables examined in improved fallows, SOC and soil base cations, had no apparent influence on forage biomass variables or forage quality. The visibly low light available to the understory beneath the dense canopy in many improved fallows suggests that light posed a significant limitation to the growth of forage species, which is consistent with the absence of effects of soil conditions on forage variables.

*Overstory-forage relationships and fallow management*

Support for the proposed hypotheses varied among the two fallow types. There was evidence that overstory competition reduced the standing biomass but not the quality of forage available in improved fallows, while in grazed fallows there was no evidence for competitive suppression of forage biomass or forage quality. In grazed fallows, selective grazing reduced the biomass of higher quality forage species as well as overall forage quality. The differences among fallow types in the observed effects of the overstory and environmental conditions on forage biomass and quality are largely attributable to differences in management of grazed and improved fallows. Grazed fallows are by definition subjected to consistent grazing and are not intentionally planted with trees or large-statured shrubs, while improved fallows in this study are ungrazed, and are planted with woody leguminous species at high density.
The hypotheses that overstory diversity and niche complementarity may either exacerbate competition with forages, or may alternatively reduce competition or enhance facilitation of forages, were not supported in either fallow type. It is possible that variation in the evenness of overstory species led to indistinct effects of tree and large shrub diversity. Thus, the potential of niche differentiation among trees and large shrubs to affect forage species growing beneath them was somewhat unclear yet nonetheless appears unlikely.

Forage variables did not bear evidence of competitive interactions between the overstory and forage species in fallows exposed to livestock grazing. The decline in the biomass of trees and large shrubs at higher grazing intensity indicated that grazers reduced biomass of large woody plants, whether directly through browsing of the overstory, indirectly by reducing recruitment of large woody species, or both. Together, these observations indicate that by reducing woody biomass, grazing may have prevented trees and large shrubs from competing with forage species. Since quality forage biomass declined significantly with grazing intensity while total forage biomass did not, higher quality forage species appear to have been preferentially reduced by selective livestock grazing. In contrast, in improved fallows the overstory appeared to compete with forage species, due to the high biomass and dominance of intentionally planted large woody species, and perhaps also the absence of grazing.

Effects of the overstory and grazing on species of higher and lower forage quality also differed among the two fallow types. In grazed fallows, the lower biomass of higher quality forage species and lower forage quality as grazing intensity increased constitute evidence that selective grazing resulted in a negative response in the palatability of the plant community. In improved fallows, forage quality did not respond to overstory variables or environmental conditions. While overstory competition reduced forage biomass in improved fallows, the ability of forage species to
withstand overstory competition was apparently unrelated to their usefulness as forage for livestock. Thus, the quantity and quality of forage biomass were regulated differently in grazed fallows, while in improved fallows higher and lower quality forage species did not displayed diverging patterns of abundance.

Yet all differences among fallow types may not necessarily be ascribed simply to the presence of livestock grazing and the planting of fallows with large woody species. Management, land use history, and their apparent effects on fallow ecological conditions differed in several ways among the two fallow types, and could have had influences of their own. The more intensively managed improved fallows are geared more toward restoration of soil fertility to support crop growth in coming seasons, while the more extensively managed grazed fallows are often retained as pasture for long periods. Improved fallows tended to be in fields of higher inherent fertility due to lower sand content, and on average have been cropped more intensively in recent years and are therefore younger than grazed fallows. Thus, the goals of management and the practices utilized differed substantively among fallow types. The extent to which additional unquantified management factors, such as the frequency and intensity of periodic coppicing of woody stems, may have influenced vegetation structure is thought to have been minimal in the study fallows, but could significantly affect interactions between the overstory and understory.

*Implications for ecosystem services*

The results have thus far been digested from the perspectives of community and ecosystem ecology, and can also be interpreted from an ecosystem services perspective. Some of the observations here may prove informative for interactions among provisioning ecosystem
services in a variety of agroforestry systems in which direct biological interactions between ESPs may occur.

The differences in possible regulatory factors affecting total forage biomass, quality forage biomass, and forage quality provide clues as to the bases of ecosystem service delivery in these systems, as do the correlations among the three forage variables themselves. The ESPs for the ecosystem service of forage production were defined here as the forage species of higher quality. Thus, total forage biomass reflects the overall abundance of all forage species, while quality forage biomass reflects the green biomass of forage ESPs, and indicates the actual amount of useful forage biomass available for feeding livestock. Information on functional traits enabled estimation of the quality and the amount of useful forage biomass, and provided an effective means of isolating forage quality from forage quantity.

The overall abundance of forage species and the amount useful of forage biomass responded similarly to the characteristics of the woody overstory in both improved fallows, and in grazed fallows, showed similar relationships with overstory biomass and grazing intensity. Relationships between forage quality and total and quality forage biomass were either non-existent (improved), or, respectively, insignificant and marginally significant (grazed). As such, effective management to produce forage for livestock in grazed fallows should ideally consider both the biomass of forage produced as well as its quality, while the quality of forage would be less of a concern in improved fallows.

Relationships among ecosystem services can be categorized in terms of whether they respond to common regulatory factors, and whether they interact with one another directly (Bennett et al. 2009). In the study systems, these criteria can be used to characterize interactions among the ecosystem services of wood production and forage production. Intentional planting of
large woody species and grazing intensity acted as shared drivers in, respectively, the improved and grazed fallow types.

The two ecosystem services interacted directly in improved fallows. When planting of woody species resulted in higher wood biomass, forage biomass was reduced more greatly due to the direct interaction of trees and shrubs competing with forage species. The negative interaction between wood ESPs and forage ESPs thus provides evidence for a trade-off between the production of wood and the production of livestock forage that prevents both ecosystem services from being maximized simultaneously.

In contrast, in grazed fallows the evidence points to an indirect interaction among wood production and forage production. The evidence from grazed fallows indicates that competitive interactions between the overstory and understory are weak or negligible under exposure to livestock grazing, and hence no trade-off was observed as in improved fallows. More intense grazing decreased not only wood biomass, but also the quality of forage, and the biomass of quality forage available. It appears unlikely that wood and forage production interacted directly in grazed fallows, although the possibility that the overstory facilitated forage species could not be dismissed. The positive relationship between quality forage biomass and overstory biomass provides evidence for a synergy among the two ecosystem services, but a synergy that is apparently correlative and attributable to the shared driver of livestock grazing, rather than arising from direct facilitative interactions among wood and forage ESPs. Changing the management of grazed fallows toward higher woody biomass clearly entails greater wood production; if the increase in woody biomass is sufficiently modest, there ought to be no impact on forage biomass or quality, and should additionally benefit soil quality in grazed fallows.
The evidence presented here demonstrates the existence of ecosystem service interactions in smallholder fallows. Trade-offs and synergies among the same pair of ecosystem services were dependent on fallow management and subsequent differences in ecological conditions. When ecosystem services interact, the linkages among services should be considered in management decisions. Improved fallows produce substantial quantities of wood, at the cost of forage production, and benefit soil quality and subsequent crop production. Grazing of fallows allows for the production of forage and wood at the same time, but intense grazing reduces the potential to produce wood and improve soil quality, and moreover reduces the quality of available forage. Accounting for these and other interactions among ecosystem services will be particularly useful when management intends to optimize production across a set of multiple ecosystem services.
Tables and Figures

*Table 3.1.* Definitions of forage variables and their significance to the ecosystem service of forage production. CP = crude protein (N content x 6.25).

<table>
<thead>
<tr>
<th>Forage variable</th>
<th>Definition</th>
<th>ES Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total forage biomass</td>
<td>Total (above- + belowground) biomass of all forage species</td>
<td>Overall abundance among all forage species; potential standing forage biomass</td>
</tr>
<tr>
<td>Quality forage biomass</td>
<td>Green biomass of forage species with green tissue CP : lignin $\geq$ 0.8</td>
<td>Edible biomass of higher quality forage species; the actual amount of biomass useful as livestock forage</td>
</tr>
<tr>
<td>Forage quality</td>
<td>Community-weighted mean green tissue CP : lignin of all forage species</td>
<td>Overall forage quality among all forage species present</td>
</tr>
</tbody>
</table>
Table 3.2. Description of forage, overstory, and environmental variables. Includes transformations applied, and summary statistics.

<table>
<thead>
<tr>
<th>Forage variable</th>
<th>Units</th>
<th>Transf.</th>
<th>Fallow type</th>
<th>n</th>
<th>Mean</th>
<th>SD</th>
<th>SEM</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total forage biomass</td>
<td>t ha(^{-1})</td>
<td>square root</td>
<td>Grazed</td>
<td>18</td>
<td>5.34</td>
<td>2.38</td>
<td>0.56</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Improved</td>
<td>21</td>
<td>3.49</td>
<td>2.13</td>
<td>0.46</td>
</tr>
<tr>
<td>Quality forage biomass</td>
<td>t ha(^{-1})</td>
<td>square root</td>
<td>Grazed</td>
<td>18</td>
<td>2.44</td>
<td>1.16</td>
<td>0.27</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Improved</td>
<td>21</td>
<td>1.69</td>
<td>1.07</td>
<td>0.23</td>
</tr>
<tr>
<td>Forage quality</td>
<td>Unitless</td>
<td>NA</td>
<td>Grazed</td>
<td>18</td>
<td>0.79</td>
<td>0.14</td>
<td>0.03</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Improved</td>
<td>21</td>
<td>0.80</td>
<td>0.10</td>
<td>0.02</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Independent variable</th>
<th>Units</th>
<th>Transf.</th>
<th>Fallow type</th>
<th>n</th>
<th>Mean</th>
<th>SD</th>
<th>SEM</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tree+Shrub biomass</td>
<td>t ha(^{-1})</td>
<td>log</td>
<td>Grazed</td>
<td>18</td>
<td>5.20</td>
<td>6.25</td>
<td>1.47</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Improved</td>
<td>21</td>
<td>46.8</td>
<td>11.0</td>
<td>2.4</td>
</tr>
<tr>
<td>Tree+Shrub species richness</td>
<td>Counts</td>
<td>log</td>
<td>Grazed</td>
<td>14</td>
<td>2.36</td>
<td>1.50</td>
<td>0.40</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Improved</td>
<td>21</td>
<td>2.67</td>
<td>1.88</td>
<td>0.41</td>
</tr>
<tr>
<td>Tree+Shrub functional diversity (FD)</td>
<td>Euclidean distance</td>
<td>NA</td>
<td>Grazed</td>
<td>8</td>
<td>8.56</td>
<td>4.09</td>
<td>1.44</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Improved</td>
<td>14</td>
<td>7.03</td>
<td>3.02</td>
<td>0.81</td>
</tr>
<tr>
<td>Soil base cations</td>
<td>meq 100g(^{-1})</td>
<td>arcsine</td>
<td>Grazed</td>
<td>18</td>
<td>4.77</td>
<td>2.18</td>
<td>0.51</td>
</tr>
<tr>
<td></td>
<td></td>
<td>square root</td>
<td>Improved</td>
<td>21</td>
<td>3.69</td>
<td>1.15</td>
<td>0.25</td>
</tr>
<tr>
<td>Soil organic carbon (SOC)</td>
<td>%</td>
<td>arcsine</td>
<td>Grazed</td>
<td>18</td>
<td>1.54</td>
<td>0.34</td>
<td>0.08</td>
</tr>
<tr>
<td></td>
<td></td>
<td>square root</td>
<td>Improved</td>
<td>21</td>
<td>1.49</td>
<td>0.31</td>
<td>0.07</td>
</tr>
<tr>
<td>Grazing intensity</td>
<td>% area (approx.)</td>
<td>arcsine</td>
<td>Grazed</td>
<td>18</td>
<td>60.3</td>
<td>22.5</td>
<td>5.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>square root</td>
<td>Improved</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
</tbody>
</table>
Table 3.3. Effects of overstory interactions and environmental conditions on forage variables in grazed fallows.

### Grazed fallows

<table>
<thead>
<tr>
<th>Mechanism(s)</th>
<th>Independent variable</th>
<th>Forage variable</th>
<th>d.f.</th>
<th>Intercept</th>
<th>Slope</th>
<th>P</th>
<th>( R^2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Overstory competition</td>
<td>Tree+Shrub biomass</td>
<td>Total forage biomass</td>
<td>16</td>
<td>2.25</td>
<td>0.183</td>
<td>0.058</td>
<td>0.157</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Quality forage biomass</td>
<td>16</td>
<td>1.67</td>
<td>0.129</td>
<td><strong>0.033</strong></td>
<td>0.208</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Forage quality</td>
<td>16</td>
<td>0.76</td>
<td>0.022</td>
<td>0.460</td>
<td>-0.026</td>
</tr>
<tr>
<td>Overstory competition or facilitation</td>
<td>Tree+Shrub species richness</td>
<td>Total forage biomass</td>
<td>12</td>
<td>2.48</td>
<td>0.104</td>
<td>0.725</td>
<td>-0.072</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Quality forage biomass</td>
<td>12</td>
<td>1.73</td>
<td>0.154</td>
<td>0.431</td>
<td>-0.027</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Forage quality</td>
<td>12</td>
<td>0.69</td>
<td>0.080</td>
<td>0.419</td>
<td>-0.024</td>
</tr>
<tr>
<td></td>
<td>Tree+Shrub FD</td>
<td>Total forage biomass</td>
<td>6</td>
<td>2.70</td>
<td>-0.005</td>
<td>0.910</td>
<td>-0.164</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Quality forage biomass</td>
<td>6</td>
<td>2.06</td>
<td>-0.011</td>
<td>0.753</td>
<td>-0.146</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Forage quality</td>
<td>6</td>
<td>0.82</td>
<td>-0.001</td>
<td>0.935</td>
<td>-0.165</td>
</tr>
<tr>
<td>Environmental conditions</td>
<td>SOC</td>
<td>Total forage biomass</td>
<td>16</td>
<td>2.15</td>
<td>2.607</td>
<td>0.758</td>
<td>-0.056</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Quality forage biomass</td>
<td>16</td>
<td>2.51</td>
<td>-5.460</td>
<td>0.302</td>
<td>0.008</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Forage quality</td>
<td>16</td>
<td>1.19</td>
<td>-3.213</td>
<td>0.192</td>
<td>0.048</td>
</tr>
<tr>
<td>Soil base cations</td>
<td></td>
<td>Total forage biomass</td>
<td>16</td>
<td>2.25</td>
<td>1.032</td>
<td>0.686</td>
<td>-0.051</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Quality forage biomass</td>
<td>16</td>
<td>1.86</td>
<td>-0.112</td>
<td>0.945</td>
<td>-0.062</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Forage quality</td>
<td>16</td>
<td>0.81</td>
<td>-0.091</td>
<td>0.905</td>
<td>-0.062</td>
</tr>
<tr>
<td>Grazing intensity</td>
<td></td>
<td>Total forage biomass</td>
<td>16</td>
<td>2.90</td>
<td>-0.477</td>
<td>0.332</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Quality forage biomass</td>
<td>16</td>
<td>2.38</td>
<td>-0.606</td>
<td><strong>0.041</strong></td>
<td>0.188</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Forage quality</td>
<td>16</td>
<td>1.09</td>
<td>-0.335</td>
<td><strong>0.013</strong></td>
<td>0.284</td>
</tr>
</tbody>
</table>
Table 3.4. Effects of overstory interactions and environmental conditions on forage variables in improved fallows.

<table>
<thead>
<tr>
<th>Improved fallsows</th>
<th>Mechanism(s)</th>
<th>Independent variable</th>
<th>Forage variable</th>
<th>d.f.</th>
<th>Intercept</th>
<th>Slope</th>
<th>P</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Overstory competition</td>
<td>Tree+Shrub biomass</td>
<td>Total forage biomass</td>
<td>19</td>
<td>7.00</td>
<td>-1.287</td>
<td><strong>0.006</strong></td>
<td>0.299</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Quality forage biomass</td>
<td>19</td>
<td>4.57</td>
<td>-0.771</td>
<td><strong>0.010</strong></td>
<td>0.263</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Forage quality</td>
<td>19</td>
<td>1.09</td>
<td>-0.077</td>
<td>0.445</td>
<td>-0.020</td>
</tr>
<tr>
<td></td>
<td>Overstory competition or</td>
<td>Tree+Shrub species</td>
<td>Total forage biomass</td>
<td>19</td>
<td>2.02</td>
<td>0.028</td>
<td>0.913</td>
<td>-0.052</td>
</tr>
<tr>
<td></td>
<td>facilitation</td>
<td>richness</td>
<td>Quality forage biomass</td>
<td>19</td>
<td>1.56</td>
<td>0.043</td>
<td>0.795</td>
<td>-0.049</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Forage quality</td>
<td>19</td>
<td>0.76</td>
<td>0.032</td>
<td>0.523</td>
<td>-0.030</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Tree+Shrub FD</td>
<td>Total forage biomass</td>
<td>12</td>
<td>1.78</td>
<td>0.033</td>
<td>0.533</td>
<td>-0.047</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Quality forage biomass</td>
<td>12</td>
<td>1.45</td>
<td>0.020</td>
<td>0.570</td>
<td>-0.053</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Forage quality</td>
<td>12</td>
<td>0.77</td>
<td>0.004</td>
<td>0.674</td>
<td>-0.067</td>
</tr>
<tr>
<td></td>
<td>Environmental conditions</td>
<td>SOC</td>
<td>Total forage biomass</td>
<td>19</td>
<td>0.65</td>
<td>11.585</td>
<td>0.208</td>
<td>0.034</td>
</tr>
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<td>0.75</td>
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<td>0.028</td>
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<td>Forage quality</td>
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<td>-2.650</td>
<td>0.137</td>
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<tr>
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<td></td>
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<td>Total forage biomass</td>
<td>19</td>
<td>2.09</td>
<td>-0.175</td>
<td>0.963</td>
<td>-0.053</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Quality forage biomass</td>
<td>19</td>
<td>1.38</td>
<td>1.197</td>
<td>0.616</td>
<td>-0.038</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Forage quality</td>
<td>19</td>
<td>0.62</td>
<td>0.919</td>
<td>0.205</td>
<td>0.035</td>
</tr>
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</table>
Figure 3.1. Relationships of total forage biomass (overall forage abundance; see Table 1 for definition and significance) with overstory biomass and diversity, and environmental conditions.
Figure 3.2. Relationships of quality forage biomass (useful forage biomass; see Table 1 for definition and significance) with overstory biomass and diversity, and environmental conditions.
Figure 3.3. Relationships of forage quality (CP : lignin; see Table 1 for definition and significance) with overstory biomass and diversity, and environmental conditions.
Chapter 4: Biodiversity and multiple ecosystem services in smallholder fallows

Abstract

Recent experimental studies provide evidence that greater species richness can increase the ability of plant communities to support multiple ecosystem functions. To better understand how and when ecosystem services depend on biodiversity, it is necessary to expand beyond experimental grassland systems. To assess whether plant diversity improves the capacity of agroecosystems to sustain multiple ecosystem services, wood production, livestock forage production, and two elements of soil formation were examined in smallholder fallows in western Kenya. In 18 grazed fallows and 21 improved fallows, stem diameter of trees and cover and height of shrubs and herbs were used to estimate biomass. Near infrared spectroscopy was used to predict soil properties (organic carbon, base cations, sand content), and steady infiltration rates were derived from asymptotic regression of ring infiltrometer data. For 4 ecosystem functions (wood biomass, forage biomass, soil base cations, and steady infiltration rates) directly tied to the 3 focal ecosystem services, fallow ecosystem service multi-functionality was quantified as (1) the proportion of functions above half-maximum (PAH), and (2) mean percentage excess above mean (EAM) function values. The objective was to examine whether plant diversity or environmental favorability (high soil organic carbon (SOC), low grazing intensity) can better predict fallow ecosystem multi-functionality. In grazed fallows, positive effects of plant diversity best explained both PAH and EAM, and PAH declined with grazing intensity but EAM did not. Diversity effects were independent of grazing, at least in moderately grazed fallows. In improved fallows, PAH
was not associated with plant diversity or SOC, however EAM increased with diversity but especially with SOC. Thus, grazed fallows yielded clearer evidence of plant diversity effects on multi-functionality, while environmental favorability may have been more influential in improved fallows. The difference in the diversity-multi-functionality relationship between grazed and improved fallows appears related to their contrasting management regimes and associated variation in disturbance, fallow species composition, and the productivity of vegetation and soils. In grazed fallows, mechanisms contributing to diversity effects may include complementary effects of species with contrasting functional traits on different ecosystem functions, and effects of multi-functional species on more than one ecosystem function. Plant diversity and site productivity may improve the capacity of smallholder fallows to provide multiple ecosystem services simultaneously, yet diversity effects are likely to vary with management, species composition, and environmental conditions.

Introduction

Biodiversity in its broad sense is responsible for the ecosystem services relied on by human societies (Duraiappah and Naeem 2005). However, the linkages among biodiversity and many ecosystem services remain poorly understood. Biodiversity conservation strategies tend to be based primarily on intrinsic and cultural values (Redford and Adams 2009), rather than these values in combination with use values (Naidoo et al. 2008, Sutherland et al. 2009). Either under- or over-estimating the utility of biodiversity to stakeholders may pose a threat to conservation efforts. Empirical information on biodiversity relationships with ecosystem services may
ultimately assist efforts to conserve biodiversity and alleviate rural poverty in developing countries. If the cumulative values attributable to biodiversity are more difficult to replace than managers expect, management decisions that excessively discount returns to biodiversity may impede delivery of ecosystem services.

In recent decades a growing body of evidence mostly from manipulative experiments has demonstrated that the diversity of species in ecological communities can significantly influence ecosystem processes and properties (Hooper et al. 2005, Balvanera 2006, Cardinale et al. 2006, Cardinale et al. 2007). Experimental manipulations of plant species and functional group diversity, predominately in grasslands, demonstrate that effects of biodiversity on ecosystem functions such as biomass production and nutrient retention are typically positive and tend to saturate at high species richness (Hooper et al. 2005, Balvanera 2006, Cardinale et al. 2006).

Several mechanisms have been proposed as contributing to positive biodiversity-ecosystem function (BEF) relationships, the two most widely acknowledged being complementarity effects and sampling or “selection” effects. Sampling effects arise from the higher probability of a species efficacious for a particular function being represented at higher species richness. Complementarity effects occur through niche partitioning among species. Complementary niches among species can reduce competition, increasing the efficiency of resource capture and utilization by the plant community. For example, a grass and a forb grown in mixture may compete less intensely with one another than with conspecifics. In addition, if the forb is leguminous, the grass may be facilitated by soil N fixed by the legume. Consequently, productivity, utilization of soil nutrients, and rates of other ecosystem processes commonly increase. In grassland plant communities, complementarity effects may be the predominant mechanism behind diversity effects on productivity (Cardinale et al. 2007).
In response to the surge in BEF studies, interest in the implications of biodiversity loss for the delivery of ecosystem services has intensified. Despite substantial progress, much work remains toward understanding how biodiversity loss may affect the functioning of ecosystems and ecosystem service delivery. For example, effects of plant and soil organism diversity on decomposition rates have been studied extensively, yet the relationship varies greatly and is notoriously difficult to characterize (Hättenschwiler et al. 2005, Gessner et al. 2010).

Currently, two major BEF research concerns are biodiversity influences on multiple ecosystem functions, and the system-specificity of research. First, from a more theoretical perspective, the focus on biodiversity effects on individual ecosystem functions does not embrace the likelihood that species affect different ecosystem functions differently (Hector and Bagchi 2007). Second, from a more ‘real-world’ perspective, the heavy emphasis on mesocosms designed to mimic natural grasslands limits applicability to ecosystems in general. Ultimately, if biodiversity is to be linked with ecosystem services in ‘real-world’ natural and managed systems, BEF research will need to account for differences between experimental grasslands and, for example, the agroecosystems and forests that provide most of the ecosystem services that human societies rely on.

BEF studies have laid a solid theoretical and empirical groundwork for research addressing multiple ecosystem functions in managed systems. While plant diversity effects on terrestrial ecosystem functioning remains largely unaddressed beyond grasslands, some studies have investigated whether biodiversity can enhance levels of multiple ecosystem functions simultaneously, or in other words ‘ecosystem multi-functionality’ (sensu Hector and Bagchi 2007).
Biodiversity and ecosystem multi-functionality

The proposition that plant diversity can increase the ability of communities to support multiple ecosystem functions finds evidence in grassland diversity manipulations in Europe (Hector and Bagchi 2007, Gamfeldt et al. 2008) and North America (Zavaleta et al. 2010). These studies overlapped somewhat in the ecosystem functions considered; all three studies included plant biomass production and indicators of N uptake, while two included primary consumer biomass production (Gamfeldt et al. 2008, Zavaleta et al. 2010), one decomposition (Hector and Bagchi 2007) and another soil C, insect species richness, and invasion resistance (Zavaleta et al. 2010).

These studies tested three distinct but related hypotheses: (1) as a greater number of ecosystem functions are considered the number of species important for one or more functions increases (Hector and Bagchi 2007); (2) species richness increases the probability that each of six ecosystem functions is sustained at half of maximum (Gamfeldt et al. 2008); and (3) species richness increases the ability of ecosystems to simultaneously sustain each of up to eight ecosystem functions at 30, 40, and 50% of function maxima (Zavaleta et al. 2010). All three studies concluded that species richness significantly enhanced the ability of grassland ecosystems to sustain multiple ecosystem functions.

Several possible mechanisms may account for the evidence these studies provide for influences of plant diversity on multiple ecosystem functions. Plant species complementarities among ecosystem functions are one mechanism. Although similar species commonly have redundant effects on a particular ecosystem function, a pair of species redundant for one function may possess traits leading to distinct (i.e., less redundant) effects on another function (Hector and Bagchi 2007). Functional uniqueness of species among ecosystem functions, and consequently
greater cumulative complementarity among the species in a community, may thus improve the overall functioning of ecosystems.

The potential of plant diversity to enhance species complementarities among ecosystem functions was well documented by Zavaleta et al. (2010), who found that species richness increased the number of functions that could be sustained at thresholds set at various percentages of function maxima. Species-poor assemblages were often able to support multiple functions at the lowest threshold level, however the ability to support several functions at the highest threshold level predominated among more species-rich plots. The change in the diversity-multi-functionality relationship as the threshold level was increased indicates that complementary effects of different plant species on different functions enabled more functions to be supported at higher levels of each.

‘Multi-functional’ species capable of contributing effectively to more than one ecosystem function simultaneously may be another mechanism. Two species of multi-purpose trees common in agroforestry systems in the study area for the present study, *Sesbania sesban* (L.) Merr. and *Calliandra calothyrsus* Meissn., serve as good examples. *Sesbania* is highly productive compared to other agroforestry trees, and both species are capable of fixing over 50% of their nitrogen content from the atmosphere, as well as preventing leaching losses of soil NO$_3^-$ (Ståhl et al. 2002). *Calliandra* has high polyphenol content in tissues both above- and belowground (Lehmann et al. 1998), and could be effective in building long-lived soil C pools, with possible long-term benefits for soil structure and hydraulic properties. Multi-functional species may possess unique combinations of functional traits, increasing functional diversity disproportionately, and their representation may increase probabilistically in more species-rich communities.
Finally, species may influence ecosystem functions indirectly. Plant species may benefit other species through facilitation or indirect positive interactions, including trophic interactions. A species redundant with others for a particular function may benefit more functionally singular species. Species unique in an assemblage in providing litter or microhabitats that suit ecosystem engineers (Jones et al. 1994, Anderson 1995) such as earthworms, termites, and other soil macrofauna may indirectly improve the performance of other species. Plant species that support different macrofauna can increase ecosystem process rates in soils and litter when in mixture (van Eekeren et al. 2009), and soil macrofauna can have strong effects, and very different effects, on soil processes in agroecosystems (Beare et al. 1997). Meanwhile, positive interactions among functionally differentiated soil macrofauna can enhance decomposition and microbial activity (Heemsbergen et al. 2004). Effects of otherwise functionally redundant plant species on soil communities could generate positive indirect effects on the performance of the plant community by improving the soil structure and fertility.

Biodiversity and agroecosystem multi-functionality

In managed systems, complementarity among plant species might influence joint levels of multiple ecosystem functions even more strongly than in experimental systems. One important characteristic of managed systems is significant disturbance in the form of land management practices such as harvesting, grazing, and periodic land use rotations. Disturbance has been reported as strengthening diversity effects on ecosystem function; partial removal of benthic invertebrates in mesocosms (Cardinale and Palmer 2002) and soil disturbance by gophers in old-field plant communities (Jouseau 2008) both enhanced apparent diversity effects.
The potential of biodiversity to buffer the functioning of ecosystems against environmental change is known as the insurance hypothesis (Naeem 2002, Loreau et al. 2003). Enhanced resilience of agroecosystem functioning is a primary rationale for the retention of biodiversity in agricultural landscapes (Tscharntke et al. 2005, Jackson et al. 2007). Higher frequency and intensity of disturbance may increase the importance of functional diversity in traits mediating plant responses to disturbance. Species able to tolerate a disturbance or re-colonize in its wake will be those that subsequently contribute to ecosystem functioning, and the post-disturbance community is likely to function differently than the previous assemblage.

Plant responses to removal of aboveground biomass are mediated by functional traits associated with two main strategies: tolerance and avoidance. The first suite of traits enables plants to withstand disturbance, such as the ability to resprout from protected organs (Bond and van Wilgen 1996, Bond and Midgley 2001), vegetative reproduction, belowground storage organs, low apical meristems, seed dormancy, and a perennial life cycle (McIntyre et al. 1999). The second suite of traits is associated with high fecundity and growth rates, providing for re-establishment and rapid growth following disturbance. Annual plants typify avoidance response, with traits for effective dispersal such as small seeds (McIntyre et al. 1999), and traits linked to rapid growth such as high specific leaf area (SLA; area per unit mass) and high leaf N (Lavorel and Garnier 2002).

The response of plant communities to grazing by large herbivores is a somewhat special case, as a wide array of responses have been documented. At the global scale, grazing typically increases the dominance of annuals (indicating avoidance), as well as short, prostrate, or stoloniferous plants (indicating tolerance), but much variation remains unexplained, and may be attributable to influences of climate and evolutionary history (Díaz et al. 2007b). Effects of
grazing on palatability vary widely, and may affect ecosystem processes by altering litter chemistry and biomass production. Grazing often reduces the abundance of forbs, while species less palatable—e.g., due to low SLA and leaf N (e.g., Quétier et al. 2007)—often increase. Negative responses of palatability tend to hold in regions with a dry climate or a long grazing history, whereas in humid regions no general trend is apparent (Díaz et al. 2007b). Positive responses of palatability in grasses of humid and sub-humid regions can occur through an overcompensatory growth response (McNaughton 1983, Augustine and McNaughton 2006), in which growth rates rise dramatically. The likely advantage of this strategy is to reach a height preventing further consumption, though the rapid growth partly results from fast-growing species exploiting a flush of newly available resources (Herms and Mattson 1992, Augustine and McNaughton 2006). Thus, responses of plant communities to grazing can be difficult to predict, yet may significantly alter ecosystem process rates.

When a biotic community is exposed to a perturbation, the importance of functional trait diversity depends on whether the traits that make species vulnerable to the perturbation (response traits) are the same traits determining species effects on ecosystem function (effect traits). When species with stronger effects are also more vulnerable, the result is a decline in ecosystem function that is greater than expected with random loss of species (Suding et al. 2008). For instance, larger bee species can be more effective as pollinators, yet are more prone to extinction, causing a disproportionate decline in pollination upon reduction of species richness (Larsen et al. 2005). If timber extraction favors tree species of high wood density, aboveground carbon storage should decline rapidly with species loss (Bunker et al. 2005). Hence, a key goal in current BEF research is to distinguish functional traits mediating the distribution and abundance of organisms, including
responses to perturbations and global change drivers, from the functional traits that determine effects on ecosystem processes (Díaz et al. 2006, Hillebrand and Matthiessen 2009).

Smallholder agricultural systems in the tropics furthermore have additional characteristics that may increase the likelihood of plant diversity influencing multiple ecosystem services. Smallholder farms tend to be more multi-functional (Altieri 1999) than commercial agriculture, with plants ranging from annual and perennial crops to forages for livestock, to tree-crops, to trees for timber and construction material. Smallholder farmers often plant multi-functional species capable of providing multiple benefits simultaneously, especially trees that improve soil quality while also producing wood, such as *Sesbania* and *Calliandra*, and tree-crops (Schroth et al. 2002). Some are perennial crops: cassava (*Manihot esculenta* Crantz) for instance, can improve soil fertility compared to annual crops (Fermont et al. 2008). Some multi-functional species are exotic to an agroecosystem or region (*Calliandra*, in the study area), while others may be desirable native species that are planted or encouraged to regenerate (*Sesbania*).

The goal of the current study is to assess whether plant diversity and environmental conditions influence the capacity of fallows in tropical smallholder systems to provide multiple agricultural ecosystem services. A set of four ecosystem functions were selected as indicators for the ecosystem services of wood production, livestock forage production, and soil formation, the latter of which moreover affects post-fallow crop production. Ecosystem service multi-functionality was quantified as (1) the proportion of functions above half-maximum (PAH), and (2) mean percentage excess above mean (EAM) function values. Two specific hypotheses were tested. The first hypothesis was that plant diversity increases the ecosystem service multi-functionality of fallows. Second, since favorable environmental conditions may benefit each of the selected ecosystem functions, it was hypothesized that multi-functionality increases with
environmental favorability in terms of lower grazing intensity and higher soil fertility (grazing intensity did not apply in improved fallows). The current study is the first to test empirically for influences of plant diversity on multiple ecosystem functions outside of experimental grassland mesocosms, and the first to test whether biodiversity influences multiple ecosystem functions directly tied to ecosystem services relevant to the livelihoods of smallholder farmers.

Methods

Study systems. The Millennium Villages Project (MVP) is an evidence-based approach to alleviating extreme rural poverty in sites throughout Sub-Saharan Africa, in which agricultural development plays a strategic role (Sanchez et al. 2007). The data for this study were collected in 2008-2009 in the Sauri MVP site in Siaya District, western Kenya.

Sauri MVP has a humid tropical climate with two rainfall peaks and potential cropping seasons yearly, and elevation ranges from 1,300 to 1,470 m. The clayey, well drained Oxisols and Ultisols are soil orders representative of soils common in Sub-Saharan Africa. The landscape in Sauri is a shifting agricultural matrix primarily composed of maize and other annual crops, with lower landscape cover of woodlots, land dedicated to grazing, and fallow fields. Land use in the area cycles between periods of annual crops, and periods of fallow intended to regenerate soil fertility and to provide wood products, green manures from foliage of woody plants, and forage for livestock, among other goods. High population density, high cropping frequency and inadequate fertilization having led to degradation since the early 20th century (Scherr 1995), and
soils in the area are relatively depleted of N and C. However, Sauri agroecosystems may currently be undergoing long-term rehabilitation.

**Fallow type.** ‘Improved’ fallows of fast-growing leguminous trees are promoted by MVP to improve soil fertility and fuelwood. They are usually planted with *Tephrosia candida* DC, and less commonly with *Crotalaria paulina* Schrank, *Calliandra calothyrsus* Meissn. or other exotics, and are not grazed with livestock. Grazed fallows, often considered ‘natural’ or ‘weed’ fallows, are less common, and contain a variety of species, most of which are native. The most common trees in grazed fallows are the native *Markhamia lutea* (Benth.) K. Schum., *Sesbania sesban* (L.) Merr., and the exotic *Psidium guajava* L. Most grazed fallows combine production of wood and green manures with livestock grazing, although heavily grazed fallows do not produce wood.

**Data collection.** Fallow fields identified for sampling ranged from 0.02 to 0.25 ha in area, with a mean size of approximately 0.1 ha. Data were collected from 18 grazed and 21 improved fallows. Data were collected using a slight adaptation of the Land Degradation Surveillance Framework (LDSF; Walsh and Vagen 2006), modified for field-scale sampling. LDSF involves characterization of vegetation structure (diameter at breast height (DBH) and height of trees, tree and shrub stem density, and vegetation cover), soil conditions (soil properties, soil infiltration capacity, rock cover and erosion), and FAO-standard land use/cover. Soils were sampled at depths of 1-20 cm (topsoil) and 20-50 cm (subsoil).

The LDSF protocol was reproduced at the scale of a single 100 m² plot located randomly in the interior of each fallow. Two 2 m² subplots were established within each 100 m² sample plot, one in the center, and one randomly located tangent to the plot edge. Soil samples were collected and soil infiltration capacity measured in both subplots. Biovolume (m³) of each plant species was characterized by visually estimating cover and average height. Cover was scored as
the mid-point of cover classes on a 5-point scale: 1-4, 4-15, 15-40, 40-65, and > 65 m². Grazing intensity was recorded by visually estimating cover for evidence of grazing—bite marks, trampling, feces, and hair—on the same 5-point scale.

*Standing biomass—large woody stems.* For all woody stems ≥ 2.5 cm DBH, aboveground standing biomass (t ha⁻¹) was estimated by using DBH measurements to calculate whole-tree biomass (Y) by the general allometric equation, \[ Y = e^{(-2.134 + 2.53 \ln(DBH))} \] for humid regions (Ponce-Hernandez 2004). To estimate belowground biomass, aboveground biomass estimates were multiplied by the mean of values from the literature for root-to-shoot ratio (RSR) of tree species common in the study site (Appendix A). Above- and belowground biomass estimates were summed to estimate total standing biomass.

*Standing biomass—small woody stems and herbaceous species.* For all woody plants < 2.5 cm DBH and all non-woody species, cover estimates were multiplied by average height to estimate biovolume by species, then multiplied by a conversion factor to estimate aboveground biomass (Appendix A). To estimate belowground biomass, aboveground biomass estimates were multiplied by the mean of values from the literature for RSR of species common in the study site (Appendix A). Above- and belowground biomass estimates were summed to estimate total standing biomass.

*Standing green biomass.* To obtain estimates of standing green biomass, the same procedure was used as for standing (total) biomass, except using conversion factors that reflect aboveground biomass for leaves and young green twigs (Appendix A).

*Soil infiltration capacity.* Infiltration was measured with ring infiltrometers 20 cm in diameter over approximately 2.5 hours, or until steady state had clearly been reached. Soil infiltration capacity was quantified as steady infiltration rates (mm hour⁻¹), the lower asymptote approached
by infiltration rate over time, and the mean was taken for the 2 nested subplots. Each ~2.5 hr measure was modeled as a random effect in a non-linear mixed effects model of the Horton equation (Horton 1940), via asymptotic regression using the `nlmer` function in the `lme4` package (Bates and Maechler 2010) in R (R Development Core Team 2008).

Soil chemistry. Soil organic carbon (SOC), soil base cations, and soil sand content were quantified by means of near infrared reflectance spectroscopy (NIRS; Shepherd and Walsh 2002, Shepherd and Walsh 2007), which utilized extensive soil libraries developed for the study site and the region to predict values of soil properties. Predictions were made by using linear mixed effects models to predict SOC, base cations, and sand from the principal components (PCs) of first-derivative NIR spectral reflectance in the 700 to 2500 nm range. Topsoil and subsoil were modeled as random effects. Cross-validation based on an independent sample set demonstrated that model fits in terms of $r^2$ were: 0.91 for SOC; 0.92 for Mg; 0.70 for Ca; 0.88 for K; and 0.92 for sand. Estimates of Mg, Ca, and K were summed to estimate base cations. For estimates of SOC, base cations, and sand contents the mean was taken for the 2 nested subplots.

Plant trait data. Samples of leaves and young green twigs were collected from a subset of study plots, and NIRS was used to predict content of N, lignins and polyphenols for the most abundant species. Dry green tissue samples—leaves for herbaceous species, and leaves combined with young green twigs for woody species. Predictions were made by using partial least squares regression models to model N, lignin, and total soluble polyphenol from PCs of first-derivative NIR spectral reflectance in the 1250 to 2500 nm range. Cross-validation based on an independent sample set demonstrated model fits in terms of $r^2$ were: 0.98 for N; 0.73 for lignin; and 0.86 for polyphenol. Mean trait values were calculated by species. For species not collected in
study plots, mean trait values by species were obtained from the Organic Resource Database (Palm et al. 2001).

**Community-weighted trait means.** Community-weighted mean (CWM) green tissue contents of N, lignins, polyphenols, and lignins+polyphenols, were calculated for each plot. CWMs were calculated with Equation 1 (Ackerly and Cornwell 2007) from species mean trait values, weighted upon species abundance in terms of standing green biomass, as

\[
f_j = \frac{\sum_{i=1}^{s} a_{ij} t_i}{\sum_{i=1}^{s} a_{ij}},
\]

where \( f_j \) is the abundance-weighted mean for trait \( t \) in plot \( j \), \( t_i \) is the value of trait \( t \) for species \( i \), \( a_{ij} \) is the abundance of species \( i \) in plot \( j \), and \( S \) is the total number of species present. Trait values were log-transformed prior to calculation of CWMs. Abundance-weighted means for tree and large shrub species, and for forage species, were similarly calculated for green tissue contents of N, lignins, polyphenols, and lignins+polyphenols, by weighting trait means on green biomass of trees and large shrubs, and green biomass of forage species.

**Wood biomass.** For the ecosystem service of wood production, the ecosystem service providers (ESPs; Kremen 2005) were taken to be the species of trees and large shrubs that were sufficiently large in a plot to serve as fuelwood for cooking. Woody biomass of trees and large shrubs includes individual stems \( \geq 2.5 \) cm DBH, and all woody species with average height \( \geq 0.7 \) m. With few exceptions, woody species of smaller stature provide insignificant quantities of useful wood.

**Forage biomass.** For the ecosystem service of forage production, the ESPs were taken to be the forage species that produce forage of higher quality, i.e. those useful for feeding livestock. Forage species were considered to include all herbaceous species, and all woody species \(< 0.7 \)
average height, and forage biomass was calculated as the summed green biomass of forage species of higher quality, in terms of the ratio of green tissue contents of crude protein (CP) (i.e., green tissue N x 6.25) to lignin (Genin and Quiroz 1993). Higher quality forage species were defined as those species with green tissue CP:lignin ≥ 0.8, which approximates the upper limit of the lowest quartile of CP:lignin values among species in the sample, and all species in the sample known to be used for feeding livestock (Dear et al. 2012) had CP:lignin > 0.8 (Sircely, pers. obs.), while all species not known to be used as forage had CP:lignin < 0.8. Forage species with lower CP relative to lignin content should be of little use as feed for livestock, as lignin reduces the ability of livestock to digest and absorb nutrients. Thus, forage biomass is indicative of the actual amount of useful forage biomass.

Species richness. The influence of species with low plot-scale abundance on ecosystem functioning is likely to be minor, and as such these species disproportionately influence evenness and are likely to bias estimation of any influences of plant diversity on ecosystem functions. Species richness was calculated as the number of species comprising ≥ 1% of standing green biomass in a fallow. While species richness and evenness were negatively correlated, when species comprising < 1% of green biomass were removed, species richness and evenness were effectively uncorrelated.

Functional diversity. Functional diversity (FD) was used as a proxy for niche complementarity among fallow plant species (Petchey and Gaston 2002). Because FD reflects dissimilarity among the species in a community, FD can be considered a measure of niche complementarity (Mason et al. 2005, Petchey and Gaston 2006). As for species richness, only species comprising ≥ 1% of standing green biomass in a fallow were included in FD estimation. FD was calculated as the summed branch length of trees generated by UPGMA average linkage
clustering of Euclidean multivariate distances among species in terms of three functional traits: green tissue contents of N, lignins, and polyphenols. Trait values were log-transformed prior to FD calculation, and re-scaled to mean and standard deviation of 1. FD calculations were robust to the traits selected; upon inclusion of maximum height, RSR, lignins+polyphenols, growth form, and woodiness, FD estimates were highly correlated with one another. As such, the conservative set of three traits was selected. Contents of N, lignins, and polyphenols exhibited little correlation across fallow plant species. In the study system, green tissue contents of N, lignins, and polyphenols may be associated with rates of production and accumulation of biomass, biological nitrogen fixation, plant species effects on soil processes, competitive and facilitative species interactions, and responses to grazing. Thus, this conservative set of traits may contain significant information on the niches of plants present in a fallow, and FD acts as an indicator of niche complementarity in terms of aspects of plant niches directly and indirectly related to these traits.

Selection of ecosystem service indicators. Ecosystem functions directly related to specific ecosystem services served as indicators of the services produced in fallows. The analysis was constrained to a handful of ecosystem functions directly related to ecosystem services that benefit farming households. The initial list of candidate functions included standing green biomass, standing woody biomass of large trees and shrubs, standing biomass of forage species, SOC content, soil content of base cations, and steady infiltration rates.

However, standing green biomass and SOC were correlated varying degrees with other ecosystem functions, creating collinearity among functions that could potentially bias analysis of ecosystem multi-functionality. For this reason, a conservative approach to ecosystem multi-functionality was adopted, and did not include standing green biomass, nor SOC or any other
general indicator of soil fertility. This approach also allowed the use of SOC as an independent variable to test for influences of environmental conditions on ecosystem multi-functionality.

The ecosystem functions selected for analysis (Table 4.1) were: standing woody biomass of trees and large shrubs (i.e., available wood), standing biomass of forage species (i.e., available forage), soil content of base cations, and steady infiltration rates (i.e., two elements of soil formation). In these agroecosystems, the selected ecosystem functions refer to specific stocks or fluxes of energy, materials, or both. Biomass of wood specifically indicates the stock of non-living aboveground biomass, and reflects the potential flux of C, energy, and nutrients in woody tissues from fallows to households for use as fuelwood, construction materials, and other uses. Biomass of forage species specifically indicates the stock of biomass available for consumption by livestock, and reflects the potential flux of C, energy, and nutrients in green tissues from fallows to livestock biomass and livestock waste. Not only do these potential fluxes constitute specific losses of energy and materials from fallows, they also denote potential contributions of energy and materials from fallows to fates subsequent to their use as fuelwood or feeding livestock. Some nutrients in fuelwood will end up in ash (except for N, which will be largely volatilized during combustion), while much of the nutrients in livestock forage will be deposited in feces and urine, some of which will be applied as fertilizer throughout the farm. Soil base cation content integrates the cycling, movements, and functions provided by Mg, Ca, and K, including soil cation retention and exchange, uptake by plants, leaching and prevention thereof, and retrieval from subsoils by deep-rooted plants. Soil infiltration capacity is an indicator of robust soil structure, avoidance of runoff and soil erosion, and soil water retention and availability for plant uptake.

**Ecosystem multi-functionality indicators.** For the 4 selected ecosystem functions, fallow ecosystem service multi-functionality was quantified by calculating 2 main indicators: (1) the
proportion of ecosystem functions above half-maximum (PAH), and (2) the mean percentage excess above mean (EAM) function values. That is, PAH is the proportion of the 4 ecosystem functions that were higher than 50% of their respective maximum values, and EAM is the mean percentage by which ecosystem functions exceeded their respective mean values. The proportion of functions above 25 and 75% of maxima were also calculated. To minimize influences of ecosystem function probability distributions on multi-functionality indicators, ecosystem functions were transformed prior to calculation of indicators (Table 4.1). The maximum for each function in the grazed and improved fallow types was defined as the mean of the 3 highest values in each fallow type. A single mean and maximum was established for each function in each fallow type among the two sampling years, as forage biomass did not differ between 2008 and 2009 (not presented), and is the only variable likely to vary with rainfall or other climatic conditions.

Statistical analysis. The response of ecosystem multi-functionality indicators to plant diversity variables and environmental variables was analyzed with univariate linear models for each individual plant diversity variable (species richness, FD) and each environmental variable (SOC, grazing intensity), and with additive bivariate linear models comprising each unique combination of a diversity variable with an environmental variable (grazing intensity did not apply in improved fallows, as they are ungrazed). Given the limited sample size and the likelihood of low statistical power, interaction terms were not specified. To support interpretation of these analyses, the incidence of pair-wise ‘jointness’ in ecosystem functions was calculated. Jointness for a specific pair of ecosystem functions was defined in two ways: when the observed values of two functions are both above 50% of their respective maxima, and when their values are both above their respective mean values. The observed pair-wise jointness for two specific ecosystem
functions was interpreted as reflecting the ability of a fallow to simultaneously sustain the two functions at or above moderate levels of each function.

Results

Correlations among the selected set of four ecosystem functions were weak in both grazed and improved fallows, with the exception of the negative correlation between wood biomass and forage biomass in improved fallows (Figure 4.1). Wood and forage biomass were positively though marginally significantly correlated ($P < 0.1$) in grazed fallows. In improved fallows, wood biomass exhibited a marginally significant negative correlation with soil base cations. Correlations were insignificant ($P > 0.1$) for all other pairs of ecosystem functions.

Ecosystem multi-functionality in terms of PAH (abbreviations given in Table 4.2) was more easily attained in improved than in grazed fallows. The proportion of ecosystem functions above 25, 50, and 75% of function maxima was higher in improved than in grazed fallows, and significantly so at the 25 and 50% levels (Figure 4.2). One improved fallow and no grazed fallows sustained more than two of the four ecosystem functions above 75% of function maxima (mean ecosystem multi-functionality in terms of EAM cannot, by definition, differ among fallow types). Both PAH and EAM were much more variable in grazed than in improved fallows (Table 4.2).

Grazed fallows had substantially higher plant diversity than improved fallows, in terms of both species richness (ANOVA, d.f. = 1,37; $F = 12.2; P < 0.01$) and functional diversity (ANOVA, d.f. = 1,37; $F = 21.3; P < 0.0001$).
In grazed fallows, PAH and EAM exhibited qualitatively similar relationships with plant diversity and environmental variables. Variance in both PAH (Figure 4.3) and EAM (Figure 4.4) was best explained by positive effects of fallow plant diversity (Table 4.3a), with FD and species richness (which were highly correlated; $r = 0.854$) explaining similar proportions of the variance. While PAH declined significantly with grazing intensity, EAM was negatively but insignificantly associated with grazing intensity. Neither PAH nor EAM was significantly associated with SOC.

In linear models combining grazing intensity with plant diversity variables, FD and species richness had marginally significant effects on PAH, and were again significant predictors of EAM, while grazing intensity was not a significant predictor of either multi-functionality indicator. For EAM, the inclusion of grazing intensity reduced the proportion of variance explained, compared to models with FD or species richness as the sole predictor, despite the additional parameter. FD was most evenly distributed (and slightly higher) at moderate grazing intensity, while the sample was small at low grazing intensity ($n = 4$), and FD varied little at high grazing intensity. As such, the moderately grazed group (i.e., ~50% of area showing evidence of grazing) provided the most meaningful test of diversity effects on multi-functionality within a single grazing group. In moderately grazed fallows, the increase in PAH (Figure 4.5; d.f. = 1,4; $R^2 = 0.582; P < 0.05$) and EAM (Figure 4.6; d.f. = 1,4; $R^2 = 0.688; P < 0.05$) with FD of fallow plants was again significant. Neither grazing intensity nor SOC correlated significantly with FD (respectively, d.f. = 1,16; $r = -0.403, 0.324; P > 0.05$) or species richness (respectively, d.f. = 1,16; $r = -0.418, 0.374; P > 0.05$). In models combining SOC with plant diversity variables, FD and species richness remained significant predictors of PAH and EAM, and SOC remained
insignificant.

**Ecosystem multi-functionality in improved fallows**

Improved fallows supported between two and three functions above 50% of function maxima, and between three and four functions above 25% of function maxima (Figure 4.2); percentage excess above mean function values did not diverge more than 25% above or below 0.

In improved fallows, ecosystem multi-functionality exhibited considerably different relationships with plant diversity and environmental conditions, depending on whether PAH or EAM was considered. PAH was not associated with fallow plant diversity, nor with SOC (Table 4.3b, Figure 4.3). In contrast, EAM increased significantly with FD, species richness, and SOC (Table 4.3b, Figure 4.4), with SOC explaining the greatest proportion of the variance in EAM. In models of EAM combining SOC with diversity variables, SOC was again the best predictor of EAM. In these models, FD and species richness were marginally significant, while SOC remained significant (Table 4.3b).

**Pair-wise jointness among fallow ecosystem functions**

Patterns of ecosystem multi-functionality in grazed and improved fallow systems can be broken down into their components by assessing the degree of jointness among fallow ecosystem functions. Here, a pair of functions exhibit jointness when the observed values of both functions are above 50% of maximum (for PAH), or above the mean (for EAM). Observed pair-wise jointness is considered to reflect the ability of a fallow to support a given pair of ecosystem functions simultaneously at or above moderate levels of each function.
Jointness is moreover indicative of co-variance among ecosystem functions and the statistical attributes of individual ecosystem functions, both of which can influence the multi-functionality of fallows in terms of PAH and EAM. For instance, consider two hypothetical ecosystem functions that are both random, normal variables that are uncorrelated with one another. A quarter of replicates in the sample would be expected to support both functions jointly above 50% of their respective maxima, and similarly above mean values. In a scatterplot of two such functions, the top-right quadrant of the figure delimits the replicates achieving jointness for the pair of functions. A strong correlation between the two functions would necessarily increase or reduce jointness: a positive correlation would increase jointness and cluster replicates in the top-right and bottom-left quadrants, while a negative correlation would reduce jointness by clustering replicates at top-left and bottom-right. In reality, since ecosystem functions can have skewed distributions and can be correlated, 25% of the sample is merely a general guideline, not a formal null expectation. The shape of the probability distributions of ecosystem functions are another potential determinant of jointness. If two functions are distributed asymmetrically, and high values of two functions co-occur, the effect is to increase the incidence of jointness; co-occurrence of low values of two asymmetrically distributed functions would reduce jointness. Thus, jointness may vary due to linear correlations among ecosystem functions suggestive of linear trade-offs (negative correlations) or complementarities (positive correlations) among functions, and may also vary in accordance with the distributional characteristics of individual ecosystem functions.

The incidence of jointness with respect to 50% of maxima differed substantially from jointness with respect to mean values. In particular, jointness at 50% of maxima was more prevalent in improved than in grazed fallows, for nearly all pairs of ecosystem functions (Figure
Jointness at mean values generally did not exhibit any such striking contrast among fallow types.

In improved fallows, the negative correlation between wood and forage biomass (Figure 4.1) is reflected in the low incidence of jointness for wood and forage biomass (Figure 4.7). Similarly low jointness with respect to mean values for wood biomass and soil base cations in improved fallows is attributable to a marginally significant negative correlation. Otherwise, there was no evidence that linear correlations among functions influenced jointness, or by extension multi-functionality, in either fallow type.

There was a tendency for the probability distributions of ecosystem functions to be skewed in favor of lower values in grazed fallows (Figure 4.8), while the reverse applied in improved fallows, with distributions of most functions skewed toward higher values (Figure 4.9). In light of the generally weak or non-existent linear correlations among functions in both fallow types, variation in pair-wise jointness was often attributable to the distributional characteristics of individual ecosystem functions. Patterns of jointness among soil base cations and steady infiltration rates are described below to illustrate distributional influences on jointness.

In grazed fallows, soil base cations and steady infiltration rates jointly exceeded 50% of maxima in 2 fallows, and exceeded mean values in 4 fallows, out of a total of 18 grazed fallows (Figure 4.1). The distributions of base cations and infiltration rates were skewed strongly leftward (Figure 4.8), and the incidence of their jointness was much lower than in improved fallows (Figure 4.9). Grazing intensity did not correlate with SOC (d.f. = 1,16; $r = 0.143; P > 0.1$), soil base cations (d.f. = 1,16; $r = 0.037; P > 0.1$), or infiltration rates (d.f. = 1,16; $r = -0.169; P > 0.1$) in grazed fallows, although steady infiltration rates were lower in grazed than in improved fallows (ANOVA, d.f. = 37; $F = 5.15; P < 0.05$). SOC was significantly correlated with base cations (d.f.
= 1,16; \( r = 0.751; P < 0.001 \)) in grazed fallows, but infiltration was not (d.f. = 1,16; \( r = 0.301; P > 0.1 \)).

In improved fallows, despite the absence of a positive linear correlation, approximately half the sample exhibited jointness among soil base cations and infiltration rates (Figure 4.7), much higher than for any other pair of functions. In improved fallows, the probability distributions of base cations and infiltration rates especially were skewed to the right (Figure 4.9). Although both of these soil properties are influenced by SOC, linear correlations of soil base cations and infiltration rates with SOC could not account for the observed incidence of jointness among base cations and infiltration rates in improved fallows. That is, although infiltration was correlated with SOC in improved fallows (d.f. = 1,19; \( r = 0.446; P = 0.043 \)), soil base cations were not (d.f. = 1,19; \( r = 0.240; P > 0.1 \)).

As the example of soil base cations and infiltration rates demonstrates, the incidence of jointness for pairs of ecosystem functions in improved and grazed fallows was often attributable to the direction and degree of skewness in the distributions of ecosystem functions.

*Correlations among plant diversity and individual ecosystem functions*

Correlations among measures of plant diversity and individual ecosystem functions are presented to further illustrate the basis for the observed biodiversity effects on multiple ecosystem functions. Note that these correlations would be inappropriate for testing influences of plant diversity on individual functions—for wood and forage biomass especially, with the possible exception of soil properties. Were this goal of interest, species richness and FD should include only those species with direct influence on specific ecosystem functions, and a different approach to calculating FD might be warranted.
Few univariate correlations among FD and individual ecosystem functions were significant. In improved fallows, wood biomass correlated negatively with FD, while forage biomass correlated positively with FD (Figure 4.10). In grazed fallows, wood biomass was rather positively correlated with FD, and forage biomass exhibited a positive marginally significant association. Correlations among species richness and individual ecosystem functions were qualitatively similar to those for FD; the sole exceptions were that in grazed fallows, both forage biomass and soil base cations were positively and significantly correlated with species richness (Figure 4.11).

More saliently, the correlations of wood and forage biomass with FD (Figure 4.10) and species richness (Figure 4.11) suggest that in the two fallow types, different subsets of the plant community are more closely association with the prevailing variation in taxonomic and functional plant diversity. In grazed fallows, most species are herbaceous, yet plant diversity was positively correlated with wood biomass as well as forage biomass, suggesting that fallow plant diversity varies with the representation of both forage species and woody species in the community. In improved fallows, negative correlations of plant diversity with wood biomass and positive correlations with forage biomass suggest that variation in plant diversity varies largely in accordance with the representation of forage species. These correlations in improved fallows likely result from the high dominance of one or few species of planted woody legumes; the majority of species were minor components of community biomass in many improved fallows, especially in older fallows with high woody biomass.
Correlations among plant traits and individual ecosystem functions: Grazed fallows

In grazed fallows, wood biomass increased with abundance-weighted mean green tissue lignin content of trees and shrubs (d.f. = 1,16; $r = 0.562; P < 0.05$), and was not significantly associated with N or polyphenol contents of tree and shrub green tissues. Forage biomass in grazed fallows increased with green tissue N content of forage species (d.f. = 1,16; $r = 0.584; P < 0.05$), and was not significantly associated with lignin or polyphenol contents of forage species. SOC and infiltration rates in grazed fallows increased with green tissue content of recalcitrant C compounds (i.e., lignins+polyphenols; see Chapter 2). Though SOC was highly correlated with soil base cations (d.f. = 1,16; $r = 0.751; P < 0.001$), in grazed fallows soil base cations and mean tissue content of lignins+polyphenols were positively but insignificantly associated (d.f. = 1,16; $r = 0.295; P > 0.1$).

Discussion

In both grazed and improved fallow types, plant diversity displayed significant positive effects on fallow ecosystem service multi-functionality. The clarity of evidence for plant diversity effects on multiple ecosystem functions was dependent on fallow type. There was clearer evidence in grazed fallows to support plant diversity influences on the capacity of falls to sustain a greater proportion of ecosystem functions above 50% of function maxima (PAH) and greater excess above mean function values (EAM), as environmental conditions could not provide a superior explanation. While significant effects of diversity on PAH were observed in improved fallows, environmental favorability appeared more influential.
Improved fallows consistently demonstrated a greater ability than grazed fallows to sustain multiple ecosystem functions above thresholds of 25 and 50% of function maxima. The general inability of both improved and grazed fallows to sustain more than two of the four ecosystem functions above the 75% threshold indicates an upper limit to multi-functionality, for the four functions examined here, in terms of providing multiple functions at high levels. Such a constraint could arise from (apparently non-linear) trade-offs among functions or among the species influencing each ecosystem function.

In grazed fallows, both PAH and EAM increased with plant diversity quantified as FD and species richness. The decline in PAH with grazing intensity explained less variance than plant diversity variables, and was not observed for EAM. Positive effects of fallow plant diversity on ecosystem multi-functionality may be stronger than negative effects of grazing, yet it was not unequivocally clear that plant diversity effects on multi-functionality were entirely independent of variation in grazing intensity. It remains possible that more intense grazing, perhaps in conjunction with variation in soil conditions, could have influenced plant diversity or altered diversity effects. Significant diversity effects within the group of fallows with moderate grazing indicated that in these fallows diversity effects on both PAH and EAM were independent of grazing.

In improved fallows, there was mixed and somewhat conflicting evidence for effects of plant diversity and environmental conditions on ecosystem multi-functionality. Improved fallows were typically capable of sustaining at least half of the four ecosystem functions at moderate levels, irrespective of either plant diversity or SOC. In contrast, EAM increased with both plant diversity variables and SOC, with SOC out-performing diversity variables as a predictor of EAM. Positive effects of SOC on EAM indicate that multi-functionality may be more easily
attained when environmental conditions are favorable for the production of biomass, the
development of soil structure and improvement of infiltration, and the deposition of base cations
in litter and retention in soils. Thus, environmental favorability may have been more influential
on multi-functionality than plant diversity in improved fallows, and the potential of diversity to
benefit multiple ecosystem functions remained somewhat uncertain. SOC was positively, but
weakly, associated with FD and species richness (d.f. = 1,19; $r = 0.202$ and 0.207, respectively; $P$
> 0.1 for both). Despite the weakness of these associations, an increase in plant diversity under
more productive environmental conditions could have influenced the observed effects of plant
diversity on EAM in improved fallows.

Pair-wise jointness among fallow ecosystem functions

Frequencies of pair-wise jointness among ecosystem functions were calculated to assist the
interpretation of results on influences of plant diversity and environmental variables on fallow
ecosystem multi-functionality. The use of the term jointness draws its inspiration from discussions
on the policy and management of multi-functional agricultural landscapes (Selman 2009, Turpin
et al. 2010) capable of providing benefits beyond agricultural production, especially conservation
of biodiversity and maintenance of supporting and regulating ecosystem services such as soil
formation and water quality. The original microeconomics usage (Baumol et al. 1981) refers to
the ability of a firm to attain ‘economies of scope,’ the reduction in average cost per unit for a
firm engaged in joint production of two or more products (*economies of scale* is more apt for a
single product). Here, a pair of ecosystem functions exhibit jointness when the observed values
for both functions are above 50% of the maximum (for PAH) or the mean (for EAM) of each
function, indicating that the fallow was capable of supporting both ecosystem functions at or above moderate levels of each simultaneously.

For most pairs of ecosystem functions, the greater incidence of pair-wise jointness at 50% of maximum among ecosystem functions in improved fallows could not be attributed to linear trade-offs among functions. The infrequency of jointness for wood and forage biomass in improved fallows reflects a trade-off attributable to large woody plants suppressing forage species growing beneath through competition for light and soil resources. In grazed fallows, large woody plants did not appear to compete with forage species, failing to generate a wood-forage trade-off. Otherwise, there were no significant linear trade-offs or complementarities among functions, yet jointness at 50% of maximum was much more prevalent in improved than in grazed fallows. Although plant diversity can reduce the severity of trade-offs among ecosystem functions (Zavaleta et al. 2010), linear trade-offs among functions could generally not account for the degree of pair-wise jointness among ecosystem functions.

In grazed fallows, skewness in the probability distributions of individual ecosystem functions toward lower values reduced the frequency of pair-wise jointness among pairs of functions at 50% of function maxima. In improved fallows, the opposite effect was observed, as skewness in the distributions of most functions toward higher values increased the frequency of jointness among functions. Thus, jointness at 50% of maximum appeared to be strongly influenced by the distributional characteristics of individual ecosystem functions. The lack of consistent differences in the incidence of jointness with respect to mean values among fallow types indicated that jointness above mean values was more robust to skewed distributions than was jointness at 50% of maximum.
Pair-wise jointness among ecosystem functions is a component of ecosystem multi-functionality quantified as PAH and EAM. However, the limited sample size contributed to the difficulty of attributing the incidence of jointness to biological mechanism. Returning to the earlier example of jointness among soil base cations and steady infiltration rates, high jointness among base cations and infiltration indicated that improved fallows were typically capable of sustaining these two elements of soil quality at moderate levels, since roughly half of the sample achieved jointness. As base cations did not correlate with SOC, there was no clear basis for attributing jointness among base cations and infiltration to linear influences of SOC in improved fallows. In grazed fallows, grazing may have influenced jointness among base cations and infiltration, for example through soil compaction due to trampling by livestock, likely the primary cause of reduced infiltration in grazed as compared to improved fallows. Since grazing intensity did not affect SOC, positive influences of SOC on infiltration may have been weaker or less detectable under grazing exposure. SOC did appear to increase soil base cations, as they were highly correlated, but intensity of grazing did not appear to affect base cations. Although there was no clear, linear explanation, effects of livestock trampling on infiltration may have reduced the incidence of co-occurrence among higher values of base cations and infiltration rates.

Ecosystem multi-functionality in grazed fallows

The results for grazed fallows are consistent with mechanisms proposed herein by which plant diversity may enhance the capacity of fallow plant communities to sustain multiple ecosystem functions simultaneously. Specifically, there was some evidence to indicate that plant diversity enhanced ecosystem multi-functionality through complementary effects of species with different functional traits on different functions, and through effects of multi-functional species
on more than one function at the same time. Disturbance from livestock grazing may have altered interactions among plant species, possibly enhancing diversity effects on multifunctionality. Complementarity and sampling effects, mechanisms by which biodiversity is known to influence individual ecosystem functions, may have also contributed to diversity effects through positive effects on specific ecosystem functions.

**Complementarity among functions.** Plant diversity appears to have increased the ability of grazed fallows to support multiple ecosystem functions, likely through greater variation in functional traits enhancing complementary benefits of plant species to different functions. Divergent effects of species on different ecosystem functions should enhance the cumulative degree of complementarity among species in a community, and should improve overall ecosystem functioning.

In grazed fallows, wood biomass clearly originates from trees and shrubs, while forage biomass is produced primarily by herbaceous species. Different functional traits were associated with and may have benefitted these components of total fallow biomass. Wood biomass increased with green tissue content of lignins, and since woody biomass declined with grazing intensity, the correlation between wood biomass and lignin content suggests that woody species less palatable to livestock may be more successful in the presence of grazing. In contrast, forage biomass increased with tissue N, suggesting that more palatable species predominate under less intense grazing pressure. Thus, not only are wood and forage produced by different subsets of the fallow plant community, they appeared to benefit from divergent functional traits, providing evidence of complementary effects of different plant species on wood and forage biomass. Therefore, co-occurrence of higher levels of both wood and forage should be found in fallows that include different species with higher tissue content of both lignins and N. As calculated here, greater FD
would meet this condition, as higher values of lignins were uncommon in general and the tissues of herbaceous species have particularly content of lignins.

While wood biomass increased with lignin content, green tissue content of polyphenols was negatively but insignificantly associated with wood biomass. Since infiltration rates and SOC (which correlated with soil base cations) responded positively to fallow vegetation with higher tissue content of lignins+polyphenols (see Chapter 2), the joint occurrence of higher levels of wood biomass with infiltration rates and soil base cations should be more likely where fallows include species with high values of both lignins and polyphenols. Again, such a combination of traits among species in the fallow plant community should coincide with higher FD. Yet regardless of plant diversity, negative effects of grazing on large woody plants as well as infiltration rates apparently reduced both wood biomass and infiltration capacity, which should decrease the degree to which higher values for these functions co-occur.

Multi-functional species. The representation of multi-functional species capable of effectively supporting more than one ecosystem function simultaneously may have further enhanced multi-functionality in grazed fallows. The increase in wood biomass with tissue lignin content paralleled the positive influence of lignin on infiltration rates and SOC, which was in turn strongly linked with soil base cations. In addition, some woody plants in the study area are known to have deep rooting systems, up to 2.5 m in depth (Mekonnen et al. 1997). These species may have prevented leaching of subsoil nutrients deeper into the soil profile (Ståhl et al. 2002), including base cations among others. Deep-rooted plants may furthermore replenish soil base cations and other nutrients through retrieval from subsoils and re-deposition in litter. Similarities in the functional traits that appear to influence wood production as well as elements of soil quality suggests that the species most greatly benefitting these ecosystem functions may overlap.
Since both woody biomass and multi-functionality (PAH) declined with grazing intensity, the loss of potentially multi-functional woody species could have contributed to negative effects of grazing on ecosystem multi-functionality. The representation of multi-functional species in biotic communities may increase probabilistically with species richness, effectively generating a sampling effect on multiple ecosystem functions. The positive correlation between FD and wood biomass indicates that plant diversity in grazed fallows increased with the representation of large woody plants in the plant community, many of which can be considered multi-functional. It is difficult to predict how multi-functional species influence FD, and their effects would likely vary with the species, traits, and functions considered. To the extent that multi-functional species possess unique combinations of functional traits, their representation in the community would increase FD disproportionately.

*Disturbance.* The presence of grazing livestock may have significantly increased the potential for plant diversity to influence ecosystem multi-functionality in grazed fallows. Greater frequency and intensity of disturbance may have increased the apparent influences of biodiversity on multiple ecosystem functions, an effect reported previously for individual ecosystem functions (Cardinale and Palmer 2002, Jouseau 2008).

In the presence of disturbance, it is not only the functional effect traits of organisms that influence ecosystem functioning. Species that cannot persist will cease to affect ecosystem processes. Thus the diversity of response traits—traits mediating responses to environmental change—can ultimately influence ecosystem functioning by determining plant species composition (Suding et al. 2008). Response traits such as resprouting ability, small stature, and inedibility that provide tolerance to grazing and other forms of disturbance tend to exhibit trade-offs at the species level with traits associated with avoidance of disturbance, including traits
bestowing high fecundity and rapid rates of growth and re-colonization. As calculated here, FD includes functional response traits since green tissue contents of N, lignins, and polyphenols affect palatability to livestock and are associated with instantaneous growth rates. Inclusion of RSR, lignins+polyphenols, growth form, and woodiness had negligible effects on FD; data for other response traits was sparse, and a more complete accounting might have been useful.

Under grazing, higher plant diversity and greater variation in the functional response traits of plant species may have enhanced the ability of fallow plant communities to maintain functioning when subjected to consistent and at times severe disturbance from grazing livestock. That is, greater representation in the plant community of species with divergent strategies for responses to disturbance may have increased the resistance and resilience of fallow ecosystem functioning to disturbance. Consequently, in grazed fallows the diversity of response traits may have indirectly contributed to apparent effects of plant diversity on ecosystem multi-functionality by acting in conjunction with the diversity of traits that directly determine plant species effects on ecosystem functioning.

The strength of positive and negative species interactions are important determinants of biodiversity effects on ecosystem processes (Hooper et al. 2005). Severe competition implies substantial niche overlap among plant species, meaning they are probably functionally redundant, and that complementary effects on ecosystem functioning are improbable. The negative relationships of grazing intensity with wood (d.f. = 1,16; \(r = -0.473; P < 0.05\)) and forage (d.f. = 1,16; \(r = -0.486; P < 0.05\)) biomass indicated that more intense grazing reduced the biomass of large woody plants as well as the biomass of forage species, resulting in the positive (marginally significant) association between wood and forage biomass (Figure 4.1). Grazing and browsing may have reduced woody plant recruitment or simply thinned the canopy, preventing or
ameliorating competitive suppression of forage species by trees and large shrubs, as was observed in improved fallows. The apparent absence of strong competition between large woody plants and the forage species growing beneath, and perhaps among plant species in general, may have been an important effect of grazing on the diversity-multi-functionality relationship.

Positive species interactions may have also contributed to plant diversity effects on ecosystem multi-functionality in grazed fallows. In the presence of grazing, less palatable species often facilitate those more palatable to grazers (Graff et al. 2007) by reducing the ability of grazers to detect and consume palatable species. By and large, grazing may have increased the prevalence of net positive interactions among species. However, intense grazing weakens facilitative interactions mediated by differences in palatability (Smit et al. 2007), an effect that could have contributed to low ecosystem multi-functionality in the most heavily grazed fallows. Abiotic stress can also shift plant species interactions away from competition and toward facilitation (Callaway et al. 2002, Brooker et al. 2008). Poor site conditions are also thought to commonly strengthen plant diversity relationships with productivity and other ecosystem processes (Hooper et al. 2005). Grazing intensity was the only environmental or management factor significantly related to multi-functionality (PAH) in grazed fallows. Among other differences, grazed fallows had on average sandier soils than improved fallows, and lower infiltration rates in grazed fallows may have restricted root access to soil water and nutrients. Thus, in some grazed fallows plants may have faced stress from unproductive soil conditions in addition to direct stress from consumption by grazers. By reducing competition and increasing the prevalence of positive interactions, grazing and poorer soils may have enhanced the response of ecosystem multi-functionality to plant diversity in grazed fallows.
Ecosystem multi-functionality in improved fallows

In improved fallows, the fact that SOC was the best predictor of ecosystem multi-functionality in terms of EAM indicates that multi-functionality may have been more sensitive to the favorability of prevailing environmental conditions. Higher SOC is indicative of favorable conditions for the vegetative growth and biomass production, as well as improvement in the structure and fertility of soils. However, multi-functionality in terms of PAH was unaffected by plant diversity or environmental variables. Nonetheless, it is probably not hasty to conclude that environmental favorability enhanced multi-functionality, since EAM appeared to be a more robust indicator. Jointness with respect to mean values was less influenced by the probability distributions of individual ecosystem functions than was jointness with respect to half-maximum, suggesting that EAM was more robust than PAH as an indicator of multi-functionality.

In addition to the evidence for environmental favorability being more influential on multi-functionality than plant diversity, there are several possible explanations for the weaker and inconsistent effects of plant diversity in improved fallows. Improved fallows are known to be highly productive (Mekonnen et al. 1997, Ståhl et al. 2002), one of the primary rationales for their establishment. Here, although productivity could not be quantified directly, differences in productivity among the two fallow types are probable. Greater productivity in improved fallows would result in greater production of woody plant biomass, and greater inputs to soils should enhance soil and root function, increasing the deposition and retention of base cations, the development of soil structure, and soil infiltration capacity. Furthermore, the apparent competitive suppression of forage species in the understory was attributable to greater biomass of highly dominant large woody plants and the absence of significant disturbance. High biomass
density and high dominance may have intensified competition and reduced facilitation, thus limiting the potential for plant species to exert complementary effects on ecosystem functions.

However, the species composition of improved fallows was not conducive to the detection of plant diversity effects on ecosystem functioning. The dominance of woody legumes planted in improved fallows, and the commonness of fallows dominated by *Tephrosia candida*, substantially reduced variation in plant diversity, functional traits, and the abundance of multi-functional species compared to in grazed fallows. Improved fallows varied little in community mean tissue contents of N, lignins, and polyphenols; limited variation in other functional traits is virtually guaranteed as well, such as biological nitrogen fixation capacity and root-to-shoot ratios. Plant diversity, in terms of species richness but especially in terms of functional diversity, was lower and less variable. Significantly, the woody legumes used for improved fallows can all be considered somewhat multi-functional, suggesting that the abundance of multi-functional species did not vary greatly in improved fallows, which would somewhat obscure the effects of these species on ecosystem multi-functionality.

It is not known whether judicious augmentation of species would further improve the ability of improved fallows to sustain more ecosystem functions at higher levels. Ndufa et al. (2009) conducted an experiment with improved fallows in monoculture and two-species combinations of larger and smaller-statured species. While monocultures and mixtures produced similar amounts of biomass, mixed fallows out-performed monocultures on average in terms of N recycled to soils and post-fallow maize yields, though the best performance was by a monoculture. Thus, the potential for niche complementarities among species to enhance multiple ecosystem services may exist in improved fallows, however this potential may be limited and dependent on species composition.
The observed relationships among plant diversity, environmental conditions, and ecosystem service multi-functionality differed substantially among grazed and improved fallows. In grazed fallows, significant effects of plant diversity on the proportion of ecosystem functions above half-maximum and the percentage excess above mean function values provided evidence consistent with plant diversity enhancing the capacity of fallows to provide multiple ecosystem services. Plant diversity effects on multi-functionality were stronger and more reliable than grazing intensity effects. In improved fallows, SOC appeared more influential than diversity, and the evidence for diversity effects on multi-functionality was scant. The ecological factors and mechanisms influencing ecosystem multi-functionality thus appeared to differ appreciably among fallow types, with plant diversity more significant in grazed fallows and environmental favorability more important in improved fallows.

Management differences between grazed and improved fallows resulted in contrasting ecological conditions that may largely explain the divergence in ecological controls over ecosystem multi-functionality. Improved fallows experienced little disturbance, as they are ungrazed, though they may have received minor periodic coppicing. In contrast, consistent disturbance from grazing livestock, including consumption of aboveground plant organs and soil compaction due to trampling, appeared to negatively affect ecosystem functioning; coppicing may have affected grazed fallows as well. The other major management difference was that improved fallows are intentionally planted with leguminous trees and large-statured shrubs, while grazed fallows are typically not planted and their species composition reflects largely unguided regeneration. These differences in fallow management appear significantly responsible for
generating the prevailing differences in biotic and abiotic ecological conditions among fallow types.

Greater frequency and intensity of disturbance may have indirectly enhanced plant diversity influences on ecosystem multi-functionality by increasing the importance of traits mediating disturbance responses and by altering the sign and strength of plant species interactions. At higher plant diversity, greater variation in the functional response traits of plant species may have enhanced the resistance and resilience of ecosystem functioning in the presence of disturbance. Thus, observed effects of diversity on multi-functionality may be attributable in part to diversity in traits determining the functional effects of plant species on the focal ecosystem functions, and partly to diversity in strategies for disturbance response. Trees and large shrubs did not seem to compete with forage species in grazed fallows, and grazing and perhaps also edaphic stress in grazed fallows may have reduced the severity of competition and increased the prevalence of facilitative interactions among species in the plant community.

Differences in the apparent intensity of competition are related to a third distinction among fallow types, the high biomass density of improved fallows. By design, improved fallows are planted with woody leguminous species, and these species exhibited high dominance. The planting of productive leguminous species, and perhaps the absence of grazing in addition, should entail substantially higher productivity in improved fallows. In improved fallows, higher productivity would accelerate production of wood and forage biomass, as well as soil processes linked with soil base cation retention, and the aggregation of soil particles and improvement of infiltration. Greater productivity may have significantly contributed to the apparently greater capacity of improved fallows to sustain multiple ecosystem functions above 50% of maximum. Further, high biomass and dominance of large woody plants apparently generated intense
competitive suppression of forage species by trees and large shrubs, which may have also competed with other large woody plants. Under such conditions facilitative interactions are likely to be weak. By accelerating ecosystem processes related to the focal ecosystem functions, and by inducing negative plant species interactions, greater productivity in improved fallows probably reduced the likelihood of plant diversity influencing multi-functionality.

Finally, the dominance of one to a few species of woody legumes in improved fallows resulted in striking differences in species composition among the two fallow types. In simplified managed systems and natural communities with high dominance or a narrowly constrained species pool, limited variation in species richness, functional diversity, and evenness are challenges to detecting influences of biodiversity on ecosystem functioning. In accordance with the dominance of woody legumes, improved fallows displayed much lower variation among replicates in species richness and functional diversity, functional traits, and the abundance of potentially multi-functional species. Each of these compositional characteristics of improved fallows may have constrained variation in ecosystem multi-functionality, and contributed to the weaker and inconsistent effects of plant diversity on multi-functionality. In contrast, in grazed fallows, the absence of planted large woody species and the presence of grazing reduced dominance and increased compositional variability among replicates. Consequently, the species composition of grazed fallows may have enhanced the potential of plant diversity to influence multi-functionality, and may have been more amenable to detection of diversity effects.

The results indicate that the management of smallholder fallows significantly affects the relationship between plant diversity and ecosystem multi-functionality through several means. The productive, multi-functional species planted in improved fallows were highly dominant, leading to apparent competition and little variation in plant diversity, functional traits, and the
abundance of multi-functional species, the likely combined effects of which are to reduce the potential for diversity effects on ecosystem service multi-functionality, and to obscure detection of any diversity effects that might exist. In grazed fallows, significant positive effects of plant diversity on multi-functionality may have been enhanced by the absence of tree and shrub planting and the presence of grazing, which may have increased the role of response trait diversity in affecting ecosystem functioning, reduced dominance and apparent competition (and possibly enhanced facilitation), and increased variation in plant diversity, functional traits, and the abundance of multi-functional species. The results from grazed fallows are furthermore consistent with plant species complementarities among functions and effects of multi-functional species being among the mechanisms underlying positive influences of plant diversity on ecosystem service multi-functionality in smallholder fallows.

To improve understanding of the relationship between biodiversity and ecosystem service multi-functionality, research investigating sources of variation in the relationship is a logical extension of the findings presented here. Disturbance and perturbations, environmental conditions, dominance, and species interactions—all recognized as potentially significant in previous BEF research—are promising avenues toward more complete elucidation of the significance of plant diversity in sustaining the ability of agroecosystems to provide multiple ecosystem services, and the roles of biodiversity in maintaining the overall functioning of ecosystems managed and natural alike.
**Tables and Figures**

*Table 4.1.* Focal ecosystem services and summary statistics for ecosystem functions serving as ecosystem service indicators in smallholder fallows. Linearizing transformations were applied prior to calculating ecosystem service multi-functionality indicators. *Maximum is the mean of the 3 highest values for each ecosystem function in the grazed and improved fallow types.

<table>
<thead>
<tr>
<th>Ecosystem service (ES)</th>
<th>Ecosystem function (ES indicator)</th>
<th>Units</th>
<th>Transformation</th>
<th>Fallow type</th>
<th>n</th>
<th>Mean</th>
<th>SD</th>
<th>SEM</th>
<th>Max.*</th>
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<td>Wood biomass</td>
<td>t ha(^{-1})</td>
<td>log</td>
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<td></td>
<td>Improved</td>
<td>21</td>
<td>1.69</td>
<td>1.07</td>
<td>0.23</td>
</tr>
<tr>
<td></td>
<td>Soil formation</td>
<td>Soil base cations</td>
<td>meq 100g(^{-1})</td>
<td>arcsine square root</td>
<td>Grazed</td>
<td>18</td>
<td>4.77</td>
<td>2.18</td>
<td>0.51</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Improved</td>
<td>21</td>
<td>3.69</td>
<td>1.15</td>
<td>0.25</td>
</tr>
<tr>
<td></td>
<td>Steady infiltration rate</td>
<td>Steady infiltration rate</td>
<td>mm hr(^{-1})</td>
<td>square root</td>
<td>Grazed</td>
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<td>261.8</td>
<td>198.1</td>
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</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Improved</td>
<td>21</td>
<td>371.0</td>
<td>148.1</td>
<td>32.3</td>
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Table 4.2. Summary statistics for indicators of fallow ecosystem service multi-functionality, and for plant diversity and environmental variables serving as linear predictors of multi-functionality.

Proportion of functions above half-maximum (PAH) is the proportion of the four ecosystem functions (Table 1) above 50% of maximum function values. Excess above mean (EAM) is the mean percentage by which ecosystem functions exceeded mean function values.

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Abbrev.</th>
<th>Units</th>
<th>Transformation</th>
<th>Fallow type</th>
<th>n</th>
<th>Mean</th>
<th>SD</th>
<th>SEM</th>
</tr>
</thead>
<tbody>
<tr>
<td>Proportion of functions Above Half-maximum</td>
<td>PAH</td>
<td>%</td>
<td>arcsine square root</td>
<td>Grazed</td>
<td>18</td>
<td>31.94</td>
<td>25.45</td>
<td>6.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Improved</td>
<td>21</td>
<td>55.95</td>
<td>17.51</td>
<td>3.82</td>
</tr>
<tr>
<td>Excess Above Mean function values</td>
<td>EAM</td>
<td>Mean %</td>
<td>NA</td>
<td>Grazed</td>
<td>18</td>
<td>0.00</td>
<td>32.99</td>
<td>7.78</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Improved</td>
<td>21</td>
<td>0.00</td>
<td>8.58</td>
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<table>
<thead>
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<th>Abbrev.</th>
<th>Units</th>
<th>Transformation</th>
<th>Fallow type</th>
<th>n</th>
<th>Mean</th>
<th>SD</th>
<th>SEM</th>
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<tr>
<td>Functional diversity</td>
<td>FD</td>
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<td>18</td>
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<td>1.16</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Improved</td>
<td>21</td>
<td>1.70</td>
<td>1.10</td>
<td>0.20</td>
</tr>
<tr>
<td>Species richness</td>
<td>Counts</td>
<td>NA</td>
<td>NA</td>
<td>Grazed</td>
<td>18</td>
<td>11.78</td>
<td>3.86</td>
<td>0.91</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Improved</td>
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<td>6.62</td>
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</tr>
<tr>
<td>Soil organic carbon</td>
<td>SOC</td>
<td>%</td>
<td>arcsine square root</td>
<td>Grazed</td>
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<td>0.34</td>
<td>0.08</td>
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<td></td>
<td></td>
<td></td>
<td></td>
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<td>0.31</td>
<td>0.07</td>
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<tr>
<td>Grazing intensity</td>
<td>% area</td>
<td>(approx.)</td>
<td>arcsine square root</td>
<td>Grazed</td>
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<td>22.51</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>Improved</td>
<td>—</td>
<td>—</td>
<td>—</td>
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</tbody>
</table>
Table 4.3a. **Grazed fallows:** Results from linear models predicting ecosystem service multifunctionality using plant diversity and environmental variables. $R^2 = \text{total model } R^2$, adjusted for number of parameters; d.f. = model, error degrees of freedom; abbreviations as in Table 2.

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Model specification</th>
<th>Predictor variable</th>
<th>d.f.</th>
<th>Intercept</th>
<th>Slope</th>
<th>t</th>
<th>P</th>
<th>$R^2$</th>
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<tbody>
<tr>
<td>PAH</td>
<td>FD</td>
<td>FD</td>
<td>1, 16</td>
<td>-0.10</td>
<td>0.04</td>
<td>2.62</td>
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<td>-0.11</td>
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<td></td>
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<td>1, 16</td>
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<td>0.467</td>
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<td>Grazing intensity</td>
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<td>Grazing intensity</td>
<td>1, 16</td>
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<td>FD + SOC</td>
<td>FD</td>
<td>FD</td>
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<td>2.39</td>
<td>0.030</td>
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<td>Species richness</td>
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<td></td>
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<td>SOC</td>
<td>1, 16</td>
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<td>FD + Grazing intensity</td>
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<td>FD</td>
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<td>1.91</td>
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<td>Grazing intensity</td>
<td>1, 16</td>
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<td>-0.13</td>
<td>-1.35</td>
<td>0.196</td>
<td>0.196</td>
</tr>
<tr>
<td>Species richness + Grazing intensity</td>
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<td>Species richness</td>
<td>2, 15</td>
<td>0.43</td>
<td>0.04</td>
<td>1.97</td>
<td>0.068</td>
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<td>Grazing intensity</td>
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<td>-0.13</td>
<td>-1.30</td>
<td>0.214</td>
<td>0.214</td>
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<td>FD</td>
<td>FD</td>
<td>1, 16</td>
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<td>3.03</td>
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<td>FD</td>
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<td>2.26</td>
<td>0.039</td>
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<tr>
<td>Specifications: EAM = Special richness + Grazing intensity</td>
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Table 4.3b. **Improved fallows:** Results from linear models predicting ecosystem service multifunctionality using plant diversity and environmental variables. $R^2 = \text{total model } R^2$, adjusted for number of parameters; d.f. = model, error degrees of freedom; abbreviations as in Table 2.

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Model specification</th>
<th>Predictor variable</th>
<th>d.f.</th>
<th>Intercept</th>
<th>Slope</th>
<th>t</th>
<th>P</th>
<th>$R^2$</th>
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</thead>
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<td>0.003</td>
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<td>0.121</td>
<td>0.076</td>
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<tr>
<td>FD + SOC</td>
<td>FD</td>
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<td>0.001</td>
<td>0.17</td>
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<td></td>
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<td>0.147</td>
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<td>SOC</td>
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<td>FD</td>
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<td>1.88</td>
<td>0.076</td>
<td>0.336</td>
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<td>0.023</td>
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<td></td>
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<tr>
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<td>Species richness</td>
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<td>2.01</td>
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Figure 4.1. Correlations among ecosystem functions. Plotted lines indicate (back-transformed) 50% of maximum (heavy lines) and mean values (light lines) of functions in grazed (solid lines) and improved fallows (broken lines). Plotted values $r$ indicate Pearson’s correlation coefficient for grazed (bold text) and improved fallows (plain text). * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, **** = $P < 0.0001$, ms = $P < 0.1$, ns = $P > 0.1$. 
Figure 4.2. Fallow type and the proportion of ecosystem functions above 25, 50, and 75% of respective function maxima. Points jittered slightly for greater clarity. Statistics presented from one-way ANOVA with d.f. = 1, 37. * = \( P < 0.05 \), ** = \( P < 0.01 \), *** = \( P < 0.001 \), **** = \( P < 0.0001 \), ns = \( P > 0.1 \).
Figure 4.3. Relationships of plant diversity and environmental variables with the proportion of ecosystem functions above half-maximum (PAH). Points jittered slightly for greater clarity.
Figure 4.4. Relationships of plant diversity and environmental variables with mean percentage excess above mean (EAM) ecosystem function values.
Figure 4.5. Grazed fallows: Relationship of fallow plant functional diversity (FD) with the proportion of functions above half-maximum (PAH) within grazing intensity groups. The plotted curve is for moderately grazed fallows. Grazing intensity groups are as follows: Light ~25%; Moderate ~50%; Heavy ~75% approximate proportional area showing evidence of grazing. Points jittered slightly for greater clarity.
Figure 4.6. Grazed fallows: Relationship of fallow plant functional diversity (FD) with percentage excess above mean (EAM) function values with grazing intensity groups. The plotted curve is for moderately grazed fallows. Grazing intensity groups as in Figure 5.
Figure 4.7. Incidence of jointness for pairs of ecosystem functions above 50% of function maxima (left), and above mean function values (right). Ecosystem function codes: C = soil base cations; I = infiltration rate; F = forage biomass; W = wood biomass.
Figure 4.8. Distributions of (transformed) ecosystem functions in grazed fallows.
Figure 4.9. Distributions of (transformed) ecosystem functions in improved fallows.
Figure 4.10. Correlations between fallow plant functional diversity (FD) and ecosystem functions.

Plotted values $r$ indicate Pearson’s correlation coefficient for grazed (bold text) and improved fallows (plain text). * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, **** = $P < 0.0001$, ms = $P < 0.1$, ns = $P > 0.1$. For grazed fallows, d.f. = 1, 16; for improved fallows, d.f. = 1, 19.
Figure 4.11. Correlations between fallow plant species richness and ecosystem functions. Plotted values $r$ indicate Pearson’s correlation coefficient for grazed (bold text) and improved fallows (plain text). * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, **** = $P < 0.0001$, ms = $P < 0.1$, ns = $P > 0.1$. For grazed fallows, d.f. = 1, 16; for improved fallows, d.f. = 1, 19.
Chapter 5: Vegetation mediation of land use effects on post-fallow maize yield

Abstract

A primary goal of fallows in smallholder farms is to improve the fertility and structure of soils to achieve a higher subsequent crop yield. The effectiveness of fallows for improving soil quality and crop yields is likely to vary with abiotic factors, the composition of fallow vegetation, whether fallows are grazed with livestock, and land use history. Soil quality is significantly affected by attributes of fallow vegetation, especially the quantity and quality of litter inputs. To assess whether the characteristics of fallow vegetation mediate effects of fallow type on post-fallow maize yield, a study was conducted in fallow fields of smallholder farms in Siaya District, western Kenya. In 18 grazed fallows and 21 improved fallows, stem diameter of trees and cover and height of shrub and herb species were measured and used to estimate biomass. Near infrared spectroscopy was used to predict soil properties (SOC and sand content), and steady infiltration rates were estimated from asymptotic regression of ring infiltrometer data. Post-fallow maize yields were hypothesized to decline with grazing due to negative effects on soil structure and infiltration capacity, to increase with standing green biomass due to greater litter input quantity, and to increase with green tissue contents of N and lignins+polyphenols (LPP) due to contrasting effects of vegetation associated with litter input quality (N content is associated with biological N fixation and greater biomass production by legumes, leading to higher soil N; LPP content reduces SOM turnover). Data on maize yields could not be linked with data on fallow conditions,
due to logistical difficulties in coordinating the research. Likely reasons behind these logistical difficulties are discussed.

Introduction

In rural areas throughout Sub-Saharan Africa, the historically predominant approach to replenishing soil fertility was to leave fields in spontaneous fallows of natural vegetation regenerating after cultivation. With rapid population growth in the 20th century, farmers have been forced to leave progressively little land out of cultivation, and consequently soil degradation and declining soil fertility have been widespread throughout the global tropics (Mosier 1998). Research into practical means of maintaining soil productivity and rehabilitating degraded soils has identified strategies of integrating cropping with production of woody and herbaceous perennials, usually N-fixing leguminous species. The effectiveness of fallows planted with woody leguminous species, often referred to as improved fallows, for improving crop yields has been debated vigorously, yet a meta-analysis demonstrated that several approaches involving the addition of leguminous species to fallows increased maize yields (Sileshi et al. 2008). Rural development projects have found that improved fallows and other ways of integrating legumes with crops hold promise for improving crop yields while also producing much-needed wood (Pretty et al. 2006, Sanchez et al. 2007).

In western Kenya, social and economic constraints on agricultural management begin with the high population density in the region and at the household scale frequently include large family sizes, periodic hunger, and limited land, capital, market access, and off-farm income
Households typically allocate fields with more productive soils to nutrient-demanding annual crops, continuously or nearly so. Fast-maturing improved fallows are sometimes planted in these fields to help maintain soil fertility. Less productive areas are typically allocated to less pressing needs: extensive grazing and wood production in natural fallows, woodlots (esp. *Eucalyptus* spp.), and production of thatch (esp. *Andropogon gayanus*). Such fields are cropped infrequently, and these land use types persist for long periods of time, perhaps because rehabilitation could require costly investments of fertilizer, improved fallow seeds, labor, etc. Some fields may be left in grazing partly because livestock, especially cattle, are rarely sold as they confer social status and an economic buffer in leaner times.

The constraints facing farmers induce them to produce goods in every field, including those not being cropped. Thus, fallows are rarely the natural fallows historically common in African agriculture, often termed ‘bush’ or ‘long’ fallows, left to undergo natural succession. Fallows in western Kenya are commonly improved fallows and extensively managed fallows, often referred to as ‘natural’, variably composed of native plants, weeds, and invasive and naturalized exotics. Improved fallows are ungrazed and produce significant quantities of wood, while most extensively managed fallows provide variable quantities of wood and forage for grazing livestock. Differences in fallow land use and management are likely to affect soil quality, in conjunction with associated differences in the frequency and duration of fallow and crop rotations. As a result, in practice the management of fallows on smallholder farms involves potential trade-offs among ecosystem services provided during periods of fallow. In this study, my focus is on the provisioning services of production of wood and forage, and the supporting service of soil formation.
After climatic and edaphic factors, the quantity and quality of litter inputs are among the predominant ecological factors that regulate the functioning of soil subsystems (Wardle 2002, Wardle et al. 2004). Net primary productivity (NPP) largely determines the amounts of organic inputs to soils, while the quality of these raw materials significantly controls rates of transformation by soil organisms and modification by physical and chemical processes (Cadisch and Giller 1997, Bronick and Lal 2005). Soil organisms process organic inputs, breaking them down chemically and physically into simpler forms, and in the process improving the fertility and structure of soils.

Litter quality is a suite of plant traits that determine the susceptibility of organic residues to decomposition. Three important and widely studied elements of litter quality are the C:N ratio, lignin content, and phenolic content (Cadisch and Giller 1997). Litters of different qualities vary in their palatability to herbivores, as well as the capacity to support the activity of soil organisms. High quality litters with low C:N (i.e., high N content) tend to have high content of labile C compounds that support rapid microbial breakdown and decomposition, and mineralization of C and nutrients in litter (Gentile et al. 2009). In contrast, lower quality litters decompose more slowly, such that C and nutrients are mineralized over a longer time period, due to high C:N or a high proportion of recalcitrant C compounds (Vanlauwe et al. 2005) resistant to microbial breakdown (de Boer et al. 2005). Recalcitrant forms of C such as lignins and polyphenols are primarily responsible for the formation of long-lived C pools in soils such as humus (Zech et al. 1997).

Soil organic carbon (SOC) performs several soil functions important for plant growth, and is an important indicator of soil quality in agricultural systems (Arshad and Martin 2002). Cycling of C and N through ecosystems tends to be coupled. In agroecosystems, agricultural
management affects the degree to which soil C and N are maintained, increased (Blair et al. 2006b), or together decline when degradation occurs (Mosier 1998), especially over long time-scales. SOC enhances the bioavailability of soil nutrients and increases nutrient retention in soils by providing cation exchange capacity (Bell et al. 1998) and binding nutrients in soil organic matter (SOM), the recalcitrance of which determines the time-scale of nutrient release (Barrios et al. 1997, Vanlauwe et al. 2005).

Soil infiltration capacity, the ability of water to enter the soil surface, is a similarly useful indicator of soil quality in agricultural systems (Arshad and Martin 2002). Infiltration rates are high when soil porosity is high and bulk density is low, and are expected to be higher for soils of a sandy texture (Siriri et al. 2006). High infiltration rates for a given soil texture are indicative of robustly structured soils that experience less soil erosion due to runoff, have greater water storage capacity (Seobi et al. 2005), and support more vigorous plant growth. Since infiltration is responsive to changes in soil aggregation, bulk density, and porosity, it is sensitive to physical soil disturbance (Salako and Kirchhof 2003, Siriri et al. 2006) and channels created by plant roots (van Noordwijk et al. 1991). By altering soil structure through inducing aggregation of soil particles and reducing soil bulk density (Martens 2000), SOM increases infiltration capacity and water retention (Seobi et al. 2005). Soil hydraulic functions can be performed by both labile (Blair et al. 2006a) and recalcitrant (Martens 2000) SOM fractions, although probably over different time-scales. Labile SOM fractions and their physical effects are more responsive to changes in inputs and soil disturbance, while the effects of recalcitrant forms are probably more lasting (Bronick and Lal 2005), on account of longer residence times.

Research conducted in the study area has found that the amount of green biomass N was the best predictor of subsequent maize yields, with *Sesbania* fallows among the most effective for...
supporting subsequent maize yield (Ndufa et al. 2009), as other studies have also found (Niang et al. 2002). Productive species with high biological N fixation capacity such as *Sesbania* (Ståhl et al. 2002) may be particularly effective for attaining high maize yields. Past land use intensity can play a significant role in the relative benefit maize yield derives from organic input N—in sites with more degraded soils, the maize yield response to higher litter N can exceed that in less degraded sites (Kimetu et al. 2008).

In western Kenya and elsewhere in the humid tropics, land use factors relevant to soil quality include grazing, fallow type (here, improved versus extensively managed fallows), and the frequency and duration of past fallow and crop rotations. In the study area, improved fallows are more productive, with leguminous species that fix N and produce of N-rich litter, thereby increasing soil N. Grazing may influence SOC stocks by reducing litter inputs or altering plant functional traits and litter quality, and may furthermore reduce infiltration rates due to trampling by livestock and soil compaction. As such, improved fallows might be expected to have greater SOC stocks and infiltration rates than grazed fallows. However, influences of land use on soils and maize yields were expected to vary according to how edaphic conditions, especially soil texture, influence agricultural management regimes.

The objective of this study was to assess whether the characteristics of fallow vegetation, by affecting soil conditions, mediate effects of fallow type on maize yield. Maize yield was hypothesized *a priori* to be lower in grazed than in improved fallows, on account of negative effects of grazing on infiltration rates. Maize yield was furthermore hypothesized *a priori* to increase with: A) standing green biomass, due to greater production of biomass leading to higher litter inputs; B) green tissue N content, due to greater fixation of N₂ and biomass production by
Methods

Study systems. The Millennium Villages Project (MVP) is an evidence-based approach to alleviating extreme rural poverty in sites throughout Sub-Saharan Africa, in which agricultural development plays a strategic role (Sanchez et al. 2007). The data for this study were collected in 2008-2009 in the Sauri MVP site in Siaya District, western Kenya.

Sauri MVP has a humid tropical climate with two rainfall peaks and potential cropping seasons yearly, and elevation ranges from 1,300 to 1,470 m. The clayey, well drained Oxisols and Ultisols are soil orders representative of soils common in Sub-Saharan Africa. The landscape in Sauri is a shifting agricultural matrix primarily composed of maize and other annual crops, with lower landscape cover of woodlots, land dedicated to grazing, and fallow fields. Land use in the area cycles between periods of annual crops, and periods of fallow intended to regenerate soil fertility and to provide wood products, green manures from foliage of woody plants, and forage for livestock, among other goods. High population density, high cropping frequency and inadequate fertilization having led to degradation since the early 20th century (Scherr 1995), and soils in the area are relatively depleted of N and C. However, Sauri agroecosystems may currently be undergoing long-term rehabilitation.

Fallow type. ‘Improved’ fallows of fast-growing leguminous trees are promoted by MVP to improve soil fertility and fuelwood. They are usually planted with *Tephrosia candida* DC, and less
commonly with *Crotalaria paulina* Schrank, *Calliandra calothyrsus* Meissn. or other exotics, and are not grazed with livestock. Grazed fallows, often considered ‘natural’ or ‘weed’ fallows, are less common, and contain a variety of species, most of which are native. The most common trees in grazed fallows are the native *Markhamia lutea* (Benth.) K. Schum., *Sesbania sesban* (L.) Merr., and the exotic *Psidium guajava* L. Most grazed fallows combine production of wood and green manures with livestock grazing, although heavily grazed fallows do not produce wood.

**Data collection.** Fallow fields identified for sampling ranged from 0.02 to 0.25 ha in area, with a mean size of approximately 0.1 ha. Data were collected from 18 grazed and 21 improved fallows. Data were collected using a slight adaptation of the Land Degradation Surveillance Framework (LDSF; Walsh and Vagen 2006), modified for field-scale sampling. LDSF involves characterization of vegetation structure (diameter at breast height (DBH) and height of trees, tree and shrub stem density, and vegetation cover), soil conditions (soil properties, soil infiltration capacity, rock cover and erosion), and FAO-standard land use/cover. Soils were sampled at depths of 1-20 cm (topsoil) and 20-50 cm (subsoil).

The LDSF protocol was reproduced at the scale of a single 100 m² plot located randomly in the interior of each fallow. Two 2 m² subplots were established within each 100 m² sample plot, one in the center, and one randomly located tangent to the plot edge. Soil samples were collected and soil infiltration capacity measured in both subplots. Biovolume (m³) of each plant species was characterized by visually estimating cover and average height. Cover was scored as the mid-point of cover classes on a 5-point scale: 1-4, 4-15, 15-40, 40-65, and > 65 m². Grazing intensity was recorded by visually estimating cover for evidence of grazing—bite marks, trampling, feces, and hair—on the same 5-point scale.
Standing biomass—large woody stems. For all woody stems ≥ 2.5 cm DBH, aboveground standing biomass (t ha⁻¹) was estimated by using DBH measurements to calculate whole-tree biomass (Y) by the general allometric equation, \( Y = e^{-2.134 + 2.53 \times \ln(DBH)} \) for humid regions (Ponce-Hernandez 2004). To estimate belowground biomass, aboveground biomass estimates were multiplied by the mean of values from the literature for root-to-shoot ratio (RSR) of tree species common in the study site (Appendix A). Above- and belowground biomass estimates were summed to estimate total standing biomass.

Standing biomass—small woody stems and herbaceous species. For all woody plants < 2.5 cm DBH and all non-woody species, cover estimates were multiplied by average height to estimate biovolume by species, then multiplied by a conversion factor to estimate aboveground biomass (Appendix A). To estimate belowground biomass, aboveground biomass estimates were multiplied by the mean of values from the literature for RSR of species common in the study site (Appendix A). Above- and belowground biomass estimates were summed to estimate total standing biomass.

Standing green biomass. To obtain estimates of standing green biomass, the same procedure was used as for standing (total) biomass, except using conversion factors that reflect aboveground biomass for leaves and young green twigs (Appendix A).

Soil infiltration capacity. Infiltration was measured with ring infiltrometers 20 cm in diameter over approximately 2.5 hours, or until steady state had clearly been reached. Soil infiltration capacity was quantified as steady infiltration rates (mm hour⁻¹), the lower asymptote approached by infiltration rate over time, and the mean was taken for the 2 nested subplots. Each ~2.5 hr measure was modeled as a random effect in a non-linear mixed effects model of the Horton
equation (Horton 1940), via asymptotic regression using the nlmer function in the lme4 package (Bates and Maechler 2010) in R (R Development Core Team 2008).

Soil chemistry. Soil organic carbon (SOC), soil base cations, and soil sand content were quantified by means of near infrared reflectance spectroscopy (NIRS; Shepherd and Walsh 2002, Shepherd and Walsh 2007), which utilized extensive soil libraries developed for the study site and the region to predict values of soil properties. Predictions were made by using linear mixed effects models to predict SOC, base cations, and sand from the principal components (PCs) of first-derivative NIR spectral reflectance in the 700 to 2500 nm range. Topsoil and subsoil were modeled as random effects. Cross-validation based on an independent sample set demonstrated that model fits in terms of $r^2$ were: 0.91 for SOC; 0.92 for Mg; 0.70 for Ca; 0.88 for K; and 0.92 for sand. Estimates of Mg, Ca, and K were summed to estimate base cations. For estimates of SOC, base cations, and sand contents the mean was taken for the 2 nested subplots.

Plant trait data. Samples of leaves and young green twigs were collected from a subset of study plots, and NIRS was used to predict content of N, lignins and polyphenols for the most abundant species. Dry green tissue samples—leaves for herbaceous species, and leaves combined with young green twigs for woody species. Predictions were made by using partial least squares regression models to model N, lignin, and total soluble polyphenol from PCs of first-derivative NIR spectral reflectance in the 1250 to 2500 nm range. Cross-validation based on an independent sample set demonstrated model fits in terms of $r^2$ were: 0.98 for N; 0.73 for lignin; and 0.86 for polyphenol. Mean trait values were calculated by species. For species not collected in study plots, mean trait values by species were obtained from the Organic Resource Database (Palm et al. 2001).
Community-weighted trait means. Community-weighted mean (CWM) green tissue contents of N, lignins, polyphenols, and lignins+polyphenols, were calculated for each plot. CWMs were calculated with Equation 1 (Ackerly and Cornwell 2007) from species mean trait values, weighted upon species abundance in terms of standing green biomass, as

\[ p_j = \frac{\sum_{i=1}^{S} a_{ij} t_i}{\sum_{i=1}^{S} a_{ij}}, \]  

where \( p_j \) is the abundance-weighted mean for trait \( t \) in plot \( j \), \( t_i \) is the value of trait \( t \) for species \( i \), \( a_{ij} \) is the abundance of species \( i \) in plot \( j \), and \( S \) is the total number of species present. Trait values were log-transformed prior to calculation of CWMs.

Maize yield. Field technicians were instructed to sample only fallows where the farmer intended to plant maize in the 2010 long rains season. Once fallows were identified and sampled, the boundary of the fallow plot was marked with 4 large wooden stakes painted blue. Under free, prior, and informed consent in Luo, their first language, farmers agreed to plant maize in cleared former fallow plots during the first 2 weeks of the 2010 long rains, to use inputs (hybrid seed and NPK fertilizer) recommended by Sauri MVP in 2010, to weed the maize at intervals of 1 and 2 months after planting, and to not harvest the maize until MVP field staff had taken a sample of maize from the former fallow plot. Since all of the farmers owning the sample fallows were consenting participants in the research, there was no danger of imposition of financial or other hardships on farmers due to participation in the research.

Sauri MVP field staff conduct annual sampling of maize yields, and were instructed to include maize fields planted in the sampled fallows among these fields. MVP maize yield sampling protocol involves collection of sample cobs and recording fresh weight of whole maize plants in square plots 16 or 25 m\(^2\) in area. Sample cobs are weighed in the laboratory, a
subsample is oven-dried to measure moisture content, and the overall weight of maize grain and cob cores are corrected for moisture content.

Results

Out of a total of 41 farms of different households where fallow sampling was conducted, maize yield data was collected in 5 farms. In the 5 farms where both fallow sampling and maize yield sampling were conducted, maize yield samples were collected from a total of 9 plots, located within 7 fields (in 2 fields, 2 maize samples were collected).

Latitude and longitude coordinates provided by MVP staff for maize yield plots indicated that, within a high degree of certainty, none of the maize yield plots where located within the boundaries of fallow fields sampled previously. For most maize yield plots the difference was clear, as maize yield plots were located an average of 100.3 m away from fallow plots. In the study site, small field sizes mean that maize was sampled between 2 and 3 fields away from the field of the fallow. Hence, no links can be made between these replicates of the fallow and maize datasets.

A few plots were close enough that they might have been in the field of the former fallow. 3 maize yield plots (in 2 fields owned by the same household) were sampled at distances of approximately 30 and 38 m away from the plot sampled in a grazed fallow. However, in this fallow the plot was located approximately 15 m from the closest boundary. The orientation of the sampled maize plots in the same direction as the closest boundary indicates that these maize plots were well over 10 m into adjacent fields. As such, although some these maize plots may have been sampled in the correct field, depending on GPS error, they were most likely not.
Discussion

Maize yields could not be linked to fallow soils, vegetation, or other factors, as maize yield plots were not located in fields sampled during the fallow period. As such, the proposed hypotheses could not be tested. There are a number of reasons that appear to have contributed to failure to obtain data adequate for testing the proposed hypotheses.

One reason could be that many of the sampled fallow fields were not in fact cleared and planted with maize. In such cases, sampling of maize yields would of course be impossible, although it has not been possible to verify which specific fallows were planted versus not. Farmers may not have known at the time which fallows they planned to clear, and simply guessed on the spot, or may have changed their management plans after the fallow was sampled. There also is some cause to suspect that communication with farmers during identification of fallows may have been problematic. Possible mis-communication could have arisen from insufficient training of field technicians, or technicians not carrying out their instructions fully in communicating with farmers. One concern is that farmers may have told field technicians what farmers imagined the technician, their supervisor, or MVP was ‘hoping to hear’, in a rather vague sense, for a variety of possible reasons.

Generally, beneficiaries of development projects should be viewed as seeking to maximize their personal or collective gain from the presence of the project. When the goals of beneficiaries align well with those of the project, the basis for an productive working relationship can be formed. This relationship requires clear communication to be established and maintained, with effective sensitization of beneficiaries as to the goals of the project, and effective feedback from beneficiaries to the project, enabling a collaborative, participatory, and adaptive approach to
decision-making. However, mis-communication and misunderstanding can arise easily. Beneficiaries may attempt to avoid possible conflicts with the project or project staff, and may not be entirely forthcoming in their communication. They may suspect that benefits received from the project depend on acceptance or active support of the project’s goals and priorities, and may be unwilling to provide negative feedback. Project staff may feel a professional drive to satisfy their supervisors, may avoid voicing criticism, and may proceed with established plans out of expediency.

It is suspected that similar dynamics influenced communication with technicians, and in communication between technicians and farmers. In some cases farmers may have indicated that certain fallow fields were to be planted with maize, yet they had no intention of doing so, and simply felt that the appearance of cooperation might be beneficial to them. This could be the case even though it was made clear that there were no financial or other personal benefits to be derived from participation. Technicians could have known that some fallows were unlikely to be planted with maize, yet may have sampled the fallow anyway, and not relayed this information upward. While these dynamics may have resulted in sampling of inappropriate fallows that the farmer did not intend to clear and plant with maize, some fallows are likely to have been planted with maize, yet must not have been sampled.

The main logistical difficulty appears to have been in the sampling of maize yields. On one or more levels, coordination with MVP field staff who were to conduct maize sampling was not effective. Currently, the precise reasons for this remain somewhat unclear. Several field staff and their supervisors were apprised of the needs of the research, and were reminded as such within one month of the 2010 long rains maize harvest. If greater coordination (e.g., daily consultations) was required to effectively implement the work, that was not clear ahead of time,
and moreover would have been difficult to carry out feasibly from overseas. Field staff could not explain afterward why maize yield data were not collected from fields sampled previously while in fallow. The instructions for maize yield sampling might not have been fully clear, perhaps due to language difficulties, and field staff may have indicated prematurely that the instructions were clear when in fact they were not. Field staff may have also not registered negative feedback as to the feasibility of the work or other concerns, and chose to ignore the situation out of expediency or a desire to focus on the most immediate, pressing concerns of the project and their supervisors (see the section above), in this case making sure that the project obtained the maize yield data to track its progress, which in any case is a crucially important objective.

Limitations on the technical capacity and training of field staff also appear to have reduced the feasibility of conducting maize yield sampling. Staff with good English skills are not difficult to find in western Kenya, but language can still be a barrier to effective coordination, especially in technical aspects. Level of education and on-the-job training are important determinants of the degree to which technicians have an effective understanding of the purpose, proper conduct, and importance of research. Even simple technical skills such as GPS navigation and data collection are constrained, since many staff members are not trained to use a GPS, or to use it with accuracy. One particularly effective staff member with excellent English, technical skills, and understanding of the research was away conducting research in Tanzania at the time. Had this individual been available at the time, they might have been able to effectively coordinate with staff on-the-ground to make the maize sampling a success. Unfortunately, limited technical capacity is a common constraint to research throughout Sub-Saharan Africa. Indeed, in Kenya the situation is reasonable compared to most countries in the region.


Bates, D. and M. Maechler. 2010. lme4: Linear mixed-effects models using S4 classes. URL http://lme4.r-forge.r-project.org/.


Appendix A: Biomass estimation methodology

Summary

To estimate biomass (t ha\(^{-1}\)) from field measures of species biovolume (m\(^3\)), conversion factors were developed based on published studies. Studies in the literature that quantified fallow biomass were identified primarily from the vicinity (~20 km) of the study site in Siaya District, western Kenya. One study was conducted in the central Kenyan Highlands (Ståhl et al. 2002), in an area with similar climate but different soil type. Growth forms were defined as: i) herbaceous (forbs, graminoids); ii) subshrubs (sub-woody shrubs and creepers); iii) shrubs (small woody shrubs and creepers); and iv) trees (tree and large shrub species).

Aboveground biomass

For all study treatments of a specific fallow compositional type, i.e., monocultures or ‘weed’/‘natural’ fallsows sharing dominant or co-dominant growth form(s), mean values for biomass:biovolume (in g m\(^{-3}\)) were calculated. For each growth form, mean values specific to fallow compositional types of the relevant growth form were then averaged, producing growth form-specific biomass:biovolume conversion factors (CFs; in g m\(^{-3}\)). Separate CFs were derived for aboveground (woody + green) biomass, and for green biomass (leaves + young green twigs).

Field measures of species aboveground biovolume (in m\(^3\)) were multiplied by the CFs for the appropriate growth form, and divided by 10,000 to estimate biomass (in t ha\(^{-1}\) / Mg ha\(^{-1}\)).
Most studies did not quantify belowground biomass, and values for root-to-shoot ratio (RSR) could not be retrieved. RSR values were taken from the subset of studies that measured belowground biomass. For all study treatments of a specific fallow compositional type, mean RSR values were calculated. For each growth form, mean values specific to fallow compositional types of the relevant growth form were then averaged, producing growth form-specific RSR values used to estimate belowground biomass from aboveground biomass. RSR values used for each fallow study treatment are indicated by subscripts in Tables A1-A4. Estimates of aboveground (woody + green) biomass were multiplied by RSR values to estimate belowground biomass, and above- and belowground biomass estimates were summed to estimate total standing biomass for each species in each plot.
Table A1. Derivation of biovolume-biomass conversion factors for herbaceous species, i.e., forbs and graminoids.

<table>
<thead>
<tr>
<th>Fallow composition</th>
<th>Abvg g m⁻³</th>
<th>Abvg green g m⁻³</th>
<th>Source</th>
<th>RSR</th>
</tr>
</thead>
<tbody>
<tr>
<td>Weed/natural fallow: mixed perennials, herbs dominant</td>
<td>531</td>
<td>531</td>
<td>Gathumbi et al. 2004</td>
<td>0.41a</td>
</tr>
<tr>
<td>Weed/natural fallow: mixed perennials, herbs dominant</td>
<td>545</td>
<td>545</td>
<td>Ndufa et al. 2009 (Migosi)</td>
<td>0.41a</td>
</tr>
<tr>
<td>Weed/natural fallow: mixed perennials, herbs dominant</td>
<td>472</td>
<td>472</td>
<td>Mekonnen et al. 1997</td>
<td>0.41a</td>
</tr>
<tr>
<td>Conversion factor (CF):</td>
<td>516</td>
<td>516</td>
<td></td>
<td>0.41a</td>
</tr>
</tbody>
</table>

* Weed/natural fallow, mixed perennials, herbs dominant (Mekonnen et al. 1997)
Table A2. Derivation of biovolume-biomass conversion factors for subshrub species, i.e., subwoody shrubs and creepers.

<table>
<thead>
<tr>
<th>Fallow composition</th>
<th>Abvg g m⁻³</th>
<th>Abvg green g m⁻³</th>
<th>Source</th>
<th>RSR</th>
</tr>
</thead>
<tbody>
<tr>
<td>Weed/natural fallow: mixed perennial herbs/subshrubs/woody</td>
<td>332</td>
<td>207</td>
<td>Ndulà et al. 2009 (Yala)</td>
<td>0.41a</td>
</tr>
<tr>
<td>Weed/natural fallow: mixed perennial herbs/subshrubs/woody</td>
<td>906</td>
<td>565</td>
<td>Maroko et al. 1999</td>
<td>0.41a</td>
</tr>
<tr>
<td>Weed/natural fallow: mixed perennial herbs/subshrubs/woody</td>
<td>698</td>
<td>449</td>
<td>Niang et al. 2002</td>
<td>0.41a</td>
</tr>
<tr>
<td>Weed/natural fallow: mixed perennial herbs/subshrubs/woody</td>
<td>898</td>
<td>577</td>
<td>Niang et al. 2002</td>
<td>0.41a</td>
</tr>
<tr>
<td>Weed/natural fallow: mixed perennial herbs/subshrubs/woody</td>
<td>283</td>
<td>182</td>
<td>Niang et al. 2002</td>
<td>0.41a</td>
</tr>
<tr>
<td>Conversion factor (CF):</td>
<td>623</td>
<td>396</td>
<td></td>
<td>0.41a</td>
</tr>
</tbody>
</table>

*a* Weed/natural fallow, mixed perennials, herbs dominant (Mekonnen et al. 1997)
Table A3. Derivation of biovolume-biomass conversion factors for shrub species, i.e., small woody shrubs and creepers.

<table>
<thead>
<tr>
<th>Fallow composition</th>
<th>Abvg g m$^{-3}$</th>
<th>Abvg green g m$^{-3}$</th>
<th>Source</th>
<th>RSR</th>
</tr>
</thead>
<tbody>
<tr>
<td>Weed/natural fallow: mixed perennial herbs/subshrubs/woody</td>
<td>623</td>
<td>396</td>
<td>Ndufa et al. 2009 (Yala); Maroko et al. 1999; Niang et al. 2002</td>
<td>0.41$^a$</td>
</tr>
<tr>
<td><em>Desmodium uncinatum</em></td>
<td>975</td>
<td>618</td>
<td>Niang et al. 2002</td>
<td>0.22$^b$</td>
</tr>
<tr>
<td><em>Macroptilium atropurpureum</em></td>
<td>1042</td>
<td>660</td>
<td>Ndufa et al. 2009 (Migosi)</td>
<td>0.44$^c$</td>
</tr>
<tr>
<td><em>Macroptilium atropurpureum</em></td>
<td>417</td>
<td>264</td>
<td>Ndufa et al. 2009 (Yala)</td>
<td>0.44$^c$</td>
</tr>
<tr>
<td><em>Macroptilium atropurpureum</em></td>
<td>375</td>
<td>238</td>
<td>Gathumbi et al. 2004</td>
<td>0.44$^c$</td>
</tr>
<tr>
<td>Conversion factor (CF):</td>
<td>708</td>
<td>449</td>
<td></td>
<td>0.37</td>
</tr>
</tbody>
</table>

$^a$ Weed/natural fallow, mixed perennials, herbs dominant (Mekonnen et al. 1997)

$^b$ *Desmodium uncinatum* (Mugabe et al. 2004)

$^c$ *Macroptilium atropurpureum* (Gathumbi et al. 2002, Gathumbi 2004)
Table A4. Derivation of biovolume-biomass conversion factors for tree species, i.e., tree and large shrub species.

<table>
<thead>
<tr>
<th>Fallow composition</th>
<th>Abvg g m(^{-3})</th>
<th>Abvg green g m(^{-3})</th>
<th>Source</th>
<th>RSR</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Calliandra calothyrsus</em></td>
<td>949</td>
<td>464</td>
<td>Ståhl et al. 2002</td>
<td>0.63(^a)</td>
</tr>
<tr>
<td><em>Crotalaria paulina</em></td>
<td>1000</td>
<td>476</td>
<td>Ndufa et al. 2009 (Migosi)</td>
<td>0.31(^b)</td>
</tr>
<tr>
<td><em>Crotalaria paulina</em></td>
<td>595</td>
<td>286</td>
<td>Ndufa et al. 2009 (Yala)</td>
<td>0.31(^b)</td>
</tr>
<tr>
<td><em>Crotalaria paulina</em></td>
<td>1057</td>
<td>357</td>
<td>Jama et al. 2008</td>
<td>0.31(^b)</td>
</tr>
<tr>
<td><em>Crotalaria paulina</em></td>
<td>557</td>
<td>191</td>
<td>Gathumbi et al. 2004</td>
<td>0.31(^b)</td>
</tr>
<tr>
<td><em>Tephrosia candida</em></td>
<td>1184</td>
<td>343</td>
<td>Jama et al. 2008</td>
<td>0.32(^c)</td>
</tr>
<tr>
<td><em>Tephrosia candida</em></td>
<td>678</td>
<td>196</td>
<td>Niang et al. 2002</td>
<td>0.32(^c)</td>
</tr>
<tr>
<td><em>Sesbania sesban</em></td>
<td>1727</td>
<td>479</td>
<td>Maroko et al. 1999</td>
<td>0.45(^d)</td>
</tr>
<tr>
<td><em>Sesbania sesban</em></td>
<td>1212</td>
<td>200</td>
<td>Ndufa et al. 2009 (Migosi)</td>
<td>0.45(^d)</td>
</tr>
<tr>
<td><em>Sesbania sesban</em></td>
<td>758</td>
<td>152</td>
<td>Ndufa et al. 2009 (Yala)</td>
<td>0.45(^d)</td>
</tr>
<tr>
<td><em>Sesbania sesban</em></td>
<td>2406</td>
<td>448</td>
<td>Niang et al. 2002</td>
<td>0.45(^d)</td>
</tr>
<tr>
<td><em>Sesbania sesban</em></td>
<td>2302</td>
<td>477</td>
<td>Mekonnen et al. 1997</td>
<td>0.45(^d)</td>
</tr>
</tbody>
</table>

Conversion factor (CF): 1288

\(^a\) *Calliandra calothyrsus* (Ståhl et al. 2002)
\(^b\) *Crotalaria grahamiana* (Ndufa et al. 2008)
\(^c\) *Tephrosia candida* (Ndufa et al. 2008)
\(^d\) *Sesbania sesban* (Mekonnen et al. 1997, Ndufa et al. 2008)