# On-farm diversity offsets environmental pressures in tropical agroecosystems: A synthetic review for cassava-based systems

**Citation:**

Delaquis, Erik; De Haan, Stefan; Wyckhuys, Kris A.G.. 2017. *On-farm diversity offsets environmental pressures in tropical agroecosystems: A synthetic review for cassava-based systems*. Agriculture, Ecosystems and Environment. 251: 226-235.

**Publisher's DOI:**

http://dx.doi.org/10.1016/j.agee.2017.09.037

**Access through CIAT Research Online:**

http://hdl.handle.net/10568/88232

For submission to *Agriculture, Ecosystems and Environment*

Send correspondence to:

Kris A. G. Wyckhuys
Institute of Plant Protection, Chinese Academy of Agricultural Sciences
No. 2 West Yuanmingyuan Rd., Haidian District,
Beijing, 100193, P. R. China
Tel: 86-10-62813685
Contact: kagwyckhuys@gmail.com

# On-farm diversity offsets environmental pressures in tropical agro-ecosystems: a synthetic review for cassava-based systems

Erik Delaquis[1], Stefan de Haan[1] and Kris A.G. Wyckhuys[1*]

[1]International Center for Tropical Agriculture (CIAT) Asia regional office, Hanoi, Vietnam

## Abstract

Ecosystem integrity is at risk across the tropics. In the quest to meet global dietary and market demands, tropical agro-ecosystems face unrelenting agricultural intensification and expansion. Agro-biodiversity can improve ecosystem stability and functioning, but its promotion in smallholder-based systems faces numerous practical hurdles. In the tropics, cassava (*Manihot esculenta* Crantz) is cultivated on over 25 million hectares and features as the third most important source of calories. Cassava crops are often maintained by resource-poor farmers who operate on marginal lands, at the fringes of sensitive, biodiverse habitats. As traditional intercropping schemes are gradually abandoned, monoculture cassava systems face stagnating yields, resource-use inefficiencies and agro-ecosystem degradation. A global literature search identified 189 cassava intercropping studies, covering 330 separate instances of intercropping systems. We employed a vote-counting approach and simple comparative measure across a subset of 95 studies to document the extent to which intercropping sustains a bundle of ecosystem services. Across geographies and biophysical conditions, a broad range of intercrops provided largely positive effects on five key ecosystem services: pest suppression, disease control, land equivalency ratio (LER), and soil and water-related services. Ecosystem services were augmented through the addition of a diverse range of companion crops. Results indicated 25 positive impacts vs. 3 negative impacts with the addition of maize, 5 vs. 1 with gramineous crops, 23 vs. 3 with four species of grain legumes, and 9 vs. 0 with trees. Appropriate intercropping systems can help to strike a balance between farm-level productivity, crop resilience, and environmental health. Our work highlights an urgent need for interdisciplinary research and systems-level approaches to identify intensification scenarios in which crop productivity, provision of ecosystem services, biodiversity conservation, and human well-being are all balanced.

**Keywords**: Food security; land-sharing; sustainable intensification; crop diversification; ecosystem services

## 1. Agricultural expansion puts tropical ecosystems at risk

Rapid population growth, shifting consumption patterns, and resource competition are increasing pressure on the world's agricultural systems and non-arable land (Godfray *et al.*, 2010). Contemporary agricultural trends have dramatically shifted farming practices, promoted rapid expansion of agricultural lands, and triggered global environmental changes that risk destabilizing whole ecosystems (Foley *et al.*, 2011). With agro-ecosystems covering 37.5 % of global national land surfaces in 2014 (FAOSTAT, 2016), environmental impacts linked to farm-level management decisions are substantial, and are expected to be exceptionally pronounced in tropical terrestrial ecosystems (Laurance *et al.*, 2014).

The pursuit of increased production through both area expansion and farming intensification has resulted in an increase of agricultural areas in the tropics of >100 million ha in the 1980-90s, occurring largely at the expense of intact or disturbed forests (Gibbs *et al.*, 2010). The limits to this expansion have simultaneously driven a need to increase productivity on limited land, sparking research into the causes of sub-optimal yields and the potential for 'yield gap closure' (van Ittersum *et al.*, 2016; Sayer and Cassman, 2013). Farmers often respond to the need for increased productivity with intensification measures, many of which have negative environmental impacts at field, farm, and agro-landscape levels (e.g., Emmerson et al., 2016). Irrational pesticide and fertilizer use and extractive management are commonplace, leading to soil and water resource degradation in many parts of the tropics (Godfray *et al.*, 2010), while exacerbating biotic and abiotic production constraints in both intensified and low-input farming systems (Poppy *et al.*, 2010).

Millions of smallholder farmers eke out a living by continuously cropping in such settings, which are characterized by shrinking natural resource bases and degraded agro-ecosystem functioning (Bai *et al.*, 2008; Barbier, 1997; Bossio *et al.*, 2010). Though they constitute the backbone of global food security, many of the world's smallholders continue to live in poverty, cultivate marginal lands, and operate on the fringes of sensitive, biodiverse habitats (Tscharntke *et al.*, 2010).

In this paper we explore how field-level diversification fosters the provision of multiple key ecosystem services (i.e., soil and water conservation, pest regulation and disease control, and land equivalency ratio) in a major tropical and subtropical food crop. More specifically, we examine the example of intercropping in cassava-based systems through an ecosystem services lens. We provide information on recent trends in cassava cultivation globally, and subsequently discuss associated environmental impacts. Next, we systematically review the literature on intercropping practices in cassava-based systems, present its impacts on multiple ecosystem services, and discuss further implications of these findings for cassava-based farming systems across the tropics.

## 2. Cassava: an adaptable 'survivor' crop

Cassava (*Manihot esculenta* Crantz) production has increased greatly in the past 50 years (Fig. 1b). This starchy, tuberous staple is now cultivated on ~ 25 million ha throughout the global tropics (FAOSTAT, 2016). Originating in the Neotropics (Olsen and Schaal, 1999), cassava is now an important food in sub-Saharan Africa and South America, while in mainland Southeast Asia it is predominantly a cash crop. Cassava is the largest calorie producer among roots and tubers, making it a critical crop in resource-poor farming settings across the global tropics (Fig. 1b). Cassava is highly adaptable to variable conditions, being grown in a wide range of agro-ecological settings: from Africa's arid Sahel and the cool highlands of Zambia to Colombia's Andean lowlands and the limestone uplands of Laos and Vietnam. A perennial woody plant primarily managed as an annual, cassava is cultivated for its starchy roots used as human food, animal feed, a source of industrial starch, and a biomass energy feedstock (Zhou and Thomson, 2009; von Maltitz *et al.*, 2009).

A hardy 'survivor' crop, cassava thrives in degraded settings, under low soil fertility, at high temperatures, and can withstand periodic droughts (El-Sharkawy, 2014). Cassava is highly resilient and adaptable in the face of ongoing climatic changes, providing options for adaptation in challenging environments (Jarvis *et al.*, 2012). Cassava's ability to grow on poor soils, under sub-optimal climatic conditions, and to provide the advantage of flexible harvest timing, make it the crop of 'last resort' across the tropics (Hillocks *et al.*, 2001) and earn it the moniker 'the drought, war, and famine crop' (Burns *et al.*, 2010).

Because intermediate yields are often attainable even in poor conditions, for example ~ 14T/ha on East and Southern African smallholder farms (Tittonell and Giller, 2013), cassava is often cultivated in monocultures, without proper addition of fertilizer or organic amendments, with complete abandonment of rotation schemes, and using low quality planting material. Cassava enjoys a theoretical yield potential (defined as the yield of a crop grown in the absence of biotic constraints, and with non-limiting water and nutrients) approaching 90 T/ha (Cock *et al.*, 1979; van Ittersum *et al.*, 2013). Despite this, average yields in the tropics remain low, and are increasing only slowly (El-Sharkawy, 2012; Tittonell and Giller, 2013). Farm yields throughout Africa as a whole average 10 T/ha, far below both the 15-40 T/ha obtained in local on-farm trials in the same agro-ecozones (Fermont *et al.*, 2009), or the average yield of 20.7 T/ha in Southeast Asia (FAOSTAT, 2016). Although substantial yield gains are predicted when farmers adopt the use of pre-emergence herbicides or appropriate soil amendments (Howeler, 2015; Fermont *et al.*, 2009), it is likely that strategic use of low-input technologies can equally achieve significant progress toward these goals while safeguarding food security, improving farmer livelihoods, and off-setting a range of environmental impacts (Pypers *et al.*, 2011; Fermont *et al*., 2009). Given the large scale of cassava's cropping, its ubiquity in sensitive tropical environments, and its importance to impoverished smallholders with limited options for investment in agricultural inputs and technologies, the environmental impacts of its cultivation is a topic that demands serious consideration.

## 3. Environmental impacts

Long thought to be largely environmentally benign due to the ability to produce acceptable yields on marginal soils with minimal external inputs, studies now demonstrate that improperly managed cassava can contribute to cycles of environmental degradation that ultimately threaten the sustainability of crop production (Reynolds *et al.*, 2015). Crop area expansion and unsustainable farming practices influence these outcomes, though patterns of variability with socio-economic factors, geography, and ecosystem composition are poorly understood.

Cassava has gained the reputation of promoting soil erosion due to its erect architecture, poor canopy cover in the early growing season coinciding with heaviest rains, soil-disturbing harvest scheme, and ability to continue producing despite mismanagement of degraded soils (Moench, 1991; Valentin *et al.*, 2008). However, those factors do not appear to be the intrinsic cause of cassava's environmental impacts. Cassava is commonly grown on erodible hillsides, drought-prone areas or acidic soils, and recently deforested land, generating negative impacts directly related to overall land use and improper management (Reynolds *et al.*, 2015). Soil exhaustion, fertility depletion, and topsoil loss challenge cassava production (and indeed that of all crops) across the tropics (Fermont *et al.*, 2009; De Vries *et al.*, 2010; Waddington *et al.*, 2010; Clement and Amezaga, 2008; Valentin *et al.*, 2008). When inadequately managed, soil biological function and plant immune responses decline, and crops become increasingly prone to arthropod pests and plant diseases (Graziosi *et al.*, 2016; Vurro *et al.*, 2010). These problems are rarely evaluated comprehensively, and symptomatic treatments are often pursued without tackling the underlying drivers or exploring the complex interplay between contributing factors.

In the period following the Columbian exchange (see Crosby, 1972), cassava spread far beyond its native range in the Americas to become an important component of agroecosystems across the global tropics. Since the 1980s, notable increases in cassava area have occurred in key production zones including Nigeria, Cambodia, and Vietnam. In West Africa, continuing agricultural expansion is leading to forest loss and degradation, with cassava cropping identified as one of several drivers (Norris *et al.*, 2010). In Cambodia, booming demand for export cassava has contributed to deforestation in upland areas, alongside other cash crops, such as rubber

(Hought *et al.*, 2012; NEPCon, 2014). Land clearance for cassava cultivation has also occurred in Latin America, but effects on local biodiversity remain poorly documented (Howeler *et al.*, 2000).

As it is grown with few interventions during a long growing cycle (8-12 months), cassava may provide stable habitat conditions for diverse biota. However, cassava monocultures sustain lower biodiversity than certain agricultural and agro-forestry habitats, or natural areas (Francesconi *et al.*, 2013). As in examples from across multiple production systems and settings (Tews *et al.*, 2004), the ability of cassava-based systems to sustain biodiversity may improve with management regimes that enhance habitat heterogeneity, which can improve and sustain biodiversity at a field, farm, and landscape level (Benton *et al.*, 2003). One of the most well-known ways to increase agrobiodiversity is through the practice of intercropping.

## 4. Intercropping as a traditional solution to restore ecosystem degradation

In the Amazonian center of origin, traditional societies grow dozens of cassava varieties on small plots, interspersed with other food, fiber, or cash crops (McKey *et al.*, 2001). This approach contrasts with the market-driven, large-scale, and genetically uniform systems promoted by industrial agriculture models. Highly diverse farming, including intercropping, prevailed in the tropics prior to the introduction of modern, globalized markets and high intensity production schemes (Hulugalle and Ezumah, 1991; Wargiono *et al.*, 2000), but currently risk being discarded in favor of increasingly uniform cropping systems (Gianessi, 2013). Despite the appeal of monoculture production systems, pockets of smallholder farmers in various parts of the world still maintain diversified cassava systems (de Carvalho *et al.*, 2009).

As cassava cropping systems shift towards simplified management regimes, they increasingly require interventions to build in resilience and safeguard ecosystem functioning. Intercropping is the production of two or more crops in the same field at the same time, augmenting structural complexity and diversity (Andrews and Kassam, 1976). The introduction of a second crop can take many forms, with spatial designs that are additive, substitutive, or a combination of both. Additive designs maintain the same spatial arrangement as in monoculture, but add an intercrop species for all or part of the production cycle. Substitutive designs entail the removal of individual plants or rows of plants and replacement with the intercrop species. While intercropping persists in subsistence or low-input, resource-limited farming systems, it is commonly under-valued (Altieri, 2004). Similarly, there exists as yet unexploited potential to pursue the development of intercropping strategies tailored specifically to highly-intensified cropping systems (Andrade *et al.*, 2012).

Diversification tactics in general, and inter-cropping specifically, are known to enhance overall system productivity, while augmenting stability, resilience, and ecological sustainability (Vandermeer, 1989; Nicholls and Altieri, 2004; Letourneau *et al.*, 2011; Lin, 2011). Intercropping may also be effective in improving water infiltration and storage, increasing carbon sequestration, reducing soil erosion, and contributing to ecological pest, weed, and disease management (Brooker *et al*., 2015; Bedoussac *et al.*, 2015). Recent research suggests that on-farm diversification supports an array of provisioning and regulating ecosystem services, especially within tropical terrestrial systems (Kremen and Miles, 2012; Oliver *et al.*, 2015; Lundgren and Fausti, 2015). Although intercropping may contribute to solutions for some of the most pressing issues in global agriculture and biodiversity conservation, quantitative syntheses of the existing research are lacking (Kremen and Miles, 2012).

Syntheses focusing on individual intercrops are relatively uncommon (Malézieux *et al.*, 2009), with examples including legumes as intercrops within cereals (including soft wheat, durum wheat and barley; Bedoussac *et al.*, 2015) and maize (Sileshi *et al.*, 2008). Mutsaers *et al.* (1993) conducted a comprehensive review of intercropping practices for cassava, focusing largely on productivity measures, but including several observations on the provision of other ecosystem services; in particular reduction of weeds and erosion through increased canopy cover. The authors noted importantly that the bulk of cassava research (including global breeding efforts) focus nearly exclusively on monoculture settings. Building on the observations of authors like Mutsaers *et al.* (1993), we apply the lens of ecosystems services specifically to cassava intercropping systems. In this study we a) carry out a global literature synthesis, across systems, components, management strategies, agro-ecozones, and field-level bio-physical conditions, b) evaluate a broad range of provisioning and regulating ecosystem services, and c) employ the formative concept of ecosystem bundles (Bennett *et al.*, 2009) to evaluate trade-offs and synergies for specific crop associations. Ecosystem service bundles provide a valuable tool for simultaneously evaluating the interactions of multiple ecosystem services in different settings, allowing for the detection of trends or patterns of interaction between services (Bennett *et al.*, 2009; Rausepp-Hearne, 2010). By grouping the effects on ecosystem services of production systems with different intercrop components, we take a broad view of the trends in ecosystem services in cassava intercropping systems.

## 5. Literature review and analysis

A literature review was employed to evaluate cassava intercropping, to assess the existing evidence for the impacts of intercropping on ecosystem services in cassava production systems, and to extract and compare findings on the functioning of these services in contrasting intercropping and monoculture settings. The cassava intercropping literature covers a wide array of systems and geographies, with experiments at differing spatial scales, temporal durations, and levels of scientific rigor. Literature was obtained in July 2015 by searching Web of Science using the keywords ‘cassava’ OR ‘*Manihot esculenta*’ AND ‘intercrop’ OR ‘polyculture’. Relevant studies were selected in which a) cassava was a focal crop, b) intercropping occurred with both spatial and temporal overlap, c) publication occurred in a peer-reviewed journal or in reports of established research centers. The resulting literature was augmented by references cited in the primary literature.

A total of 189 references were found (complete list available in online supporting material), of which 170 investigated intercropping for one or more ecosystem services response variables; the remainder being reviews not specific to cassava or reports of intercropping with no experimental data. A total of 20 studies were reviews of intercropping theory or mechanisms not attached to any geographic location. Publications covered the 1975-2015 time period and originated from 27 countries. Overall 63 % of cases evaluated intercropping systems with only 2 components, a further 26 % evaluated three component systems, and the remainder investigated various more complex arrangements. In 62 % of cases the intercropping system included a legume. Only 17 % of experiments combined cassava with perennial species alone, while a further 21 % of combinations included both a perennial and an annual, and the remainder with only annual species. Of the 330 species combinations across these studies, 122 included maize (*Zea mays* L.), 52 included cowpea (*Vigna unguiculata* L. Walp), 48 included trees, 38 included peanut (*Arachis hypogaea* L.), and 36 included grass/forages. Other intercrops, including rice (*Oryza* sp.), soybean (*Glycine max* L. Merrill), and variety mixtures, were less frequently mentioned.

Intercropping schemes with annual crops generally took advantage of the initial space provided by the establishment of the relatively long-duration cassava crop. Studies were classified according to type of ecosystem service (TEEB, 2010) evaluated (provisioning, regulating, cultural) (Fig. 2).

For further analysis of the effects on ecosystem services, a subset of papers was selected for the inclusion of an appropriate cassava monoculture control, robust methods and description of data, examination of land productivity expressed as land equivalent ratio (LER) or area-time equivalent ratio (ATER), soil services (soil cover, erosion, changes in content of N,P,K, organic matter, or earthworm activity), water services (infiltration, runoff, soil moisture content), and pest regulation or disease control. Only 95 studies met all of the above criteria (for information about their geographic origin see Fig. 1c). We analyzed these studies using vote-counting and synthesized multiple independent studies by summing the numbers of (statistically significant) positive and negative effects. More statistically powerful syntheses based on weighted combination of effects are recognized, but quality and applicability of meta-analysis in agronomy has often been questioned (Philibert *et al.*, 2012), and its application to intercropping issues to date remains scarce (Brooker *et al.*, 2015). Robust analysis of ecosystem services in intercropping systems (based on historical published results) will require greater understanding of trends in research and findings, in order to guide the formulation of analytical methods and approaches specific to this application. Considering the lack of directly comparable measures for many of the ecosystem services reported and the absence of recent systematic reviews on this topic, the authors selected vote-counting as a first measure for compiling an overview of the existing research (Cooper, 1998). Vote-counting is a coarse method of evaluation that does not attempt to generate composite effect sizes, but does permit making comparisons across a wide range of indicators and variables. For studies in which data were solely presented in graphical form, data were extracted using WebPlotDigitizer software (Rohatgi, 2011). Due to the common practice of reporting multiple separate experiments in a single journal article, data was extracted from each ‘experiment’. In cases where the intercropping arrangement was kept constant but another variable varied (for example, fertilizer application rate or management scheme), the range is represented by horizontal bars. For cases in which a single journal article presented results from completely separate experiments, these were represented as separate points. For multi-year studies, values were averaged over the whole study period. Non-significant results appear on the bisector. For vote-counting only the directionality of results was considered, with differentiation between 4 categories: benefit, dis-benefit, mixed, and no effect. Studies in which no statistically-significant effects of intercropping were reported were catalogued under the ‘no effect’ category, while those with significant yet inconsistent effects (e.g., between years, locations, climatic conditions, soil types) were listed as ‘mixed effect’.

## 6. Ecosystem service bundles in diversified systems

### 6.1. Land use efficiency: LER and ATER

A large share of intercropping studies covered provisioning services (Fig. 2). As proxies for land productivity we used two well-established measures: LER and ATER. LER is a common yardstick for measuring relative land use and is widely employed in intercropping (Bedoussac and Justes, 2011), calculated as a ratio of the relative land area required when growing sole crops to produce the yield from an intercrop (Willey and Osiru, 1972). Due to the prolonged growth period of cassava, the disparity between cultivation cycles of component crops can lead to an overestimation of intercropping advantage (Hiebsch and McCollum, 1987; Fukai, 1993). Hence, an alternative measure, ATER, which calculates the sum of the relative yields of the intercrop components corrected for the differences in duration of growing period, may be more appropriate (Hiebsch and McCollum, 1987; Fukai, 1993; Mutsaers *et al.*, 1993). Despite this, LER remains a more often reported metric in intercropping studies (Bedoussac and Justes, 2011), and for this reason was the focus of our literature review. Overall, 43 and 17 measures of LER and ATER were reported in 30 and 7 studies, respectively.

A positive relationship (represented by a ratio above 1) was found between intercropping and overall system productivity, with an overall range from 0.79 – 1.84. LER measures were above parity in nearly all cases (37/43), with consistent over-yielding observed in a number of species combinations (Fig. 3). One notable exception is pigeonpea (*Cajanus cajan*), for which average LER values below 1 were recorded. Maize and bean-based systems performed particularly well due to their relatively short growing seasons, while peanut and rice-based systems give mixed results and are therefore inconclusive. Within a given intercrop system, substantial variation was observed due to environment, varieties, treatments and management practices. ATER measures were also at or above parity in 13/17 reported cases (not shown).

LER and ATER do not reflect economic yield. If couched in a system in which cassava is much more valuable on the market than its intercrop, even a small yield penalty may reduce overall profits. In the majority of cases cassava root yield was depressed by intercropping, but intercrop production was able to compensate for these losses. Similar findings have been previously reported for intercropping in a set of different systems and geographies (e.g., Ngwira *et al.*, 2012). Some systems (particularly those not bound by the onset of a rainy season, which can encourage root rot) may also present opportunities for cassava to remain in the field after intercrop harvest, making up for yield losses incurred by early intercrop competition (Tsay *et al.*,

1988) and possibly benefiting from higher off-peak root prices. This may be increasingly feasible for smallholders gaining early income from harvest of an intercrop.

### 6.2. Pest and disease suppression

Plants grown in association regularly benefit from reduced arthropod pest pressure and stronger immune responses through so-called associational resistance mechanisms (Barbosa *et al.*, 2009; Letourneau *et al*., 2011). Particular plant associations experience a reduced likelihood of detection or vulnerability to herbivores, as affected by a plethora of biotic and abiotic factors. Not only can plant associations enhance abundance or activity patterns of natural enemies, thus benefiting biological control (e.g., Khan *et al*., 1997), but they can also directly regulate pest densities (e.g., Ben Issa *et al*., 2016). These benefits are further amplified at larger scales, in which inter- and intraspecific diversity at field or farm level can contribute to a substantial lowering of pest populations and disease incidence (Boudreau, 2013; Lundgren and Fausti, 2015; Gurr *et al.*, 2016).

In our global review, 63 % (n=15/24) of experiments reported a decrease in pest indicators within intercropped systems (Fig. 4). Across whitefly species the average population change with intercropping was a reduction of 27 %, while in mealybugs the average was a reduction of 37 %. We combined metrics that reflect pest pressure, including abundance ratios of various developmental stages or feeding damage ratings. Pests of global relevance, such as mealybugs, mites, and whitefly, were affected to varying extents by intercropping. Whitefly and mealybugs experienced population reductions in 73 % and 60 % of cases (n= 11/15 and 3/5), respectively. The effect of intercrops on herbivorous mites was solely studied for the invasive green mite, *Mononychellus tanajoa* in Africa, reporting slightly lowered (average -5 %) pest populations; however in 3/5 cases no effect was found. Whether the observed population reductions translate into economic gains is under-investigated. Few authors have hypothesized about the mechanistic basis for this reduced vulnerability to pests, and the relative contribution of abiotic or biotic factors (including natural enemies) has not been thoroughly assessed (but see Gold *et al.*, 1989, 1990). In this review we focused on pest populations, for which the available data are more robust; in the few studies which attempted to evaluate higher-order interactions with predators or parasitoids (Gold *et al.*, 1989; Toko *et al.*, 1996; Schulthess *et al.*, 2004; Onzo *et al.*, 2014), mixed and inconsistent results were reported (not shown). Although past work has failed to adopt holistic, community-level perspectives (e.g., Memmott, 2009; Wood et al. 2015; Wyckhuys et al., 2017a), our findings suggest that further research is required into the myriad ways in which diversification can enhance crop resilience to pest attack.

The impact of intercropping on arthropod pest suppression has direct implications for incidence, virulence and spread of insect-vectored diseases, such as cassava mosaic disease (CMD). Transmitted by different species of whitefly, cassava geminiviruses are debilitating pathogens of cassava worldwide and cause important productivity losses in Africa and South Asia. We noted a consistently beneficial effect of intercropping on CMD, with all five cases reporting a 10-40 % reduction in disease incidence in diversified plots (data not shown) (Agbobli, 1987; Fondong *et al.*, 1982; Night *et al.*, 2011). Addition of an intercrop affects pathogen-host-vector interactions through changes in plant morphology and system complexity, resulting in behavioral modification of the insect vector, and subsequent changes in temporal and spatial aspects of disease spread (Fondong *et al.*, 2002; Night *et al.*, 2011). Similar trends were observed for non-viral diseases, such as cassava bacterial blight (n= 2/3 studies; data not shown). As plant pathogens are propagated by wind, rainfall, or soil, an added intercrop can alter bacterial disease dynamics by impeding infection, disease development or dispersal (Gurr *et al.*, 2016). Analysis of these encouraging results should be tempered by the limited attention the subject has received in cassava, and the likely effects of variable management, genetic, and abiotic factors or the interplay with resident pest populations (e.g., Wyckhuys et al., 2017b). Despite those interfering factors, intercropping may bring about significant farm-level savings as multiple cassava biotic stressors inflict tangible yield losses (e.g., Nwanze, 1982; Legg & Fauquet, 2004).

### 6.3. Soil- and water-regulating services

Our review included 21 studies examining soil variables covering a range of edaphic parameters including measures of soil fertility, erosion, ground cover, moisture content, water infiltration, soil macro-fauna, and organic matter levels (Fig. 5). Excessive erosion has cascading negative effects on carbon cycling, results in substantial nutrient effluxes, and has compounding impacts on a host of soil properties (Quinton *et al.*, 2010; Powlson *et al.*, 2011). Intercropping brought about sharp reductions in erosion levels in a wide range of biophysical settings (n=8/9), with levels regularly halved and beneficial impacts strongly modulated by management tactics (*e.g.,* cultivation, sowing or harvesting timing). This is of primary importance as cassava fields on steep slopes can lose topsoil at a staggering rate of 221 tons per annum (Pimentel *et al.*, 1995); soils that are effectively ‘non-renewable’ over human timescales.

Little effect was observed in studies investigating N, P, K, pH, or soil organic matter. While legume intercrops increase overall biomass production, contribute to C sequestration, and help meet the nitrogen needs of the standing crop (Bedoussac *et al.*, 2015; Sileshi *et al.*, 2008), this was not reflected in the results of the present review. In short-term experiments, intercropping did not contribute to changes in nutrient storage or soil carbon stocks. Many of the included studies had conspicuously short durations by the standards of soil science (3 years or less). Due to the often multigenerational scale of processes involved with soil fertility regulation (Powlson *et al.*, 2011), closer scrutiny should be paid to long-term records of nutrient balances, analysis methodology, and incorporation of surface crop residues. When residues are removed soil benefits are expected to be minimal (Lal, 2010; Makinde *et al.*, 2006). Over the long term, gradual accumulation of organic matter is expected if sufficient crop biomass is reincorporated into the field, mitigating one of the key constraints to cassava crop productivity.

Soils are dynamic systems in which decomposition of organic matter occurs through diverse faunal communities (e.g., Bardgett & van der Putten, 2014). Prolonged vegetative cover maintains structure and function of trophic soil food webs and helps to explain the important increases of earthworm activity in intercropped systems (Curry, 2004; Fig. 5). The contribution of diversification to microbially-mediated nutrient cycling processes is also expected to be positive (Brooker *et al.*, 2015), but requires further investigation in cassava-based systems. Cassava's particularly low P demand and high use efficiency is a result of an efficient obligate symbiosis with P-scavenging mycorrhizae, making soil health particularly salient to maintaining robust production (Howeler *et al.*,1982).

In six of the seven cases of water-related services reported, the effects of intercropping were considered beneficial, with no effect in the seventh case (Figure 6). Soil moisture content and infiltration were either not affected or increased, while runoff was reduced by 59 % in the single study evaluating this metric (Ghosh *et al.*, 1989). A significant gap in research is evident in that none of the studies evaluated investigated water-related services in cassava - grain legume systems, despite this being one of the most commonly promoted intercrops for cassava (n=40). Lastly, with increased soil moisture and water infiltration rates, judicious intercropping systems may be increasingly adaptable to changes in climate as they possess several key attributes to sustain productivity under prolonged drought conditions.

### 6.4. Composite measures of ecosystem function

In the above sections, we demonstrate how intercropping helps to sustain specific ecosystem services. We compiled these data to visualize how integration of a specific companion crop (or plant family) contributes to provision of a bundle of ecosystem services in the most commonly reported systems. The concept of *ecosystem service bundles* takes into account service trade-offs and synergies (Bennett *et al.*, 2009), to provide a balanced picture of system-level benefits and costs. Four common intercropping systems were compared by vote-counting of an ecosystem service bundle in Fig. 6. Vote-counting was undertaken at the global scale. No obvious trends were detected between specific ecosystem services and geographic location. Due to the paucity of studies on certain ecosystem services (e.g., soil microfauna, fertilizer use efficiency) and imbalance of geographic distribution of research (see Figure 1c), the present study cannot draw any conclusions regarding geographic trends. Nevertheless, overall benefits were identified in five ecosystem services, as ranked under supporting, regulating, and provisioning service categories (i.e., pest regulation, disease control, LER, soil- and water-related services) (see Bommarco *et al*., 2013). Though the small number of studies for particular systems (e.g., water and disease control for grass systems) precluded drawing broader generalizations, the following exceptions were recorded: 1) pest control with the addition of maize (no effect in 8/16 studies), 2) LER under legume systems (mixed results in 8/20 studies), and 3) soil-based services for tree intercrops (no effect in 6/12 studies). Despite these anomalies, our work illuminates the under-recognized role of intercropping for ecological remediation within degraded settings. Human-mediated recovery of agro-ecosystems could concurrently help to restore ecological functioning, to rebuild crop yields and to play a role in the on-farm conservation of biodiversity; a strategy which has received no scientific attention in the case of cassava.

Benefits of intercropping are widely thought to be highly variable, context-specific, and dependent upon management and crop components (Brooker *et al.*, 2015). Though not explicitly addressed in our study, management factors and genotype x environment interactions do indeed shape the performance of intercropping systems, and in many cases make the difference between relative advantage and disadvantage. Despite certain biases, our study shows that ecosystem service bundles are sustained with a diverse range of companion crops in cassava systems, with 25 positive impacts vs. 3 negative ones for maize (total n= 43), 5 vs. 1 for other Poaceae (total n= 10), 23 vs. 3 for four species of grain legumes (total n= 40), and 9 vs. 0 for trees (total n= 24), respectively. Half of the global studies on maize intercrops showed no significant effects for pest suppression, while 6 (out of 16) reported positive impacts. Land productivity ratios of the cassava-grain legume systems include studies with pigeonpea, all of which were conducted at a single location in Australia. While these trials may hint at incompatibility of cassava with perennial legumes, they may not be representative of the potential performance of these systems in other geographical and agro-ecological settings. The comparatively weak impact of trees on soil parameters may be due to variable spatial and temporal coverage, methodological effects of studies focused primarily on designing over-yielding forage or mulch systems, and the inclusion of a wide range of tree types and species. Variability in spatial and temporal coverage may be particularly important in tree-based systems, as studies were commonly done with a range of naturally-occurring trees (with inherent seasonal leaf shedding) at close proximity to cassava plantations. Tree species included leguminous species, such as *Flemingia macrophylla* (Willd.) Merr., *Gliricidia sepium* (Jacq.) Steud, and *Leucaena leucocephala* (Lam.) de Wit, and nonleguminous species such as *Eucalyptus* spp., and *Cocos nucifera*. Tree mixtures are also sometimes employed; one study from Brazil included a mixture of 37 species of indigenous trees intercropped with cassava (Daronco *et al.*, 2012). Perennials have been heavily promoted to build underground carbon storage, soil health and fertility in degraded farming systems in Africa, focusing on the use of N-fixing legumes (Glover *et al.*, 2012). The outspoken variability in the effects of different tree species under particular agro-climatic or biophysical conditions suggests that (trait-based, locality-specific) decision-support systems to choose the right companion crops for complementation of one or more particular ecosystem services likely have considerable merit.

Caution needs to be taken when interpreting the results of this study, not solely due to our analytic approach (i.e., vote-counting) but also due to a range of other factors. Many agronomic studies are ‘answer-driven,’ and seek solutions to production problems. Designed to identify ‘improved’ production systems, these risk over-representing positive results, with experiments guided by evidence from systems designed by farmers and practitioners. Of further importance is the risk of publication bias, in which experiments reporting significant results are favored for submission and/or publication (Dickersin, 1990). Cultural ecosystem services, such as traditional uses and networks (Coomes, 2010), food cultures (Lancaster *et al*., 1982), and local perceptions (Kamau *et al*., 2011) that could have been captured through participatory approaches, were generally underreported in the literature. Despite these pitfalls our findings echo those of several comprehensive global reviews focused on other crops (Andow, 1991; Malézieux *et al.,* 2009; Kremen and Miles, 2012).

## 7. Conclusion

Intercropping can add complexity and diversity to the world's agro-production systems. With roots in traditional systems, intercropping holds considerable potential in cassava production systems if attention is given to key barriers to broad-scale adoption. Intercropping has received a fair amount of research attention, but past work primarily consists of on-station trials with a nearly exclusive emphasis on identifying potential for over-yielding. Our work documents the value of this practice to wider ecosystem functioning in a crop of global significance.

The present study elucidates intercropping's potential to meet growing food production needs with minimal environmental costs. Over a wide array of companion plants diversified cassava systems can enhance levels of land productivity and sustain key ecosystem functions and services. Benefits are not only concurrent while intercrops are in place (as shown in this study), but importantly also deliver medium to long-term effects on soil fertility, erosion prevention, and both pest and beneficial insect communities. These long-term benefits are particularly important for soil conservation and erosion prevention, as soils are effectively 'non-renewable' over human timescales. Historical evidence suggests that intercropping can be adapted to smallholders' diverse biophysical and socio-economic contexts. However, the allure of the ecosystem service benefits must be counterbalanced against general reductions in focal crop yields, additional labor costs, and economic considerations. Adoption can be hampered by challenges related to e.g., mechanization, labor requirements, incentive systems, and ultimately the overall economic productivity of a crop producing low-value products. Component crops must each perform well within the agro-ecological niche in which the intercropping system is found, and factors such as spacing, arrangement, input types and levels, and relative harvest timing may significantly influence overall productivity. Nevertheless, even with the existing compelling drivers of monoculture, a research-informed evaluation of overall system profitability and the development of optimized management regimes will increase the practicability of diversification schemes.

Our exercise also suggests a need for methodological, experimental, and conceptual approaches linking productivity, system resilience, and broader environmental preservation within the cassava agro-ecosystem. A weak mechanistic understanding of variable context-dependent ecological processes (*e.g.* plant-plant, and plant-soil interactions) presently constitutes one of several barriers to more widespread promotion and adoption. The path forward for cassava-based farming systems does not solely lie in advancing technical innovations, but in a combination of policies, institutional engagement, markets, and practices. Interdisciplinary, transdisciplinary, and systems-level approaches will be instrumental for identifying intensification scenarios in which cassava productivity, provision of ecosystem services, biodiversity conservation, and human well-being are all balanced, and in providing (smallholder) farmers with selection aides to evaluate appropriate practices to optimize their unique production realities.

## 8. Acknowledgements

This initiative was conducted as part of an EC-funded, IFAD-managed, CIAT-executed program (CIAT-EGC-60-1000004285). Additional funding was also provided through the CGIAR-wide Research Program on Roots, Tubers and Banana (CRP-RTB).

## 9. References

Altieri, M.A., 2004. Linking ecologists and traditional farmers in the search for sustainable agriculture. Front Ecol. Environ. 2, 35-42.

Andow, D.A., 1991. Yield loss to arthropods in vegetationally diverse agro-ecosystems. Environ. Entomol. 20(5), 1228-1235.

Andrade, J. F., Cerrudo, A., Rizzalli, R.H., Monzon, J.P. 2012. Sunflower–soybean intercrop productivity under different water conditions and sowing managements. Agron. J. 104, 1049-1055.

Andrews, D.J., Kassam, A.H., 1976. The importance of multiple cropping in increasing world food supplies. ASA Special Publication, American Society of Agronomy.

Bai, Z.G., Dent, D.L., Olsson, L., Schaepman, M.E. 2008. Proxy global assessment of land degradation. Soil Use and Management 24, 223-234.

Barbier, E.B. 1997. The economic determinants of land degradation in developing countries. Phil. Trans. R. Soc. Lond. B. 352, 891-899.

Barbosa, P., Hines, J., Kaplan, I., et al., 2009. Associational resistance and associational susceptibility: having right or wrong neighbors. Annu. Rev. Ecol. Evol. S. 40, 1-20.

Bardgett, R.D., van der Putten, W.H. 2014. Belowground biodiversity and ecosystem functioning. Nature 515, 505-511.

Bedoussac, L., Journet, E.P., Hauggaard-Nielsen, H., et al., 2015. Ecological principles underlying the increase of productivity achieved by cereal-grain legume intercrops in organic farming. A review. Agron. Sustain. Dev. 35(3), 911-935.

Bedoussac, L., Justes, E., 2011. A comparison of commonly used indices for evaluating species interactions and intercrop efficiency: Application to durum wheat-winter pea intercrops. F. Crop Res. 124, 25-36.

Ben Issa, R., Gautier, H., Gomez, L., 2016. Influence of neighbouring companion plants on the performance of aphid populations on sweet pepper plants under greenhouse conditions. Agric. For. Entomol. 19, 181-191.

Bennett, E.M., Peterson, G.D., Gordon, L.J., 2009. Understanding relationships among multiple ecosystem services. Ecol. Lett. 12, 1-11.

Benton, T.G., Vickery, J.A., Wilson, J.D., 2003. Farmland biodiversity: is habitat heterogeneity the key. Trends Ecol. Evol. 18, 182-188.

Bommarco, R., Kleijn, D., Potts, S. G. 2013. Ecological intensification: harnessing ecosystem services for food security. Trends in Ecol. Evol., 28(4), 230-238.

Bossio, D., Geheb, K., Critchley, W. 2010. Managing water by managing land: addressing land degradation to improve water productivity and rural livelihoods. Aricultural Water Management 97(4), 536-542.

Boudreau, M.A., 2013. Diseases in intercropping systems. Annu. Rev. Phytopathol. 51, 499-519.

Brooker, R.W., Bennett, A.E., Cong, W.F., et al., 2015. Improving intercropping: a synthesis of research in agronomy, plant physiology and ecology. New Phytol. 206, 107-117.

Burns, A., Gleadow, R., Cliff, J., et al., 2010. Cassava: The drought, war and famine crop in a changing world. Sustainability 2, 3572-3607.

Clement, F., Amezaga, J.M., 2008. Linking reforestation policies with land use change in Northern Vietnam: why local factors matter. Geoforum 39, 265-277.

Cock, J.H., Franklin, D., Sandoval G., Juri, P., 1979. The ideal cassava plant for maximum yield. Crop Science 19(2), 271-279.

Coomes, O.T. 2010. Of stakes, stems, and cuttings: the importance of local seed systems in traditional Amazonian societies. Prof. Geogr. 62(3), 323-334.

Cooper, H. 1998. Synthesizing Research: A Guide for Literature Reviews, 3rd edn. Sage Publications, Thousand Oaks, CA.

Crosby, Alfred W. 1972.The Columbian Exchange: Biological and Cultural Consequences of 1492, Westport: Greenwood Press.

Curry, J.P. 2004. Factors affecting the abundance of earthworms in soils. Earthworm Ecology, Volume 9, 113 p.

de Carvalho, F.M., Silveira Viana, A.E., Leite Cardoso, C.E., et al., 2009. Sistemas de produção de mandioca em treze municípios da região sudoeste da Bahia. Bragantia 68, 699-702.

De Vries, S.C., van de Ven, G.W.J., van Ittersum, M.K., Giller, K.E., 2010. Resource use efficiency and environmental performance of nine major biofuel crops, processed by first-generation conversion techniques. Biomass and bioenergy 34, 588-601.

Dickersin, K., 1990. The existence of publication bias and risk factors for its occurrence. J. Amer. Med. Assoc. 263(10), 1385-1389.

El-Sharkawy, M.A., 2012. Stress-Tolerant Cassava: The Role of Integrative Ecophysiology-Breeding Research in Crop Improvement. Open J. Soil Sci. 2, 162-86.

El-Sharkawy, M.A., 2014. Global warming: causes and impacts on agro-ecosystems productivity and food security with emphasis on cassava comparative advantage in the tropics/subtropics. Photosynthetica 52, 161-178.

Emmerson, M., Morales, M.B., Oñate, J.J., et al., 2016. Chapter Two-How Agricultural Intensification Affects Biodiversity and Ecosystem Services. Adv. Ecol. Res. 55, 43-97.

FAOSTAT, 2016. Food and Agriculture Organization of the United Nations - Statistics Database. http://faostat3.fao.org/ (accessed 15.05.2016).

Fermont, A.M., van Asten, P.J.A., Tittonell, P., et al., 2009. Closing the cassava yield gap: An analysis from smallholder farms in East Africa. Field Crop Res. 112, 24-36.

Foley, J.A., Ramankutty, N., Brauman, K.A., et al., 2011. Solutions for a cultivated planet. Nature 478(7369), 337-42.

Fondong, V.N., Thresh, J.M., Zok, S., 2002. Spatial and temporal spread of cassava mosaic virus disease in cassava grown alone and when intercropped with maize and/or cowpea. J. Phytopathol. 150, 365-374.

Francesconi, W., Nair, P.K.R., Levey, D.J., et al., 2013) Butterfly distribution in fragmented landscapes containing agroforestry practices in Southeastern Brazil. Agroforest. Syst. 87, 1321-1338.

Fukai, S., 1993. Intercropping - bases of productivity. F. Crop Res. 34, 239-245.

Gianessi, L.P., 2013. The increasing importance of herbicides in worldwide crop production. Pest Manag. Sci. 69(10), 1099-1105.

Gibbs, H., Ruesch, A.S., Achard, F., et al., 2010. Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. P Natl. Acad. Sci. USA 107, 16732-16737.

Glover, J.D., Reganold, J.P., Cox, C.M., 2012. Plant perennials to save Africa’s soils. Nature 489, 359-361.

Godfray, H.C.J., Beddington, J.R., Crute, I.R., et al., 2010. Food security: the challenge of feeding 9 billion people. Science 327, 812-818.

Gold, C.S., Altieri, M.A., Bellotti, A.C., 1989. The effects of intercropping and mixed varieties of predators and parasitoids of cassava whiteflies (Hemiptera: Aleyrodidae) in Colombia. Bull. Entomol. Res. 79, 115-121.

Gold, C.S., Altieri, M.A., Bellotti, A.C., 1990. Effects of intercropping and varietal mixtures on cassava hornworm, Erinnyis ello L. (Lepidoptera: Sphingidae), and the stemborer, Chilomima clarkei (Amsel) (Lepidoptera: Pyralidae), in Colombia. Trop. Pest Manage. 34 (4), 362–367.

Graziosi, I., Minato, N., Alvarez, E., et al., 2016. Emerging pests and diseases of South-east Asian cassava: a comprehensive evaluation of geographic priorities, management options and research needs. Pest Manag. Sci. 72(6), 1071-1089.

Gurr, G.M., Lu, Z.X., Zheng, X.S., et al., 2016. Multi-country evidence that crop diversification promotes ecological intensification of agriculture. Nature Plants 2, 16014.

Hiebsch, C.K., McCollum, R.F., 1987. Area×Time Equivalency Ratio: a method for evaluating the productivity of intercrops. Agron. J. 79, 15-22.

Hillocks, R.J., Thresh, J.M., Bellotti, A.C., 2001. Cassava biology, production and utilization. CAB International, Wallingford, UK.

Hought, J., Birch-Thomsen, T., Petersen, J., de Neergaard, A., Oelofse, M., 2012. Biofuels, land use change and smallholder livelihoods: A case study from Banteay Chhmar, Cambodia. Appl. Geogr. 34, 525-532.

Howeler, R.H., 2015. Sustainable cassava production in Asia for multiple uses and for multiple markets: Proceedings of the ninth regional workshop held in Nanning, Guangxi, China PR, 27 Nov-3 Dec 2011. 336 p. International Center for Tropical Agriculture, CIAT.

Howeler, R.H., Cadavid, L.F., Burckhardt, E., 1982. Response of cassava to VA mycorrhizal inoculation and phosphorus application in greenhouse and field experiments. Plant Soil 69, 327-339.

Howeler, R.H., Oates, C.G., Allem, A.C., 2000. Strategic environmental assessment. An assessment of the impact of cassava production and processing on the environment and biodiversity, vol. 5. FAO, IFAD.

Hulugalle, N.R., Ezumah, H.C., 1991. Effects of cassava-based cropping systems on physico-chemical properties of soil and earthworm casts in a tropical Alfisol. Agric. Ecosyst. Environ. 35, 55-63.

Jarvis, A., Ramirez-Villegas, J., Herrera Campo, B.V., et al., 2012. Is cassava the answer to African climate change adaptation? Trop. Plant Biol. 5, 9-29.

Kamau, J., Melis, R., Laing, M., et al., 2011. Farmers’ participatory selection for early bulking cassava genotypes in semi-arid Eastern Kenya. J. Plant Breed. Crop Sci. 3(3), 44-52.

Khan, Z.R., Ampong-Nyarko, K., Chiliswa, P., Hassanali, A., Kimani, S., Lwande, W., Overholt, W.A., Pickett, J.A., Smart, L.E., Woodcock, C.M. 1997. Intercropping increases parasitism of pests. Nature 388, 631-632.

Kremen, C., Miles, A., 2012. Ecosystem services in biologically diversified versus conventional farming systems: Benefits, externalities, and trade-offs. Ecol. Soc. 17, 40.

Lal, R. 2010. Managing soils for a warming earth in a food-insecure and energy-starved world. J. Plant Nutr. Soil Sci. 173, 4–15.

Lancaster, P.A., Ingram, J.S., Lim, M.Y., et al., 1982. Traditional cassava-based foods: survey of processing techniques. Econ. Bot. 36(1), 12-45.

Laurance, W.F., Sayer, J., Cassman, K.G., 2014. Agricultural expansion and its impacts on tropical nature. Trends Ecol. Evol. 29, 107-116.

Legg, J.P., Thresh, J.M., 2000. Cassava mosaic virus disease in East Africa: a dynamic disease in a changing environment. Virus Research, 71, 135-149.

Laurance, W.F., Sayer, J., Cassman, K.G., 2014. Agricultural expansion and its impacts on tropical nature. Trends Ecol. Evol. 29, 107-116.

Letourneau, D.K., Armbrecht, I., Salguero Rivera, B., et al., 2011. Does plant diversity benefit agro-ecosystems? A synthetic review. Ecol. Appl. 21, 9-21.

Lin, B.B., 2011. Resilience in agriculture through crop diversification: adaptive management for environmental change. BioScience 61, 183-193.

Lundgren, J.G., Fausti, S.W., 2015. Trading biodiversity for pest problems. Sci. Adv. 1(6), e1500558.

Makinde, E.A., Oluwatoyinbo, F.I., Ayoola, O.T. 2006. Intercropping and Crop Residue Incorporation: Effects on Soil Nutrient Status. J. Plant Nutr. 29, 235-244.

Malézieux, E., Crozat, Y., Dupraz, C., et al., 2009. Mixing plant species in cropping systems: concepts, tools and models. A review. Agron. Sustain. Dev. 29, 43-62.

MAPSPAM, 2016. http://mapspam.info/ (accessed 22.06.2016).

McKey, D., Emperaire, L., Élias, M., et al., 2001. Gestions locales et dynamiques régionales de la diversité variétale du manioc en Amazonie. Genet. Sel. Evol. 33, S465-S490.

Memmott, J., 2009. Food webs: a ladder for picking strawberries or a practical tool for practical problems? Phil. Trans. R. Soc. B 364(1524), 1693-1699.

Moench, M., 1991. Soil erosion under a successional agroforestry sequence: a case study from Idukki District, Kerala, India. Agroforest. Syst. 15, 31-50.

Mutsaers, H.J.W., Ezumah, H.C., Osiru, D.S.O., 1993. Cassava-based intercropping: a review. Field Crop Res. 34, 431-457.

NEPCon, 2014. Forest-land conversion and conversion timber estimates: Cambodia case study. Nature Ecology and People Consult (NEPCon), Copenhagen, Denmark.

Ngwira, A.R., Aune, J.B., Mkwinda, S. 2012. On-farm evaluation of yield and economic benefit of short term maize legume intercropping systems under conservation agriculture in Malawi. Field Crop Res. 132, 149-157.

Nicholls, C.I., Altieri, M.A., 2004. Designing species-rich, pest-suppressive agroecosystems through habitat management. Agronomy 43, 49-62.

Night, G., Asiimwe, P., Gashaka, G., et al., 2011. Occurrence and distribution of cassava pests and diseases in Rwanda. Agric. Ecosyst. Environ. 140, 492-497.

Norris, K., Asase, A., Collen, B., et al., 2010. Biodiversity in a forest-agriculture mosaic – The changing face of West African rainforests. Biol. Conserv. 143, 2341-2350.

Nwanze, K.F. 1982. Relationships between cassava root yields and crop infestations by the mealybug, Phenacoccus manihoti. Int. J. Pest Man., 28(1), 27-32.

Oliver, T.H., Heard, M.S., Isaac, N.J., et al., 2015. Biodiversity and resilience of ecosystem functions. Trends Ecol. Evol. 30, 673-684.

Olsen, K.M., Schaal, B.A. 1999. Evidence on the origin of cassava: phylogeography of *Manihot esculenta*. PNAS 96(10), 5586–5591.

Onzo, A., Hanna, R., Toko, M., 2014. Mix-planting pubescent and glabrous cassava affects abundance of *Typhlodromalus aripo* and its prey mite *Mononychellus tanajoa*. J. Appl. Entomol. 138, 297-306.

Philibert, A., Loyce, C., Makowski, D., 2012. Assessment of the quality of meta-analysis in agronomy. Agric. Ecosyst. Environ. 148, 72-82.

Pimentel, D., Harvey, C., Resosudarmo, P., Sinclair, K., Kurz, D., McNair, M., Crist, S., Shpritz, L., Fitton, L., Saffouri, R., Blair, R., 1995. Environmental and economic costs of soil erosion and conservation benefits. Science 267, 1117-1123.

Poppy, G.M., Chiotha, S., Eigenbrod, F., et al., 2014. Food security in a perfect storm: using the ecosystem services framework to increase understanding. Philos. T. R. Soc. B. 369(1639), 1-14.

Powlson, D.S., Gregory, P.J., Whalley, W.R., Quinton, J.N., Hopkins, D.W., Whitmore, A.P., Hirsch, P.R., Goulding, K.W.T., 2011. Soil management in relation to sustainable agriculture and ecosystem services. Food Policy 36, S72-S87.

Pypers, P., Sanginga, J.-M., Kasereka, B., et al. 2011. Increased productivity through integrated soil fertility management in cassava–legume intercropping systems in the highlands of Sud-Kivu, DR Congo. F. Crop Res. 120, 76–85.

Quinton, J.N., Govers, G., Van Oost, K., Bardgett, R.D., 2010. The impact of agricultural soil erosion on biogeochemical cycling. Nature Geosci. 3, 311-314.

Raudsepp-Hearne C., Peterson G.D., Bennett E.M., 2010. Ecosystem service bundles for analyzing tradeoffs in diverse landscapes. Proc. Natl. Acad. Sci. USA 107: 5242–7.

Reynolds, T.W., Waddington, S.R., Anderson, C.L., et al., 2015. Environmental impacts and constraints associated with the production of major food crops in Sub-Saharan Africa and South Asia. Food Security 7, 795-822.

Rohatgi, A., 2011. WebPlotDigitizer version 3.9.

Sayer, J., Cassman, K.G., 2013. Agricultural innovation to protect the environment. Proc. Natl. Acad. Sci. USA 110, 8345-8348.

Schulthess, F., Chabi-Olaye, A., Gounou, S., 2004. Multi-trophic level interactions in a cassava-maize mixed cropping system in the humid tropics of West Africa. Bull. Entomol. Res. 94, 261-272.

Sileshi, G., Akinnifesi, F.K., Ajayi, O.C., et al., 2008. Meta-analysis of maize yield response to woody and herbaceous legumes in sub-Saharan Africa. Plant Soil 307, 1-19.

TEEB, 2010. The Economics of Ecosystems and Biodiversity: Ecological and Economic Foundations. Taylor & Francis, Oxford, UK.

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M., Jeltsch, F., 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. J. Biogeogr. 31, 79-92.

Tittonell, P., Giller, K.E., 2013. When yield gaps are poverty traps: The paradigm of ecological intensification in African smallholder agriculture. Field Crop Res. 143, 76-90.

Toko, M., Yaninek, J.S., O’Neil, R.J., 1996. Response of *Mononychellus tanajoa* (Acari: Tetranychidae) to cropping systems, cultivars, and pest interventions. Environ. Entomol. 25, 237-49.

Tsay, J. S., Fukai, S., and Wilson, G. L. 1988. Effects of relative sowing time of soybean on growth and yield of cassava/soybean intercropping. F. Crop. Res. 19, 227–239.

Tscharntke, T., Clough, Y., Wanger, T.C., et al., 2012. Global food security, biodiversity conservation and the future of agricultural intensification. Biol. Conserv. 151(1), 53-9.

Valentin, C., Agus, F., Alamban, R., et al., 2008. Runoff and sediment losses from 27 upland catchments in Southeast Asia: impact of rapid land use changes and conservation practices. Agr. Ecosyst. Environ. 128, 225-238.

van Ittersum, M.K., van Bussel, L.G.J., Wolf, J., et al., 2016. Can sun-Saharan Africa feed itself? PNAS 113(52), 14964-14969.

Vandermeer, J.H., 1989. The ecology of intercropping (Cambridge University Press).

von Maltitz, G.P., Haywood, L., Mapako, M., Brent, A., 2009. Analysis of opportunities for biofuel production in sub-Saharan Africa. Environment brief. CIFOR, Bogor, Indonesia.

Vurro, M., Bonciani, B., Vannacci, G., 2010. Emerging infectious diseases of crop plants in developing countries: impact on agriculture and socio-economic consequences. Food Security 2, 113-132.

Waddington, S.R., Li, X., Dixon, J., et al., 2010. Getting the focus right: production constraints for six major food crops in Asian and African farming systems. Food Security 2(1), 27-48.

Wargiono, J., Widodo, Y., Hadi Utomo, W., 2000. Cassava agronomy research and adoption of improved practices in Indonesia – major achievements during the past 20 years. Cassava's Potential in the 21st Century: Present Situation and Future Research and Development Needs. 6th Regional Workshop, eds. Howeler, R., Tan, S. International Center for Tropical Agriculture, CIAT.

Willey, R.W., Osiru, D.S.O. 1972. Studies on mixtures of maize and beans (*Phaseolus vulgaris*) with particular reference to plant population. J. Agri. Sci. 79, 517-529.

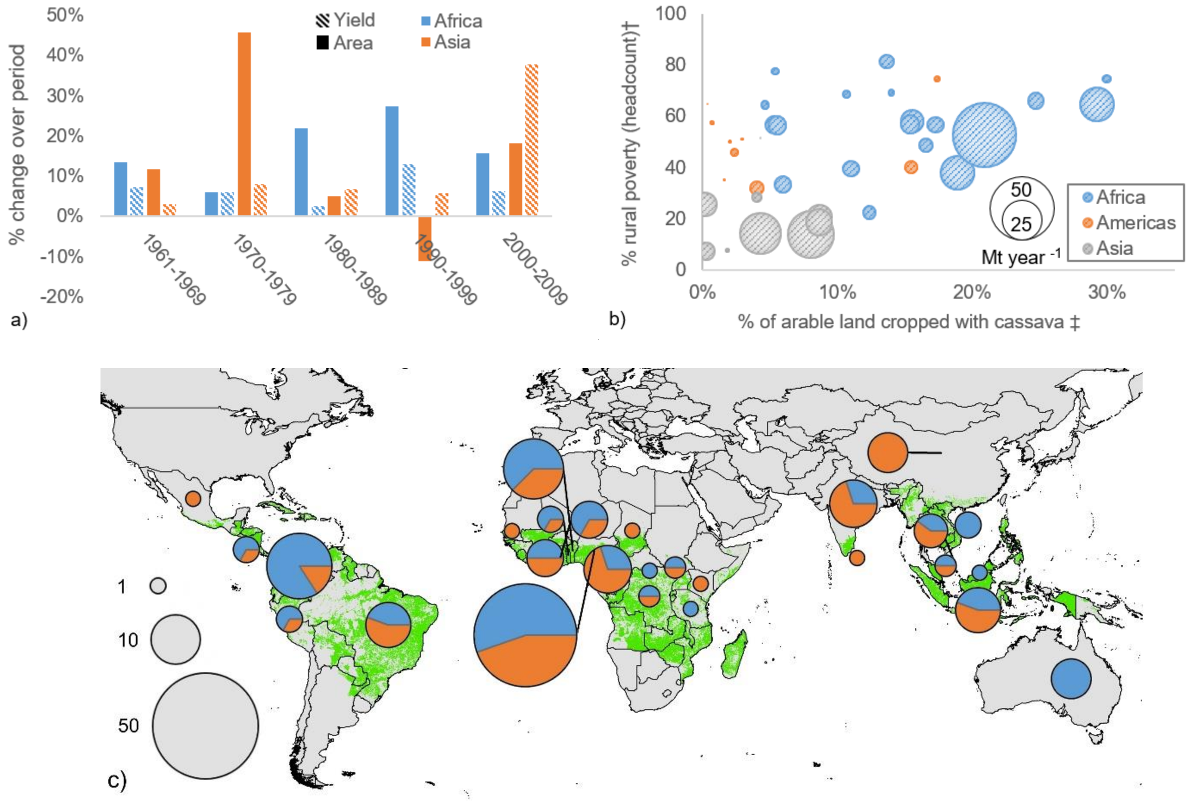
Wood, S.A., Karp, D.S., DeClerck, F., Kremen, C., Naeem, S., Palm, C.A., 2015. Functional traits in agriculture: agrobiodiversity and ecosystem services. Trends Ecol. Evol. 30(9), 531-539.

Wyckhuys, K.A.G., Burra, D.D., Tran, D.H. et al. 2017a. Soil fertility regulates invasive herbivore performance and top-down control in tropical agro-ecosystems of Southeast Asia. Agric. Ecosyst. Environ 249, 38–49.

Wyckhuys, K.A.G., Graziosi, I., Burra, D.D., Walter, A.J. 2017b. Phytoplasma infection of a tropical root crop triggers bottom-up cascades by favoring generalist over specialist herbivores. PLoS ONE 12(8): e0182766.

Zhou, A., Thomson, E., 2009. The development of biofuels in Asia. Appl. Energ. 86, S11-S20.

# Figures



† World Bank, Global Poverty Working Group. Rural poverty headcount at national poverty lines. Accessed June 2015. http://data.worldbank.org/

‡Calculated from 2014 cassava area data (FAOSTAT, 2016) total agricultural area (FAO, electronic files and web site), online table at http://wdi.worldbank.org/table/3. 'Arable land' using FAO definition.

Figure 1. Trends in cassava production and research: cassava production has intensified over the past 5 decades, both in terms of area and yield (a). Countries across the developing-world tropics have a high degree of dependence on cassava in their agricultural systems and high levels of rural poverty as seen in (b) where each bubble represents a single country (FAOSTAT, 2016). Studies on cassava intercropping originate from a wide geographic area (c). The green backdrop indicates harvested cassava area in 2014 (MAPSPAM, 2016), while bubble size indicates total number of studies and blue segments indicate the proportion selected for final ecosystem services analysis.

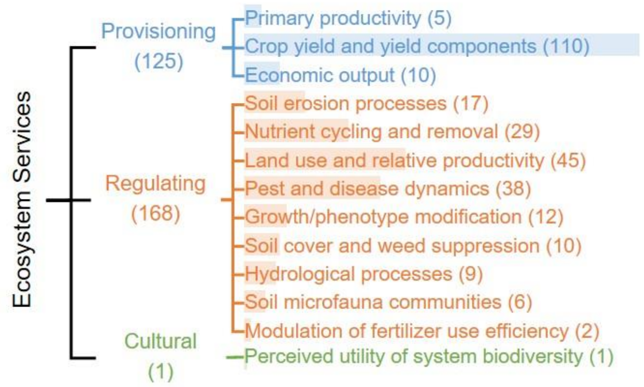


Figure 2. Categories of ecosystem services investigated by cassava intercropping literature. Numbers in brackets indicate the overall number of studies identified. Complete list of references available in online supplementary material.

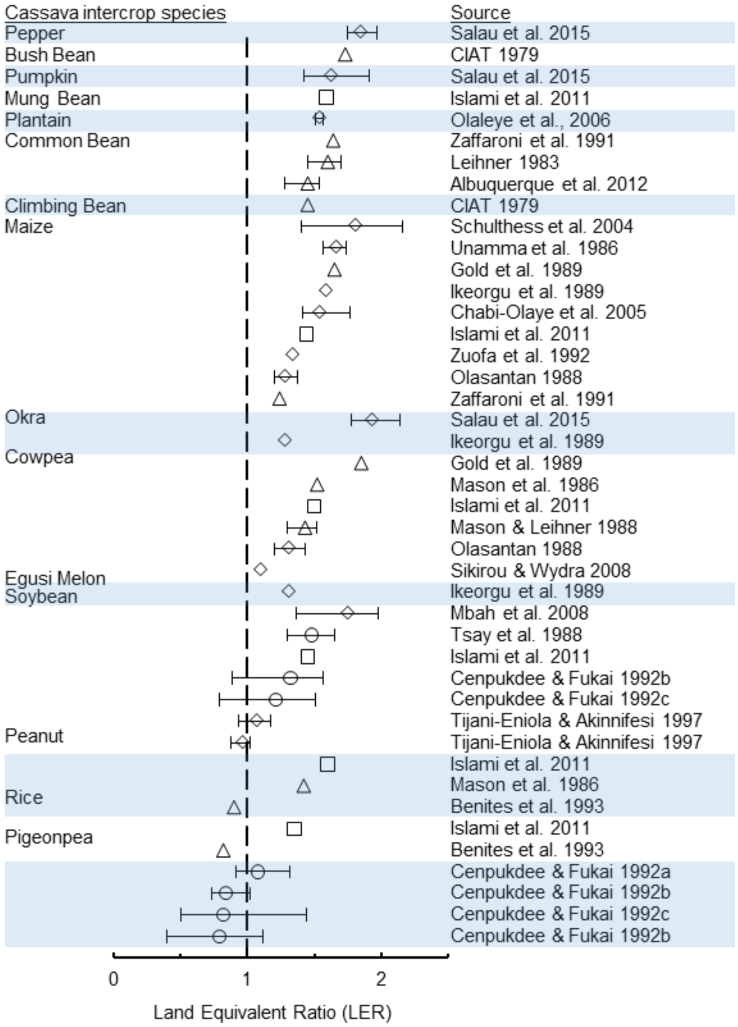


Figure 3. Land Equivalent Ratios of 2-crop combinations reported in cassava intercropping literature. Diamond-Africa, Square-Asia, Triangle-Americas, Circle-Oceania/Pacific. Horizontal bars indicate ranges for studies reporting multiple values. In cases where the intercropping arrangement was kept constant but another variable varied (for example, fertilizer application rate or management scheme), the range is represented by horizontal bars. Results from separate experiments within a given study are represented as separate points. For multi-year studies, values were averaged over the whole study period.

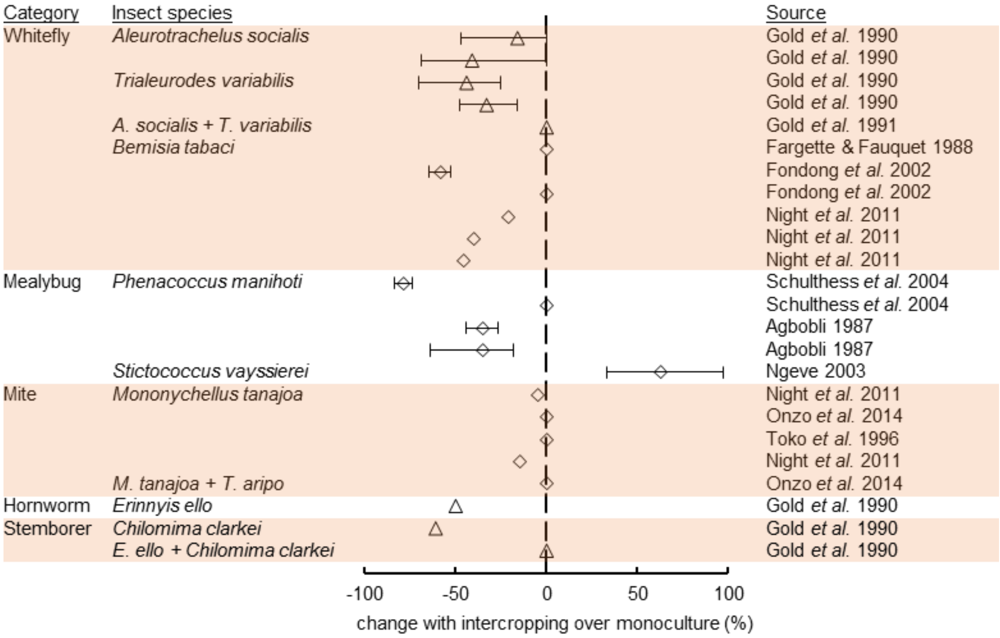


Figure 4. Means and ranges of effects on pest indicators reported in cassava intercropping literature relative to their respective monoculture controls. Nonsignificant results are located on the median line and horizontal bars indicate ranges found in studies with multiple means reported. Studies that contained separate 'experiments' are presented as separate points. Diamond-Africa, Square-Asia, Triangle-Americas, Circle-Oceania/Pacific.

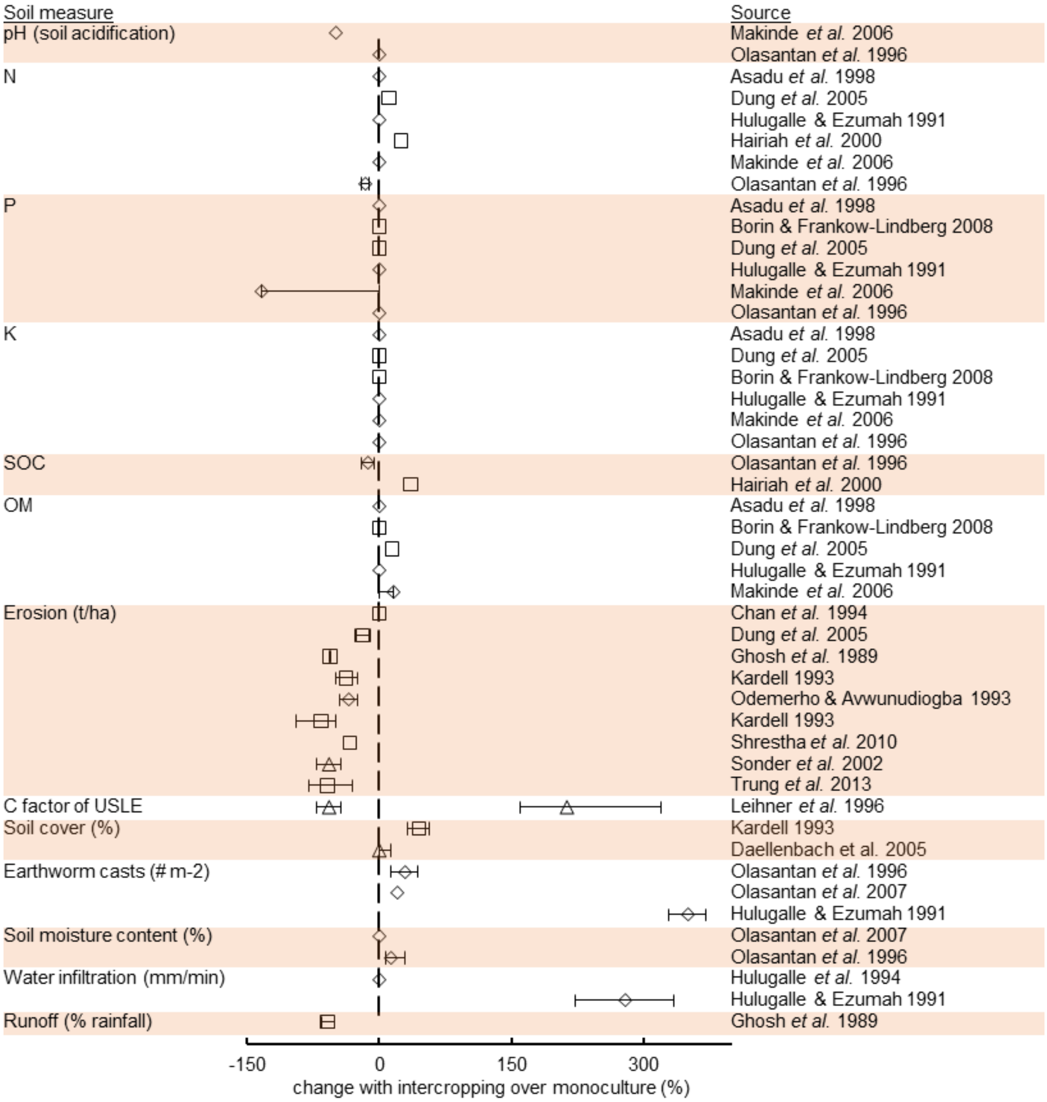


Figure 5. Means and ranges of effects on soil and water indicators reported in cassava intercropping literature relative to their respective monoculture controls. pH is measured as the percentage difference in acidification of soils under monoculture and intercrop, with negative percentages indicating that intercropping leads to less acidic soil for this particular study. SOC= Soil organic carbon, OM=Organic matter, C factor of USLE= crop management factor of universal soil loss equation. Cover % indicates percentage of total soil coverage achieved. Nonsignificant results are located on the median line and horizontal bars indicate ranges found in studies with multiple means reported. Diamond-Africa, Square-Asia, Triangle-Americas, Circle-Oceania/Pacific.

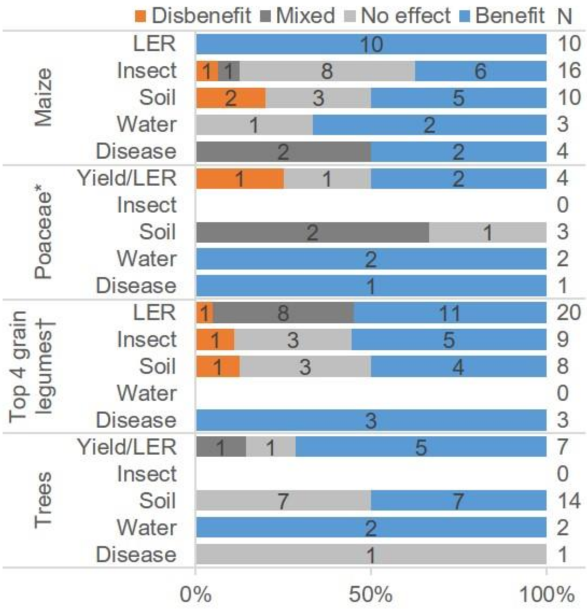


Figure 6. Vote-count of study findings for key ecosystem services and key intercrop species in cassava. Numbers on bars indicate number of studies, N= total studies evaluated for each trait/crop combination. *Poaceae excepting maize, †Soybean, peanut, cowpea, and pigeonpea.