

POLLINATOR DIVERSITY

Mutually beneficial pollinator diversity and crop yield outcomes in small and large farms

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Ecological intensification, or the improvement of crop yield through enhancement of biodiversity, may be a sustainable pathway toward greater food supplies. Such sustainable increases may be especially important for the 2 billion people reliant on small farms, many of which are undernourished, yet we know little about the efficacy of this approach. Using a coordinated protocol across regions and crops, we quantify to what degree enhancing pollinator density and richness can improve yields on 344 fields from 33 pollinator-dependent crop systems in small and large farms from Africa, Asia, and Latin America. For fields less than 2 hectares, we found that yield gaps could be closed by a median of 24% through higher flower-visitor density. For larger fields, such benefits only occurred at high flower-visitor richness. Worldwide, our study demonstrates that ecological intensification can create synchronous biodiversity and yield outcomes.

More than 2 billion people are reliant on smallholder agriculture (farms with less than 2 ha) in developing nations, representing 83% of the global agricultural population (1, 2). In such countries, human population is growing faster than in developed nations, while many of the rural inhabitants are poor, undernourished, and live in conditions where the environment is either degraded or being degraded (2–4). As a result, improving the livelihoods of smallholders through higher and more stable crop yields, while minimizing negative environmental impacts, is essential for achieving global food security and poverty reduction (3, 5). Ecosystem services enhanced through biodiversity (such as nutrient cycling, biotic pollination, or pest control) can replace, complement, or interact synergistically with external inputs (such as fertilizers, introduction of pollinator colonies, and pesticides) and should create mutually beneficial environmental and food-supply scenarios (6, 7). Despite advocacy for such “ecological” intensification (6–8), its effectiveness in small versus large holdings is largely unknown. Moreover, smallholding crop systems in developing countries have been largely neglected in ecosystem-services research (2, 4).

Yield gaps, defined here as the difference in crop yield between high- and low-yielding farms of a given crop system (Fig. 1), are pervasive for small holdings in many developing countries (7–9). This definition of yield gaps is particularly relevant for smallholders, as the attainable yields in field trials and research centers usually result

from applying different technologies (e.g., nutrients provided as manure in crop-livestock smallholding systems versus synthetic fertilizers used in large monocultures in research centers) (3, 7). Such empirical estimates of attainable yields are more conservative than modeled potential yields (10), but they are likely achievable with current technology (9). Indeed, the marginal returns from additional inputs can make modeled potential yields nonprofitable for farmers (9). Yield gaps can be partially closed through the provision of optimal amounts and quality of resources, such as water, nutrients, and pollen (9, 11). Although fruit or seed set of many crops relies on wild pollinators (12), management for improved pollination services is uncommon in these systems (13), likely contributing to yield gaps globally (11). Indeed, pollination has been neglected even in studies analyzing the continental or global drivers of yield gaps (5, 7, 9, 10). Pollinator deficits may be more relevant than before, as (i) other resources (e.g., nutrients) are increasingly provided (e.g., fertilizers) to crops (6, 8); (ii) cultivated area of pollinator-dependent crops is expanding more rapidly than the area of pollinator-independent crops (11); (iii) cultivated area of pollinator-dependent crops is also expanding more rapidly than the stock of managed honey bee colonies (14); and (iv) populations of wild pollinators are increasingly threatened (15, 16). Furthermore, pollinator-dependent crops provide essential micronutrients to humans in those regions of the world where micronutrient deficiencies are common (4). To date, it is uncertain to

what degree local populations of pollinators need to be enhanced (“flower-visitor density gap”), and how much of the yield gaps (kg ha^{-1}) can be closed by such management (Fig. 1).

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We recorded flower-visitor density, flower-visitor richness, and crop yield in 344 fields of 33 crop systems across small and large holdings in Africa, Asia, and Latin America (figs. S1 and S2). To avoid the limitations of different methodologies, and considering the global nature of our focus, we performed coordinated experiments (17) over a 5-year period (2010–2014)—a collaborative approach that encompassed large geographic ranges involving a standardized protocol. This sampling protocol (18) used fields with contrasting flower-visitor density and richness

not confounded with management variables other than the ones that were employed to influence flower-visitor assemblages (table S1). Therefore, crop systems are defined as a crop species in a particular year and region subject to similar management, except for flower-visitor density and richness (table S1). Following this protocol (18), flower-visitor density was measured by scan sampling a fixed number of open floral units (hereafter “flowers”) in each of four subplots in each field, on at least four dates during the main flowering period (19). Flower-visitor spe-

cies richness was measured by netting all visitors of crop flowers along six 25-m-long and 2-m-wide transects for herbaceous crops (or six pairs of adjacent trees for orchard crops). Crop yield was measured by harvesting all the fruits or seeds of 5 to 10 entire plants (kg plant^{-1}) and then multiplying those values by plant density (plants ha^{-1}), or by harvesting 1 to 5 m^2 , according to the crop (18). Crop yield ($\log_{10} \text{kg ha}^{-1}$) was analyzed through (hierarchical) mixed-effects models with fields nested within crop systems. Fixed effects were flower-visitor density (number of visitors in

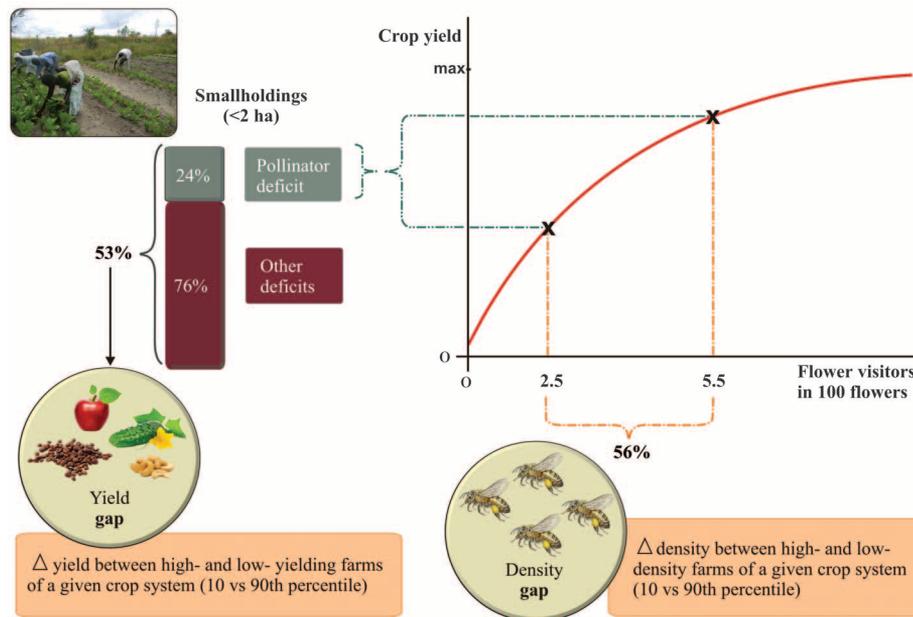


Fig. 1. Pollinator deficit is defined here as the amount of yield gap that can be accounted by closing flower-visitor density gap. Worldwide, for <2-ha fields, our study shows that yield gaps could be closed by a median of 24% (mean = 31%) through higher flower-visitor density (table S2). For larger fields, such a level of yield benefits only occurred if they sustained high flower-visitor richness (Fig. 2). Although the relation between crop yield and flower-visitor density is expected to be positive but asymptotic (11), our study supports a linear relation, demonstrating that the highest levels of flower-visitor density observed around the world are still at nonsaturating values.

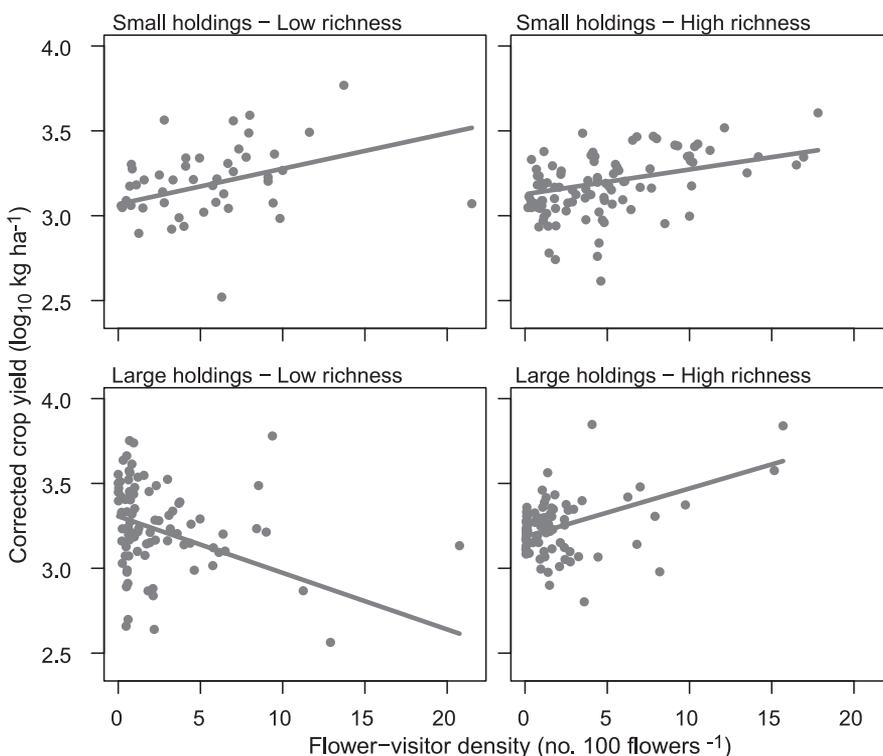


Fig. 2. Worldwide, the benefits of flower-visitor density to crop yield are greater for smaller than larger holdings, and when flower-visitor richness is higher. Moreover, high richness can compensate this negative influence of field size. Each point is a field within a crop system; lines are the fixed-effect predictions from the best hierarchical model without covariables. Small (<2 ha) versus large holdings, and low (<3 species) versus high richness, are categories only for graphical purposes, while the model considers field size and species richness as quantitative variables. By using the same protocol, we could express density as number of visitors in 100 crop flowers, avoiding standardizations to integrate results from different crop systems. Because yield (kg ha^{-1}) is harvested in different magnitudes for different crop species (e.g., coffee versus tomatoes), we present the crop yield after subtracting the random intercept for each crop system.

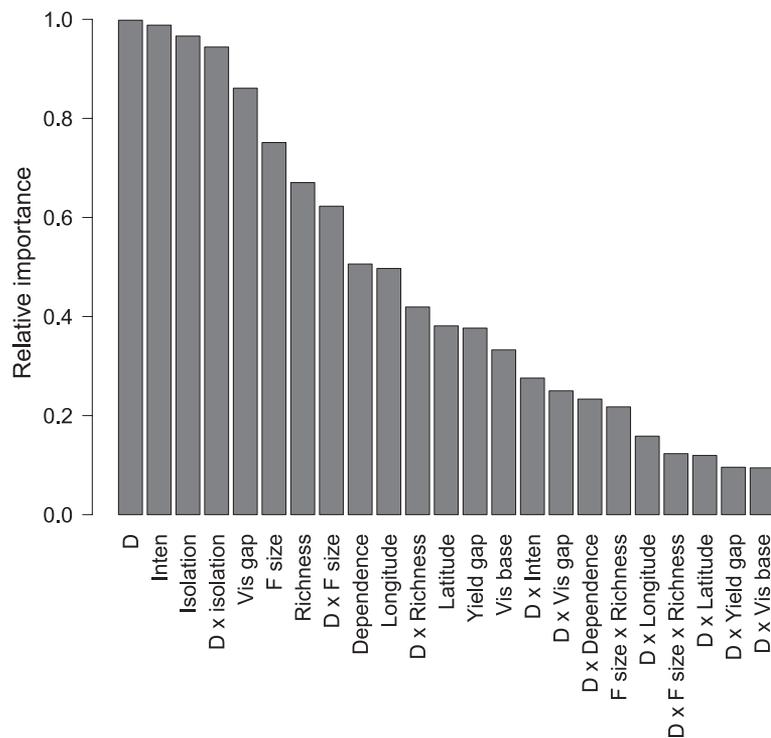


Fig. 3. Flower-visitor density (D) was the most important predictor of crop yield for pollinator-dependent crops globally. The relative importance is the sum of the Akaike information criterion weights of the models with each predictor. Inten, level of conventional intensification; Isolation, distance to seminatural or natural areas; Vis gap, magnitude of flower-visitor gap; F size, field size; Richness, flower-visitor richness; Dependence, crop pollinator dependence; Vis base, baseline level of flower-visitor density.

100 crop flowers), flower-visitor richness (number of species per field in 30 min of net sampling), field size (\log_{10} ha), and their interactions (19). Random effects were intercepts and slopes for each crop system for the relation between crop yield and flower-visitor density and richness. Although our focus was on developing countries, research partners from Norway followed the same protocol in three crop systems, and their data were included in the analyses for comprehensiveness.

Globally, yield gaps were large and common across fields in each crop system (Fig. 1 and table S2). Crop yield in low-yielding fields (10th percentile) was, on average, only 47% of the value in high-yielding fields (90th percentile; see table S2 for kg ha^{-1}). Differences in flower-visitor density (i.e., flower-visitor density gaps) were similarly large (Fig. 1 and table S2). The fields with low flower-visitor density (10th percentile: 2.5 flower visitors in 100 flowers on average across crop systems) had only 44% of the individuals of the fields with high values (90th percentile: 5.5 flower visitors in 100 flowers on average across crop systems). These results indicate that even for crops of a given variety planted within a particular region and year, and managed similarly, there are large opportunities to increase flower-visitor densities and yields to the values of the best farms (90th percentile).

The effects of flower-visitor density on crop yield were largely influenced by field size (which ranged from 0.1 to 327.2 ha in our study) and flower-visitor richness (which ranged from 0 to 11 species in our study), as reflected by a three-

way interaction (Fig. 2 and table S3). For small-holdings worldwide, crop yield increased linearly with flower-visitor density, suggesting that inadequate pollination quantity and/or quality is partly responsible for yield gaps (11, 20). These benefits were irrespective of flower-visitor richness. In contrast, for larger holdings, the benefits of flower-visitor density on crop yield were greater in fields with higher flower-visitor richness (Fig. 2 and table S3). Therefore, greater flower-visitor richness could compensate the negative influence that field size had on the relationship (slope) between crop yield and flower-visitor density. For example, in fields with only one flower-visitor species, the increase in crop yield per unit of flower-visitor density was 106% higher for fields of 2 ha than for those of 20 ha. However, this difference was reduced to only 16% when four flower-visitor species were present. Globally, our results suggest that the effectiveness of ecological intensification (represented here by flower-visitor density) differs between small and large holdings, being greater for small holdings and when species richness is enhanced.

To test if these results could be explained by environmental and management aspects that covary with flower-visitor density, flower-visitor richness, or field size (table S1), we added to the previous mixed-effects model the following fixed effects: level of conventional intensification (a quantitative index based on the presence of monocultures, synthetic fertilizers, herbicides, pesticides, and fungicides) (19); isolation from seminatural

or natural habitats (\log_{10} km); crop pollinator dependence (%); latitude (decimal degrees); longitude (decimal degrees); baseline level of flower-visitor density (10th percentile: number per 100 flowers); magnitude of yield gap (%); magnitude of flower-visitor gap (%); and the two-way interactions between each of these covariables and flower-visitor density (19). The best-fitting model (i.e., lower corrected Akaike's information criterion, AICc) (19) was then derived from evaluation of all possible combinations of predictors and covariables, including a model without predictors. The influences of flower-visitor density, flower-visitor richness, field size, and their interactions were still included as predictors of crop yield in the best model, in addition to the intensification level, isolation from natural habitats, and flower-visitor gap (table S3). Importantly, fixed-effect values (and standard errors) for these predictors were of similar magnitude in the models with and without covariables (table S3), reflecting their independent contribution from the covariables in predicting crop yield [see also VIF (variance inflation factor) values in table S3]. The sum of the AICc weights of all the models for each predictor and covariable was used as an estimate of its relative importance (19). Notably, among all the variables we tested, flower-visitor density was the most important predictor of crop yield (Fig. 3). As expected (21), the level of conventional intensification was an important predictor of crop yield (Fig. 3), showing a positive relation (table S3). Crop yield decreased with isolation from natural habitats, and more so when flower-visitor density was lower (table S3). Worldwide, our data show that effects of flower-visitor density, flower-visitor richness, and field size are highly relevant in the context of, and not confounded by, other environmental and management variables affecting crop yield.

Our best-fitting model (table S3) allows the estimation of the degree to which yield gaps (kg ha^{-1}) can be closed by enhancing local populations of flower visitors for a given field size and several other key management and environmental covariables (note the high coefficient of determination, R^2 , of 0.97 in table S3). In fields of less than 2 ha, the enhancement of flower-visitor density in fields with the lowest values (10th percentile) to those of the best fields (90th percentile) should close yield gaps by a median of 24% (Fig. 1 and table S2). The remaining 76% of the yield gap may be partially closed by technologies oriented to the optimal provision and efficient use of other resources (e.g., radiation, nutrients, water), including sowing date, plant density, genetic material, conservation agriculture, and integrated pest management, among many others (5–7, 9, 10). In contrast, for larger fields, such level of yield benefits from enhancement of flower-visitor density occurs only if these fields have high flower-visitor richness (Fig. 2 and table S2). In our study, the influences of field size were not confounded by several important environmental and management variables affecting crop yield (table S3). Lower benefits from flower-visitor density in larger fields may reflect the fact that they are only

pollinated by flower visitors with large foraging ranges, which are usually generalist species, such as honey bees (12). In accordance with this hypothesis, we found greater dominance of *Apis* spp. in larger holdings regardless of species richness (fig. S3), and that flower-visitor density effects were enhanced when richness increased in large fields (Fig. 2). Such synergistic influences among pollinator species on crop yield (kg ha^{-1}) are likely due to different nonexclusive mechanisms (22), including pollination niche complementarity (23, 24), interspecific interactions (25, 26), or raising the chances of providing effective pollinator species (i.e., sampling effects of biodiversity) (27, 28).

Pollinator deficits have been neglected from previous global or continental yield gap analyses (5, 7, 9, 10). However, here we found that they are responsible to a large degree for yield gaps of pollinator-dependent crops in small holdings (Fig. 1 and table S2), even after considering several environmental and management predictors of crop yield (Fig. 3). Indeed, flower-visitor density was the most important predictor of crop yield. Closing flower-visitor density gaps is a realistic objective, as our figures are based on the densities observed in real-world farms (i.e., the difference between the 90th and 10th percentiles). Unfortunately, recent studies suggest that flower-visitor assemblages in agroecosystems are increasingly threatened because of declining floral abundance and diversity, as well as increasing exposure to pesticides and parasites (15, 16). Such trends can be reversed by a combination of practices, the effectiveness of which is context dependent, including sowing flower strips and planting hedgerows, providing nesting resources, more targeted use of pesticides, and/or restoration of seminatural and natural areas adjacent to crops (table S1) (13, 29).

Enhancing smallholder livelihoods through greater crop yields while reducing negative environmental impacts from agriculture is one of the greatest challenges for humanity (3, 5). Moreover, from a food-security point of view, pollinator-dependent crops provide essential micronutrients to human health where needed (4). Our data indicate that the effectiveness of ecological intensification through pollination services was greater for small, rather than large, holdings. Using pollination services as a case study, we demonstrated that ecological intensification can create mutually beneficial scenarios between biodiversity and crop yields worldwide.

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SUPPLEMENTARY MATERIALS

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Materials and Methods
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Database S1

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SMALL RNAS

Biogenesis and function of tRNA fragments during sperm maturation and fertilization in mammals

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Several recent studies link parental environments to phenotypes in subsequent generations. In this work, we investigate the mechanism by which paternal diet affects offspring metabolism. Protein restriction in mice affects small RNA (sRNA) levels in mature sperm, with decreased let-7 levels and increased amounts of 5' fragments of glycine transfer RNAs (tRNAs). In testicular sperm, tRNA fragments are scarce but increase in abundance as sperm mature in the epididymis. Epididymosomes (vesicles that fuse with sperm during epididymal transit) carry RNA payloads matching those of mature sperm and can deliver RNAs to immature sperm *in vitro*. Functionally, tRNA-glycine-GCC fragments repress genes associated with the endogenous retroelement MERVL, in both embryonic stem cells and embryos. Our results shed light on sRNA biogenesis and its dietary regulation during posttesticular sperm maturation, and they also link tRNA fragments to regulation of endogenous retroelements active in the preimplantation embryo.

Accumulating evidence indicates that parental environments can affect the health of offspring. For example, paternal nutrition influences offspring metabolism in mammals (1). Our prior published work showed that male mice consuming a low-protein diet

fathered offspring exhibiting altered hepatic cholesterol biosynthesis, relative to the offspring of control males (2). The mechanisms by which paternal conditions reprogram offspring phenotype remain elusive, as males can influence offspring via the sperm epigenome, microbiome

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More-diverse pollinators improve crop yields

It is known that increased pollinator diversity can improve the yield of agricultural crops. However, how best to both produce food and maintain diversity is still debated. Garibaldi *et al.* show that on small farms, which provide food for the most vulnerable populations globally, pollinator diversity can significantly increase productivity. Thus, the management of crops and surrounding areas for ecological health is likely to benefit both wild pollinator populations and farmers.

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