Global growth and stability of agricultural yield decrease with pollinator dependence

Lucas A. Garibaldi[a,b,1], Marcelo A. Aizen[a], Alexandra M. Klein[c], Saul A. Cunningham[d], and Lawrence D. Harder[e]

[a]Laboratorio de Ecotono, Instituto de Investigaciones en Biodiversidad y Medioambiente-Consejo Nacional de Investigaciones Científicas y Técnicas de Argentina and Centro Regional Universitario Bariloche-Universidad Nacional del Comahue, 8400 Bariloche, Río Negro, Argentina; [b]Departamento de Métodos Cuantitativos y Sistemas de Información, Facultad de Agronomía, Universidad de Buenos Aires, 1417 Buenos Aires, Argentina; [c]Institute of Ecology, Ecosystem Functions Section, Leuphana University of Lüneburg, 21335 Lüneburg, Germany; [d]Commonwealth Scientific and Industrial Research Organization Ecosystem Sciences, Canberra, ACT 2601, Australia; and [e]Department of Biological Sciences, University of Calgary, AB, Canada T2N 1N4

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Human welfare depends on the amount and stability of agricultural production, as determined by crop yield and cultivated area. Yield increases asymptotically with the resources provided by farmers' inputs and environmentally sensitive ecosystem services. Declining yield growth with increased inputs prompts conversion of more land to cultivation, but at the risk of eroding ecosystem services. To explore the interdependence of agricultural production and its stability on ecosystem services, we present and test a general graphical model, based on Jensen's inequality, of yield–resource relations and consider implications for land conversion. For the case of animal pollination as a resource influencing crop yield, this model predicts that incomplete and variable pollen delivery reduces yield mean and stability (inverse of variability) more for crops with greater dependence on pollinators. Data collected by the Food and Agriculture Organization of the United Nations during 1961–2008 support these predictions. Specifically, crops with greater pollinator dependence had lower mean and stability in relative yield and yield growth, despite global yield increases for most crops. Lower yield growth was compensated by increased land cultivation to enhance production of pollinator-dependent crops. Area stability also decreased with pollinator dependence, as it correlated positively with yield stability among crops. These results reveal that pollen limitation hinders yield growth of pollinator-dependent crops, decreasing temporal stability of global agricultural production, while promoting compensatory land conversion to agriculture. Although we examined crop pollination, our model applies to other ecosystem services for which the benefits to human welfare decelerate as the maximum is approached.

diminishing returns | environmental degradation | global pollination crisis | food security | land use change

Exponential growth of the human population imposes major challenges for meeting increasing global demand for diverse nutritional diets, despite worsening environmental degradation. During the last 50 y, the human population increased 128% from 3.0 to 6.9 billion people (1), whereas cultivated area and crop yield increased globally by 33% and 57%, respectively (2). Concomitantly, natural habitat cover decreased (3–5), and global stocks and flows of water (6), nutrients (7), and pollinators (8, 9) were altered, reducing the capacity of many ecosystem services to support human activity (3, 10). Such environmental degradation can constrain the amount and stability of crop yield, which are essential components of human food security (11). Low stability (i.e., high interannual variation) causes unpredictable food shortages, which impact human health and survival, and also threatens farmers' livelihoods (11). However, the consequences of variation in ecosystem services for both average agricultural output and its stability have received little attention.

The fundamental challenges for agricultural production are evident from various aspects of the generalized relation of yield (production ha^{-1}) to the availability of "resources," such as water, nutrients, and pollen (Fig. 1). According to this model, some minimum resource availability is required to support any yield, and increased availability above this threshold improves yield asymptotically (12, 13) (although excess resource availability, e.g., flooding, can diminish yield, we focus on the more common effects of resource scarcity). The details of this relation reflect both intrinsic biological properties of the crop and extrinsic abiotic and biotic features of the environment that govern yield. For many crops, two general resource sources contribute to realized yield: an "ecosystem service" (14) available naturally (Fig. 1, black lines); and an anthropogenic component supplied agriculturally (Fig. 1, gray lines). Human inputs supplement the resources available naturally, and this underlying ecosystem service varies among systems. Within this context, environmental degradation can impact yield by reducing naturally available resources ($-\Delta$ in Fig. 1*A*; e.g., soil depletion) and/or maximal yield capacity (Δ in Fig. 1*B*; e.g., invasive weeds or herbivores), which may be mitigated by increased subsidies (e.g., fertilizers and pesticides, respectively), genetic "improvement" (e.g., artificial selection for resource efficiency and genetic engineering of Bt toxin, respectively), and/or modified agricultural practices (e.g., precision agriculture, intercropping). Alternatively, because production is the product of yield and cultivated area and yield improvement decreases with increasing resource augmentation (Fig. 1), the effects of environmental degradation may be compensated agriculturally by conversion of more area to cultivation. However, increased cultivation could aggravate environmental degradation (15–17), creating positive feedback that encourages further agricultural intensification.

This characterization of the resource dependence of yield (Y) also reveals likely consequences of annual resource variability on the mean and stability of yield. If yield improvement decelerates with increased resource input, a "good" year with resource conditions Δ units above the long-term average ($+\Delta$ in Fig. 1*A*) improves yield less than it is reduced during a "bad" year with resource conditions Δ units below average ($-\Delta$ in Fig. 1*A*). In addition to the direct consequences of such resource variability in reducing yield stability, this asymmetrical response reduces the average yield over years (Fig. 1*A*, $\bar{Y}$) compared with that expected if resource availability was constant at the long-term average (Fig. 1*A*, horizontal solid line), a general result known as Jensen's (18) inequality (19). The decrease in $\bar{Y}$ and variability in Y depend positively on resource variability. Furthermore, because yield varies asymptotically with resource availability, these effects depend on average resource availability, being more severe when resources are limited. Similar effects arise from spatial variation, whereby Jensen's inequality reduces average yield below that expected from the average resource input. Given such relations, when anthropogenic degradation reduces mean re-

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[1]To whom correspondence should be addressed. E-mail: garibald@agro.uba.ar.

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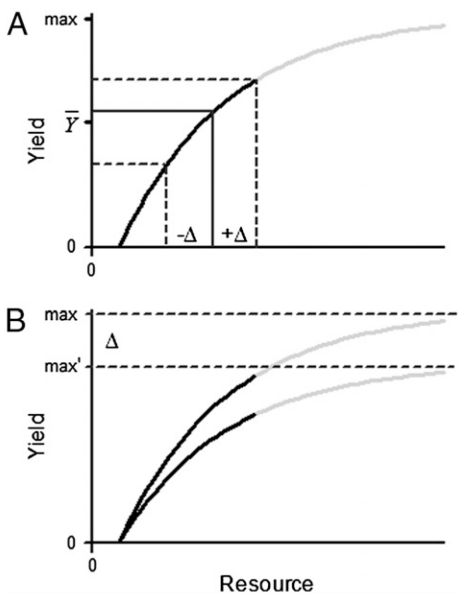

Fig. 1. General relations of yield (production area^{-1}) to environmental (black lines) and anthropogenic (gray lines) resource availability and the effects of (*A*) resource variability and (*B*) altered maximum yield (*max*).

source availability and/or increases its spatial and temporal variability, it will also reduce the contribution of ecosystem services to yield mean and stability.

Here we provide evidence, based on data from the Food and Agriculture Organization (FAO) of the United Nations (*Materials and Methods*), for this view of the dependence of agricultural production and its stability on ecosystem services, focusing on animal pollination as a resource influencing production of seed and fruit crops. Approximately 70% of 1,330 tropical crops (20) and 85% of 264 crops cultivated in Europe (21) benefit from animal pollination. Furthermore, pollinators can increase the production of ≈75% of the 115 most important crops worldwide, as measured by food production (15, 22) and economic value (23). Not surprisingly, given its relevance to production of the human food supply, the value of the ecosystem service provided by pollinators has been subject to heated debate by scientists and public media (22–28). We developed the conceptual framework described above to help structure such discussion and clarify expectations. This framework applies directly to agricultural pollination, because fecundity of flowering plants varies asymptotically with pollen receipt, as depicted in Fig. 1 (29–31). In addition, the extensive variation among crops in their dependence on vector-mediated pollination, especially that provided by flower-visiting animals (22), allows assessment of more specific predictions of this hypothesis concerning yield and its stability.

Pollination as an Ecosystem Service

Unlike crop interaction with weeds, herbivores, pathogens, and their vectors, which are usually highly regulated by agricultural practices, crop pollination is often subject to little direct management and so is provided almost entirely as an ecosystem service. Biotic pollination of most crops relies on wild pollinators and managed honey bees (20–22, 32); however, the abundance and diversity of wild pollinators are declining in many regions (9, 33, 34), raising concern that pollination shortage is limiting crop yields (9, 25, 26). For example, the diversity of wild pollinators and pollinator visitation rate to crop flowers commonly decline with distance from natural or seminatural habitats (35).

Managed honey bees (*Apis mellifera*) have long provided partial independence from wild pollinators for some crops (20–22, 32). The number of managed hives continues to grow globally (8), but this growth does not imply that agricultural production is not pollen limited for three reasons. First, the demand for agricultural pollination services grows increasingly relative to the supply, because cultivation of pollinator-dependent crops outpaces growth in the global stock of domesticated honey bees (8). Second, honeybee numbers have increased unevenly among countries, with strong growth in major honey-producing countries, such as Argentina, China, and Spain, but declines elsewhere, including the United States, Britain, and many western European countries (8, 36). Pollination occurs locally, so this heterogeneity likely has uneven consequences for agricultural pollination among (and within) countries. Finally, in most countries, except the United States (32), honey bees are raised primarily to produce honey, in which case their ancillary agricultural role as pollinators is more of an ecosystem service than an intentional agricultural input.

Importantly, pollination shortage (i.e., limitation of crop yield by incomplete pollination) could even constrain yield of highly pollinator-dependent crops in the absence of any "pollination crisis" (i.e., temporally increasing pollen limitation due to recent decreases in biotic pollination; *SI Text: Does the FAO Dataset Provide Evidence of a Global Pollination Crisis?* and Fig. S1*A*). Highly productive crops flower intensively for brief periods (20, 37), so that resident pollinator communities may not satisfy requirements for ovule fertilization. Indeed, pollination shortage occurs frequently even in nondegraded pollinator communities and natural ecosystems (38), just as crops can be nutrient limited in nondegraded soils (12).

Specific Model and Predictions

Crops differ greatly in the degree to which animal pollination improves yield (22), from pollinator-independent crops, such as obligate wind- or self-pollinated cereals and species cultivated for vegetative parts, to those for which animal pollination is essential, such as melon, kiwi, papaya, Brazil nut, and cocoa. Most fruit and seed crops lie between these extremes (22). In general, a crop can be classified as *x%* dependent on animal pollination according to the yield reduction caused by pollinator exclusion compared with the asymptotic yield (*max*, Fig. 1*A*) resulting from hand pollination or management of adequate pollinator numbers (Fig. 2*A*). Consideration of only the ecosystem service provided by animal pollination reveals that the direct impact of a given change in this service on yield should vary positively with pollinator dependence (Fig. 2 *B* and *C*, *SI Text: Model Simulations*, and Fig. S2). Similarly, variation in animal pollination should reduce average yield (via Jensen's inequality) and yield stability most for pollinator-dependent crops. These effects will tend to limit the magnitude and consistency of yield improvement associated with agronomic advances unrelated to pollination (i.e., improvements that increase the asymptotic yield from max′ to max in Fig. 1*B*). This model of variable and incomplete pollen delivery predicts that compared with crops with low pollinator dependence, crops with greater pollinator dependence exhibit (*i*) lower mean relative yield and slower yield growth; (*ii*) higher temporal coefficient of variation (CV) (i.e., less stability) in yield and yield growth; and (*iii*) faster growth in cultivated area to compensate lower yield growth. Furthermore, as a result of area compensation (*iv*) the mean and CV of production (and production growth) vary less with pollinator dependence than do yield or area alone.

Results and Discussion

Pollination Dependence and Yield Variation. In agreement with prediction *i*, crops with greater pollinator dependence had lower relative yield than less-dependent crops (Fig. 3*A*), suggesting greater deficit between realized and maximal (*max*, Fig. 1*A*) yield caused by pollen limitation (Fig. 2). Overall, crop yield (Mt ha^{-1}) increased by an average of 1.3% year^{-1} (Fig. 3*B*; see also ref. 39), reflecting agronomic advances since 1961. Among countries, yield growth of pollinator-independent and -dependent crops varied positively (Spearman's correlation, $r_s = 0.517$, $P < 0.001$, $n = 80$ countries), probably reflecting differences in environmental and economic conditions, agricultural policies, and farmers' education. Yield grew significantly (i.e., >1) for all pollinator-dependence classes; however, yield improvement weakened with increasing dependence on pollinators (prediction *i*) for all but the six crops for

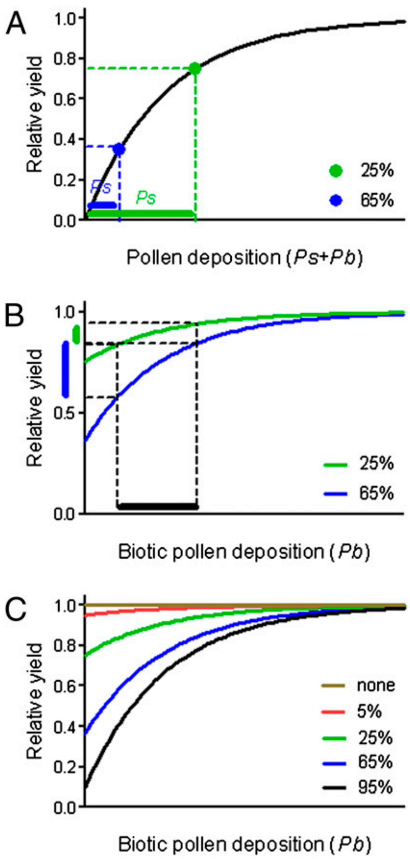

Fig. 2. General relations of relative yield (seeds ha^{-1}/maximum yield) to either total pollen receipt by stigmas (*A*) or pollen receipt caused by animal pollination (*Pb*: *B* and *C*). *A* and *B* show two examples of plants differing in pollinator dependence (i.e., percent reduction in seed production in the absence of biotic pollination). In *A*, the bars denote the total self- and abiotic pollination (*Ps*) that causes 25% (green) and 65% (blue) pollinator dependence, respectively. *B* illustrates both higher and more stable yield for a given range of variation in biotic pollination (black bar) if a plant has 25% pollinator dependence (green bar) than if it has 65% dependence (blue bar). *C* illustrates the variation in relative yield associated with the entire range of biotic pollination for crops in five pollinator-dependence classes.

which animal pollination is essential [Fig. 3*B*; previous analyses contrasting pollinator-independent crops with -dependent crops as a group found little difference (28, 39) because of heterogeneity among crops with different dependence (40)].

Yield stability (Fig. 4*A*) and the consistency of yield growth (Figs. 4*B* and 5) decreased (i.e., increased CV) with increasing pollinator dependence, in accord with prediction *ii*. The yield CV for crops with high dependence on animal pollination is twice that of pollinator-independent crops (13.2% vs. 6.6%), suggesting that interannual variation in pollination service causes approximately half of the yield instability for dependent crops. These results are consistent with observations of interannual variation in pollen limitation for many wild plant species (38) and provide the most direct evidence of pollen limitation in animal-pollinated crops available in the FAO data. Furthermore, these results imply that Jensen's inequality contributes to the negative relation between mean yield and pollinator dependence (Fig. 3*A*). That consistency in yield growth also declines with increasing pollinator dependence (Figs. 4*B* and 5) further indicates that pollination variability contributes to the limited yield improvement of crops that rely on animal pollination (Fig. 3*B*).

Area Compensation for Changes in Crop Yield. Cultivation of more land can compensate for reduced production owing to pollen limitation of yield (15–17). As expected from the negative effect of pollinator dependence on yield growth (Fig. 3*B*; prediction *iii*), cultivated area generally expanded faster for more-dependent crops (Fig. 6*A*) (39), but again the six most dependent crops were exceptions (Fig. 6*A*) (40). Similarly, the greater acceleration of yield with increasing pollinator dependence correlated with greater deceleration in cultivated area (*SI Text*: *Does the FAO Dataset Provide Evidence of a Global Pollination Crisis?* and Fig. S1*B*). On average, crops from all pollinator-dependence classes showed negative yield-area correlations (Fig. 6*B*), but compensation was stronger for crops with greater pollinator dependence (Fig. 6*B*), indicating greater need to mitigate lower yield im-

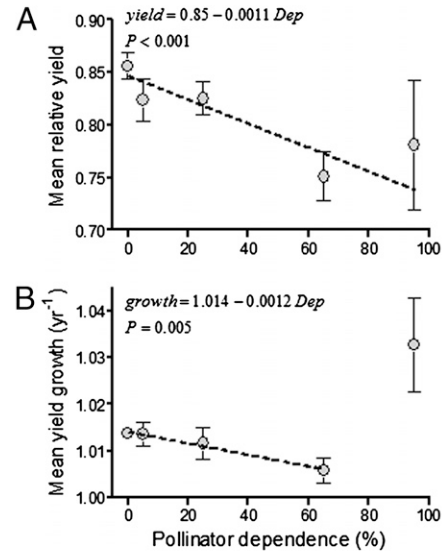

Fig. 3. Global trends in (*A*) mean (±SE) relative yield (detrended yield in year *t*/detrended maximum yield) and (*B*) mean annual yield growth (yield ratio for consecutive years: Y_t/Y_{t-1}) between 1961 and 2008 for 99 crops categorized by pollinator dependence. Dashed lines depict linear regressions based on individual crops.

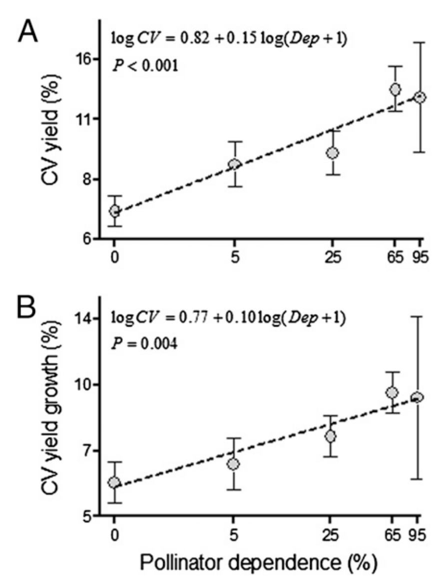

Fig. 4. Global trends in mean (±SE) temporal stability of (*A*) crop yield and (*B*) yield growth, as measured by the coefficients of annual variation (CV) of detrended data between 1961 and 2008 for 99 crops differing in pollinator dependence. Dashed lines depict linear regressions based on individual crops (note the $\log_{10}$ scaling of both axes).

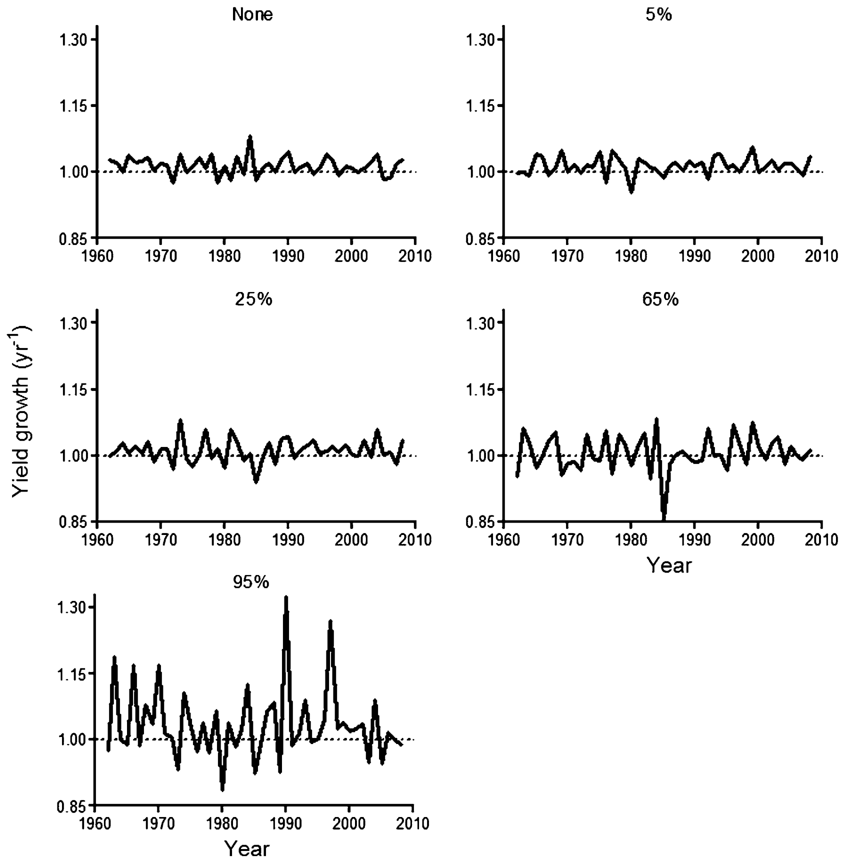

Fig. 5. Global temporal trends in mean yield growth between 1961 and 2008 for 99 crops categorized by pollinator dependence.

provement. Mean production growth also increased with pollinator dependence (Fig. 6*C*) but not as strongly as crop area (Fig. 6*A*), as expected from yield-area compensation (prediction *iv*). Because yield improvement decelerates with resource addition (Fig. 1*A*), labor and/or economic costs of adding resources when yield is almost maximized are more likely to exceed the benefit obtained from increased yield. Therefore, cultivation of more land may provide a more rewarding tactic in the short term, despite negative consequences in the longer term. Yield can also be improved by increasing the yield maximum (Fig. 1*B*), so compensation by cultivation should be more intense for crops with slower yield growth, an expectation supported by our results.

Temporal stability in agricultural production depends on the consistency of both yield and cultivated area (prediction *iv*). In general, CVs for yield and cultivated area correlate positively among crops (Pearson's $r = 0.53$, $P < 0.001$, $n = 99$ crops), as do CVs for yield and production ($r = 0.45$, $P < 0.001$, $n = 99$ crops). The former result is expected from the within-crop correlations between yield and area (Fig. 6*B*), whereas the latter reflects production being the product of area and yield (41). Furthermore, pollinator dependence positively influences CVs of cultivated area [$\log CV = 0.92 + 0.10\log(Dep + 1), P = 0.004$], yield (Fig. 4*A*), and overall production [$\log CV = 1.09 + 0.045\log(Dep + 1), P = 0.12$], but the latter trend is weak, as expected from yield-area compensation (prediction *iv*). Similar patterns exist between interannual growth in yield and cultivated area ($r = 0.70$, $P < 0.001$, $n = 99$ crops) and production ($r = 0.89$, $P < 0.001$, $n = 99$ crops) and among pollinator dependence classes (Figs. 4*B* and 6*D*). Production growth of crops with greater pollinator dependence was less stable (Fig. 6*E*), but this variation was smaller than CVs of yield (Fig. 4*B*) or area (Fig. 6*D*) alone (prediction *iv*).

Recent trends in crop cultivation also foreshadow aggravated pollination shortages in the future. The area cultivated with pollinator-dependent crops doubled from 1961 to 2008, whereas cultivation of pollinator-independent crops changed little (Fig. S3) (15, 39). Continuation of such growth necessarily increases demand for pollination services. However, the global stock of domesticated honey bees grew slower than the area cultivated with pollinator-dependent crops (8). Furthermore, ongoing deforestation and land degradation (3–5) are expected to hasten declines in the abundance and diversity of wild pollinators (9, 24). The increasing disparity between agricultural demand for pollination and the capacity of managed and wild pollinators to deliver this service warns that current agricultural practices cannot sustain growth in the production of pollinator-dependent crops.

Possible Alternative Explanations. Crop performance depends on both ecosystem services and human inputs, so the observed associations may reflect economic and sociological aspects of agriculture unrelated to pollinator dependence. To assess this possibility, we now consider the apparent impacts of several human factors on yield and cultivated area.

The observed yield trends may reflect application of less effort to yield improvement of pollinator-dependent crops, because they are economically less important. For example, (log) global cultivated area during 2008 varied negatively with increasing pollinator dependence ($t_{97} = 3.4$, $P = 0.001$), reflecting a parallel trend in importance in the human diet. However, yield growth did not vary significantly with cultivated area after accounting for pollinator dependence ($t_{90} = 1.8$, $P > 0.05$) and yield growth declines with increasing pollinator dependence, regardless of whether cultivated area is included as a covariate ($t_{90} = 2.4$, $P = 0.015$). In addition, prices of pollinator-dependent crops average five times higher than those of nondependent crops (23), so agricultural inputs (e.g., fertilizers, herbicides, pesticides) are not expected to be lower than in pollinator-independent crops. Thus, the negative relation of yield improvement to pollinator dependence is more likely a consequence of greater constraints on

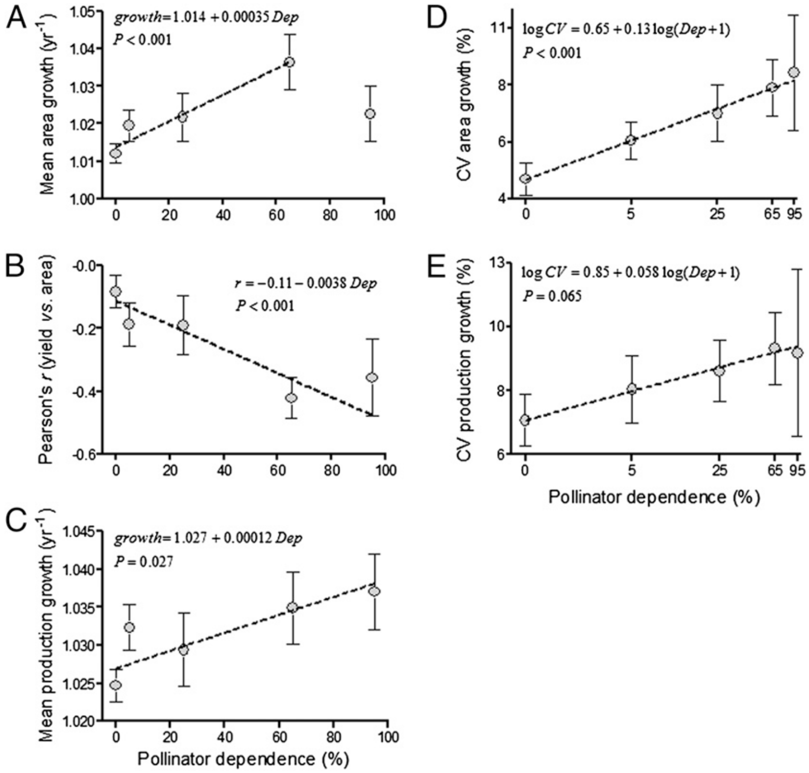

Fig. 6. Global trends in the mean (±SE) growth and temporal stability of crop area (*A* and *D*, respectively) and production (*C* and *E*, respectively) between 1961 and 2008 for 99 crops differing in pollinator dependence and the relation of the correlation between detrended yield and area growth to pollinator dependence during the same period (*B*). Dashed lines depict linear regressions based on individual crops (in *A* the six crops for which animal pollination is essential were excluded from the regression analysis). Note the $\log_{10}$ scaling of both axes in *D* and *E*.

the capacity for yield improvement, whether by altered growing regimes or genetic development, caused by pollen limitation associated with pollinator dependence.

Paradoxically, this explanation is also supported by the strong yield improvement shown by the six crops for which animal pollination is essential, namely (*i*) Brazil nut, (*ii*) watermelon, (*iii*) cantaloupe, (*iv*) pumpkin, squash, gourd, marrow, and zucchini, (*v*) cocoa, and (*vi*) vanilla. Their exceptional yield growth (Fig. 3*B*) likely reflects more intensive pollination management (40) than is applied for less pollinator-dependent crops. Vanilla is produced commercially by hand pollination (20, 42), and cucurbits are frequently pollinated by managed bees in large-scale production (33, 43). Cocoa is frequently managed in agroforestry systems that usually provide habitat for their pollinating midges (20, 44), and Brazil nuts are harvested only in seminatural forests where pollinators are available. In these cases, new agricultural methods and varieties could improve yield while pollination management reduces the influence of insufficient pollination as a yield constraint. This interpretation implies that more attention to pollination management for crops that depend moderately on animal pollination could amplify the success of other yield-improvement innovations.

Changes in cultivated area may also reflect fluctuations in prices and production costs, among other factors; however, this explanation for the positive relation of growth in cultivated area to pollinator dependence is not supported by commodity price dynamics. For example, for Argentina, Brazil, China, India, the Russian Federation, and the United States which together accounted for 48% of the area cultivated globally in 2007 (2) the prices paid to producers did not grow differently among pollinator-dependence categories for a representative set of crops (Fig. S4), except for the Russian Federation during 1993-2007. In the latter case, price increases (Fig. S4) were consistent with global growth in cultivated area (Fig. 6*A*); however, this country modified its agricultural sector substantially after the collapse of the Soviet Union during the early 1990s (e.g., ref. 45). On the other hand, agreement of our results (Figs. 3–6) and four predictions supports the key role of dependence on an ecosystem service.

Final Remarks. The mean and variance in the delivery of ecosystem services influence the mean and stability of agricultural productivity. Although we used biotic pollination to illustrate our framework for interpreting this influence, the underlying principles are not process specific, so it should apply generally to ecosystem services that have a decelerating influence on the productivity of managed biological systems.

Our findings for agricultural pollination indicate that greater reliance on an ecosystem service reduces the stability of productivity and the capacity for production improvement through enhanced management practices unrelated to the service. Specifically, the lower growth and stability in yield of crops with greater pollinator dependence from 1961 to 2008 may have motivated the disproportionate increase in their cultivated areas. The consequences of such effects may be of long standing, because they may have guided plant domestication and development of some crops as staple food sources and others as complementary components of the human diet. As a result of this history, ≈70% of agricultural area grows crops with no dependence on pollinators (Fig. S3), and the expected direct reduction of total agricultural production in the absence of animal pollination ranges from only 3% to 8% (15).

Historically, demand for increased crop production has been satisfied by expansion of cultivated area and yield improvements through genetic innovation, increased external inputs (e.g., fertilizers, herbicides, pesticides), and new agricultural practices. However, this combination of approaches imposes tradeoffs for agricultural production, such as between cultivated area and habitat for wild bees, between pesticide application and pollinator health, and between monoculture and diversified resources for pollinators (20, 46). Because yield growth and stability vary negatively with pollinator dependence, yield and its improvement should benefit considerably from more active management of wild pollinators and their habitats, the use of honey bees as pollinators rather than as honey producers, and increased application of other managed pollinators for specific crops. Such practices would weaken the feedback between environment quality and crop productivity, as the resulting improved yield may alleviate the need for increased cultivation.

Materials and Methods

We tested our predictions (Fig. 2) with data collected annually from 1961 to 2008 by the FAO concerning crop yield, cultivated area, and production, which we analyzed at a global scale. Our analysis considered 99 crops that accounted for 95% of global cultivated area during 2008 (2). Each crop was categorized following Klein et al. (22) into one of five pollinator-dependence classes: none (no yield reduction without pollinators, 39 crops), little (yield reduction without pollinators >0 but <10%, 20 crops), modest (10–39% reduction, 16 crops), considerable (40–89% reduction, 18 crops), and essential (≥90% reduction, 6 crops). For each crop we estimated mean relative yield as the average ratio of annual yield (Y_t) to the maximum yield observed during the analysis period (*max*, Fig. 1*A*). We removed long-term trends by analyzing the residuals from linear regressions of yield on year for each crop. We also calculated annual yield growth (y^{-1}) as the average ratio of yield for consecutive years ($Y_t/Y_{t\text{-}1}$). To quantify temporal stability in yield and yield growth, we estimated the among-year CV of residuals for each crop: a large CV represents low stability (47). The same analyses were performed for crop area and production. Statistical assumptions were satisfied in all cases [in some cases after suitable transformation (Figs. 4 and 6)].

Because the data were collected independently by member countries of the FAO, they may be subject to considerable variation, owing to different collection methods and intensity among countries and years, but this variation probably has limited impact on the patterns we observed for several reasons. First, reporting errors or biases from particular countries should have little influence, because we used a global analysis, summing production or area for each crop over all countries (yield is the ratio of total production to total area). Second, we considered many (99) diverse crops over a long period (48 y) and used relative data for each crop, which further homogenizes the effect of reporting inconsistencies. Finally, for reporting difficulties to affect our results, biases would have to vary with pollinator dependence in a manner that paralleled the four predictions that we tested. The improbability of such correspondence lends confidence that the observed patterns reflect the influence of pollinator dependence on crop performance.

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