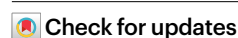


The productivity–stability trade-off in global food systems

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Historically, humans have managed food systems to maximize productivity. This pursuit has drastically modified terrestrial and aquatic ecosystems globally by reducing species diversity and body size while creating very productive, yet homogenized, environments. Such changes alter the structure and function of ecosystems in ways that ultimately erode their stability. This productivity–stability trade-off has largely been ignored in discussions around global food security. Here, we synthesize empirical and theoretical literature to demonstrate the existence of the productivity–stability trade-off and argue the need for its explicit incorporation in the sustainable management of food systems. We first explore the history of human management of food systems, its impacts on average body size within and across species and food web stability. We then demonstrate how reductions in body size are symptomatic of a broader biotic homogenization and rewiring of food webs. We show how this biotic homogenization decompartmentalizes interactions among energy channels and increases energy flux within the food web in ways that threaten their stability. We end by synthesizing large-scale ecological studies to demonstrate the prevalence of the productivity–stability trade-off. We conclude that management strategies promoting landscape heterogeneity and maintenance of key food web structures are critical to sustainable food production.

Agricultural production has historically pursued a high-growth, high-yield model to feed a growing human population^{1–3}. At the coarsest level, this has occurred by replacing slower growing forests or more diverse grasslands with simplified ecosystems (monocultures) of smaller, rapidly growing and shorter-lived (annual), edible plants^{4,5}. Although greater food yields from monocultures make sense from a productive capacity perspective, potential systemic trade-offs are seldom considered⁶. Creation of widespread monocultures through deforestation is argued to be a leading contributor to global biodiversity decline⁷, suggesting fundamental changes in

ecosystem biostructure (the composition and interaction structure of ecosystems⁸) both on fields and their adjacent lands. Diversity generates increased weak interactions (energy fluxes) in food webs that contribute to their overall resilience⁹. Simplified lower-diversity systems with increased average interaction strengths are primed for explosions of inedible and/or destructive populations such as diseases and pests, where such rapid exponential growth is a hallmark of instability (Box 1).

Furthermore, the productive efficiency of crop systems has been amplified in the past century with the widespread adoption of inorganic

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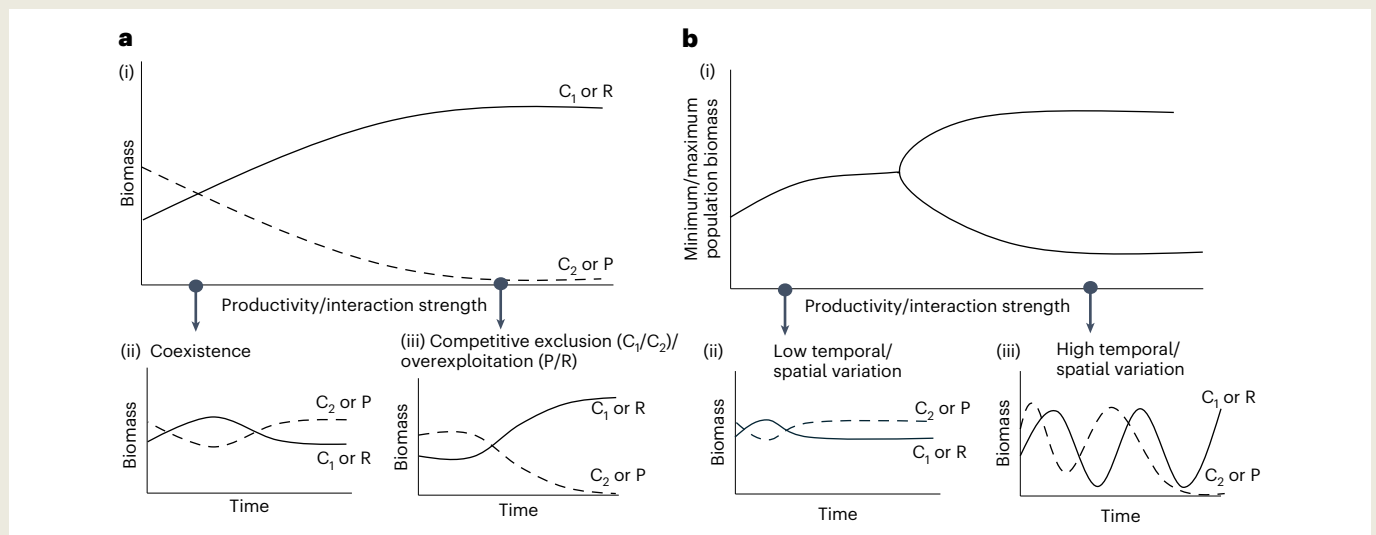
BOX 1

Defining stability: mean and variance-driven stability loss

Here, we define instability in two forms, mean-driven and variance-driven instability, which broadly capture two general forms of stability loss in theoretical models and can be easily applied in empirical systems. Broadly speaking, in ecosystem models, local species extinctions indicate a loss of the interior equilibrium such that the system no longer persists as is, due to mean-driven and/or variance-driven stability loss processes⁹⁰. Mean-driven instability is characterized as substantial declines in mean population density through mechanisms such as competitive exclusion and overexploitation, that ultimately leads to local extinction⁹⁰ (Box 1 Fig. a). Notably, theoretical work has shown that these mechanisms are more likely with increasing productivity^{12,75,173}. For example, increasing fisheries productivity (that is, higher rates of fish removal to increase yields) has led to overexploitation and resulted in dramatic declines and collapses of key large-bodied predatory fish species^{30,67,174}, in turn driving trophic cascades that result in population explosions of small, faster growing species that can outcompete slower growing species and cause subsequent further species loss through competitive exclusion^{175,176}. Conversely, variance-driven instability is characterized by increasing oscillatory dynamics that necessarily imply that a population or community will attain low densities and increase risk of local extinction⁹⁰ (Box 1 Fig. b). This idea originates from Rosenzweig's paradox of enrichment, in which increasing carrying capacity, a metric of productivity, tends to alter the structure of consumer–resource interactions in ways that drive

wildly oscillating population dynamics (through a Hopf bifurcation¹¹; Box 1 Fig. b(i)). Since these early ideas, both theoretical and empirical work have documented evidence of such variance-driven instability across space and/or time and at different levels of biological organization (for example, populations and communities) through further mechanisms, such as increasing growth rates and increasing population synchrony^{73,74,104,105}. For example, in this paper, we show, through historical pollen analysis, how increasing agricultural productivity resulted in significant increases in temporal variation of plant community dynamics. Overall, the above losses in stability alter ecosystem biostructures and whole energy flows in ways that ultimately result in unstable ecosystems that are more vulnerable to further perturbations, which, in the context of food production, indicate a serious threat to food security.

Empirically, mean-driven stability loss and variance-driven stability loss can be identified using metrics such as the coefficient of variation (CV, s.d./mean), changes in population size across space/time and evidence of species loss (for example, through loss of diversity). CV can capture both mean and variance-driven instability as increasing CV can result from large increases in the underlying variation (s.d.) or through reductions in mean densities (mean-driven instability). In general, increasing CV is an indication of stability loss; however, it must be partitioned into its component parts to fully elucidate the mechanism driving alterations in population/community dynamics.



Box Fig. 1 | Conceptual representation of mean and variance-driven instability. a, b. Conceptual representation of biomass dynamics of predator–prey interactions (predator P/resource R) or competitive interactions (competing species C₁/C₂) across gradients of productivity/interaction strength and associated time series under mean-driven instability (a) and variance-driven instability (b). The bifurcation diagram in b(i) shows local minima and maxima of a population's (P/R/C₁/C₂) depending on interaction) biomass dynamics (in which a solid line indicates a stable equilibrium), indicating a transition from a stable equilibrium to oscillatory dynamics (a Hopf bifurcation) across gradient of productivity/interaction strength.

fertilizers, altering nutrient cycling and agro-ecosystem metabolism^{3,10}. More than 50 years ago, ecologists argued that the change in nutrient dynamics with the liberal application of inorganic nutrients to foster increased productivity precipitates stability loss through the generation of destructive oscillations in population dynamics (Box 1)¹¹. Similarly, ecologists have also shown that high productivity can drive

instability from competitive exclusion, especially at local scales^{12,13}. The increasing need and use of fertilizers and pesticides to maintain food production¹⁴ in these unstable systems hint at the underlying costs associated with eroded ecosystem stability. Given that these analyses demonstrate the potential existence of a productivity–stability trade-off and the costs associated with managing such a trade-off, it

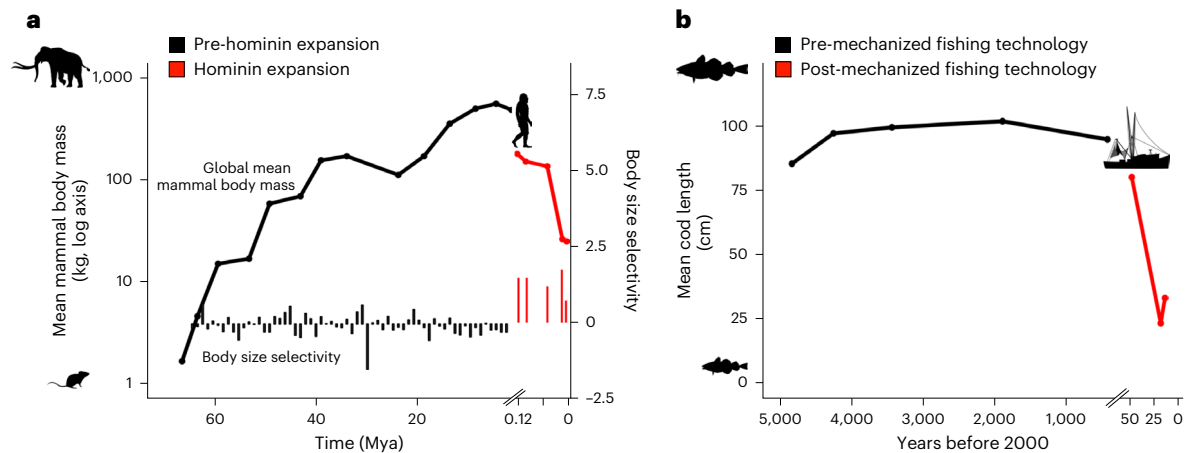


Fig. 1 | Historic trends in terrestrial mammal and Atlantic cod body size.

a. Global mean terrestrial mammal body size and hominin body size selectivity from 65 million years ago (Mya) to present. Black line indicates change in global mean mammal body mass and selectivity before hominin expansion and red line indicates change in body size and selectivity following expansion of hominins out of Africa 125,000 years ago. Data were extracted and adapted from ref. 28. **b.** Mean body length of Atlantic cod from kelp forests in the coastal Gulf of Maine

over the last 5,000 years. Black line indicates change in mean cod length before the onset of mechanized fishing and red line indicates trends in body size after the onset of mechanized fishing. Data were extracted and adapted from ref. 30. Credit: Animal silhouettes obtained from PhyloPic under a Creative Commons CC0.1.0 Universal licence; fishing boat silhouette obtained from rawpixel under a Creative Commons CC0.1.0 Universal licence.

is concerning that this phenomenon is little considered in discussions around global food production and security.

While food production has historically altered average community composition towards smaller and more productive plant species on land, the human drive for food has also altered body size distributions indirectly in commercially harvested aquatic ecosystems by tending to preferentially harvest larger-bodied species/individuals^{15–17}. Larger species/individuals typically have lower growth rates and are, therefore, unable to withstand the high mortality associated with commercial harvesting, in turn driving selection for smaller, faster growing individuals within and across species^{17,18}. As a result, this kind of harvesting has driven skewed losses of large species and concomitant increases in smaller-bodied species, an example of shifting biostructure. Long-standing empirical allometric observations have shown that decreases in average community body size coincide with increases in maximum per capita population growth rates (r), an effect that theory predicts generally ought to destabilize the whole ecosystem^{19,20}. More recent arguments from marine fisheries have shown that collections of several stressors, including terrestrial run-off (nutrients) and climate change, contribute to a rise in high-growth-rate life-history strategies²¹. The overall result is that fisheries are on a similar trajectory as agriculture in that we observe reduced fish body size within populations and whole communities, leaving behind smaller, faster growing, more productive species (and thus a more productive community)²² that alter aquatic ecosystem biostructure in ways that are predicted to be destabilizing²³.

Here, we synthesize empirical and theoretical findings to demonstrate the existence, consequence and potential mitigation of the productivity–stability trade-off in food production systems, both past and present. First, we explore historical patterns in agricultural production and wild animal harvest using long-term fossil, fishery and pollen time series records to show that both body and plant size reductions are common in food-producing ecosystems. We also show how agriculture not only transitioned precipitously from trees to smaller plants but also simultaneously to decreased stability, as shown by increased variability in plant pollen dynamics. Towards developing a full understanding of how food production impacts ecosystems, we then review the empirical literature to show that food production has consistently altered ecosystem biostructure, resulting in rewired food webs²⁴. This rewiring occurs as food production collectively reduces diversity, organism size and trophic position, while simultaneously

homogenizing spatial structure, resulting in simplified food webs dominated by fewer energy channels with increased average interaction strengths (energy fluxes from resources to consumers²⁵). We synthesize existing theory that suggests that these structural changes tend to decrease stability. Finally, we synthesize empirical studies of food production systems across large spatiotemporal gradients to show how increasing food production intensity (for example, fishing pressure and agricultural intensity) drives losses of stability of surrounding ecosystems through changes in biostructure.

The need to provide food security, end hunger and maintain sustainable development of food are part of the calls to action of the UN Sustainable Development Goals (SDGs)²⁶ and we argue that to meet these goals it is critical to recognize the fundamental trade-off between productivity and stability. Ecosystem structure, function and dynamics (stability) are inextricably inter-related, yet we tend to ignore this when developing solutions towards increasing the resilience of food systems²⁷. The productivity–stability trade-off we demonstrate here reveals the need for a different and broader framework of action to address the relevant SDGs.

A brief history of food production and stability

There is a long agricultural and food harvesting history from both terrestrial and aquatic environments that has driven the replacement of large slow-growing species with smaller faster growing species^{2,28} (Fig. 1). Terrestrial fossil records, for example, indicate that, as hominins swept across the globe in the Late Quaternary, a dramatic global downgrading of mammal body size resulted²⁸ (with a truncation of more than two orders of magnitude, Fig. 1a). This process was precipitous and markedly different from the pre-hominin Cenozoic era (Fig. 1a)²⁸, suggesting that a growing hominid population and the use of tools and fire intensified hunting pressure. Notably, we see that even early humanity could place intense top-down pressure on whole ecosystems, driving selection toward species of smaller body size. Such was the extent of this impact that the fossil evidence indicates that ecosystems became homogenized at the continental scale, primarily through the loss of large iconic mammalian species (for example, mastodons, sabre-toothed tigers and giant sloths)²⁸.

This early loss of large terrestrial mammal species is mirrored more recently in aquatic ecosystems where fishing has led to reductions in body size, increases in the speed of growth and increased productivity

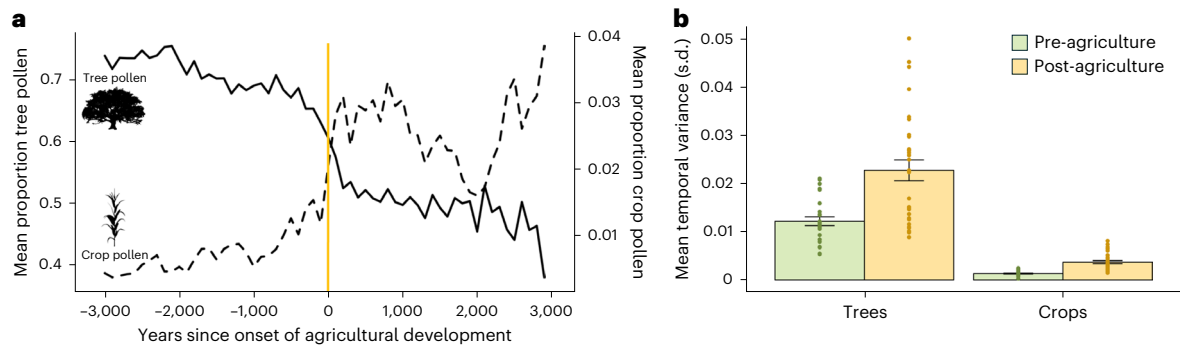


Fig. 2 | Pollen dynamics in relation to agricultural development in Europe.

a, The mean proportion of tree pollen (solid line) and crop pollen (dashed line) across Europe in relation to the onset of agricultural development. A total of 180 pollen records from the European Pollen Database standardized by time of agricultural development onset were used to generate mean trends. **b**, Mean temporal variance (s.d.) in mean pollen proportions for trees and crops pre- and post-onset of agricultural development ($n_{\text{pre}} = 26$, $n_{\text{post}} = 30$, for each

plant group). Points represent s.d. over each 500 year moving window used to calculate mean; error bars indicate s.e. Results from two-sample two-tailed t -tests for trees—mean_{pre} = 0.0122, mean_{post} = 0.0228, 95% confidence interval (CI) = (0.00584, 0.0153), $t_{38.88} = 4.526$, $P < 0.001$; and crops—mean_{pre} = 0.00133, mean_{post} = 0.00369, 95% CI = (0.00168, 0.00307), $t_{35.69} = 7.009$, $P < 0.001$. Credit: Silhouettes obtained from PhyloPic under a Creative Commons CC0.1.0 Universal licence.

in some fisheries^{16,29–31}. Fisheries researchers have, for example, shown that, over time, commercial harvesting tends to reduce the average body size of both individual species and communities^{15,17,18,32}. As an example, historical losses of larger body-sized Atlantic cod from the Gulf of Maine followed the transition and expansion of mechanized fishing technology (Fig. 1b)³⁰. Here, again, the impact of humans is rapid as the expansion of mechanized fishing coincides almost perfectly with the period of dramatic decline in mean cod body length, demonstrating the strong top-down effect of humans on body size of species targeted for food.

The above examples demonstrate strong evidence of the loss of large-bodied species in response to hunting and fishing pressure. They are, however, limited in their capacity to detect resultant changes in ecological stability (for example, population variability over time). Historical land-use data from Europe support the hypothesis that deforestation precipitated the loss of large-bodied species; providing early suggestions of human-driven landscape homogenization, as the proportion of arable land used for agriculture, fuel and construction increased substantially over the last 3,000 years across Europe (Supplementary Fig. 1)⁵. To demonstrate these changes more explicitly, we use a long-term, high-resolution European pollen-record time series (Supplementary Fig. 2) to reveal that the impact of humans was rapid, as the onset of agricultural development (transition from foraging to farming) coincides almost perfectly with the decline of larger-bodied, slower growing tree species and increases in smaller-bodied, faster growing cultivated crop species (62.9% decline and 187.9% increase, respectively, since onset of agricultural development; Fig. 2a). The high temporal resolution of these data also allows us to describe changes in ecological stability (here measured as temporal variability, that is, s.d.) in tree and crop populations following the establishment of agriculture. We see that the temporal variabilities of both tree and crop pollen increased significantly following the onset of agricultural development (Fig. 2b). Interestingly, non-cultivated, small, fast-growing plant species exhibited similar changes to cultivated crops following agricultural development (Supplementary Fig. 3). This increased variability in pollen dynamics (presumably mirrored by plant population dynamics) implies a loss of stability since the onset of agriculture across Europe and is the first major signature of the productivity–stability trade-off—a trade-off that has deep implications for the sustainability of biodiversity, food security and economies.

Evidence from marine systems demonstrates similar losses of population stability because of fishing-driven body size reductions^{16,29,33}. These exact changes in body size were found to erode stability in a well-studied commercially fished ecosystem¹⁶. Moving through several

hypotheses, the authors found that their data aligned most with the explanation that greater instability resulted from reduced body size composition and increased per capita growth rates (r) (ref. 16). This result echoes the historical results from terrestrial systems, again suggesting that food production both on land and in water may be inherently part of a trade-off between food production and ecosystem stability.

Although it is recognized that agriculture and wild animal harvesting tend to replace larger species with smaller more productive species^{5,15,34}, the full implications of how food production drives changes in ecosystems and their stability seems largely underappreciated in the food security literature. Some aspects of the resilience of food systems are linked to a suite of issues, including the diversity of the crops we rely on (for example, refs. 35–37) but overall the food security literature is relatively silent on the specific mechanisms by which changes in food web structure lead to instability. In what follows, we review this productivity–stability trade-off from a whole food web perspective by first examining the broad structural food web changes that tend to come with food production before briefly reviewing the stability theory on the consequences of these structural changes.

Food production consistently rewires whole food web flows

Food production activities modify a suite of ecosystem characteristics often to maximize productivity and consistency of single species; gross patterns have consistently emerged that have clear implications for whole food web dynamics. Studies have detected widespread signatures of human impacts such as trophic downgrading³⁸, habitat simplification^{39–41}, biodiversity loss⁷, biotic homogenization^{42–49} and body size reduction^{17,28,50,51}. These effects work in concert to alter biostructure in ways that rewire both the topology and interaction strength distributions among species and, therefore, the energy flow²⁴ of whole food webs in both aquatic and terrestrial systems (Fig. 3). Here, we consider these changes together and synthesize their implications for food web structure before discussing their consequences for food web stability.

One of the most fundamental signatures of human-caused global change has been the systematic loss and fragmentation of habitat⁴⁰. The corollary of fragmentation for the purpose of food production is the creation of large stands of homogeneous habitat in between fragmented remnants of old ecosystems^{40,41,52}. Such landscape homogenization leads to extensive biotic homogenization of both aboveground and belowground communities^{53–55}, where regional species losses tend to be compartmentally skewed such that losses/declines are dominated by certain functional groups (for example, specialists and large

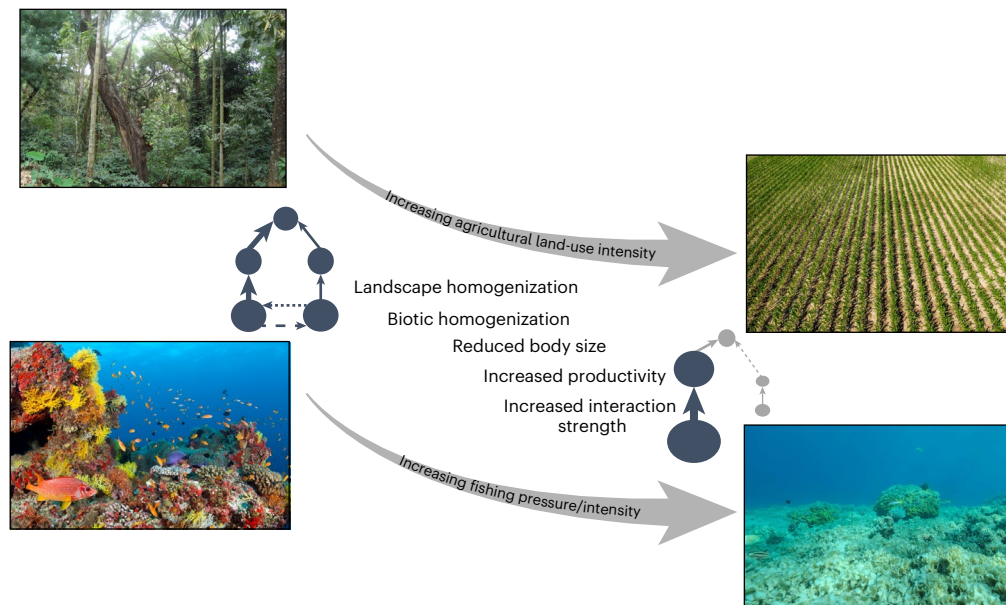


Fig. 3 | Food production-driven changes in ecosystem biostructure. Increasing agricultural land-use intensity and fishing pressure/intensity homogenize diverse terrestrial and aquatic ecosystems through landscape and biotic homogenization, which is associated with reduced body sizes (and thus increasing growth rates) and increased productivity. These changes alter food web structure towards highly simplified, truncated single energy

channel webs with strong interactions. Credits: Photo of coral reef reproduced with permission from WaterFrame_FBA/Alamy Stock Photo and photo of algal covered reef reproduced with permission from Zuma Press/Alamy Stock Photo; forest and corn photos obtained from rawpixel under a Creative Commons CC0.1.0 Universal licence.

mobile top predators) or whole energy channels (see Supplementary Table 1 for literature synthesis of examples)^{56,57}. Such losses generate food webs that tend to be dominated by single energy channels^{58–61}. Additionally, the erosion of heterogeneity across landscapes has been shown to increase interaction strengths, as habitat diversity and spatial complexity generate more diverse foraging landscapes that support higher diversity of prey and an associated increase in the proportion of weak interactions^{62,63}. Further, habitat heterogeneity provides refugia for prey which in turn reduces capacity of predators to access and overexploit prey, a stabilizing characteristic that is lost in systems with single energy channels and high biomass potential (for example, high-productivity systems)⁶⁴. Consequently, these low-diversity, homogenized, single-channel dominated systems erode spatial and temporal portfolio effects generating instability across aggregate communities and whole food webs. Collectively, landscape homogenization tends to drive skewed species losses that shift ecosystem biostructure towards low-diversity, truncated (reduced food chain length)^{15,38}, single energy channel dominated food webs with higher average interaction strengths.

Similarly, commercial fisheries, through intensive harvest methods have homogenized aquatic ecosystems. For example, bottom trawling has homogenized entire benthic zones in some areas in a manner consistent in scale with agricultural deforestation⁶⁵. In tandem with invasive species, often introduced for sport and commercial fisheries⁶⁶, these ecosystem modifications tend to induce biotic homogenization^{42,48,49}. As in terrestrial systems, biotic homogenization and overall biodiversity declines in aquatic systems tend to be compartmentally skewed, exemplified by the loss of large-bodied mobile top predators through harvesting or the shift towards dominance of pelagic energy channels in heavily trawled benthic communities (the loss of macroalgae energy channel)^{38,61,67}. In combination with harvesting, homogenization drives compartmented losses within food webs, reducing food chain length (reduced trophic position) and coupling between macrohabitats in aquatic food webs¹⁵.

At the same time, researchers have found a disturbing and consistent trend that the reduction in species body size associated with food

production, both within species and across whole communities and food webs (larger species are lost or dramatically reduced in relative quantity, akin to trophic downgrading³⁸), is being compounded by climate change^{50,68}. Although outliers occur, the empirical data are generally so strong that some have suggested this as a law of climate change for terrestrial and aquatic ecosystems⁵⁰. Notably and discussed above, this reduction in size also occurs in plants from agriculture and after extensive harvesting as increasing productivity tends to select for small, fast-growing species⁶⁹.

The result of this reduction in body size is more species at lower trophic level with greater productive potential^{19,70} and concomitant greater interaction strengths (Fig. 3). This productive potential manifests in high population maximal growth rates, r (refs. 20,70). Allometric patterns in r have shown historically and consistently that, as body size or plant size decreases, population maximal growth rates increase as smaller organisms have higher metabolic cost per unit biomass and therefore must increase consumption to maintain positive growth^{19,20,71,72}. Theory from simple consumer–resource models predicts that these increases in population growth rates necessitate that maximum growth from intake must outweigh increased metabolic costs and, thus, that interaction strengths necessarily increase^{72–74}. Further, smaller, high-growth-rate species tend to outcompete larger slower growing species in simplified, disturbed environments, leading to competitive exclusion and contributing to diversity loss^{12,56,57,75,76}.

Finally, the large-scale homogenization of habitat tends to drive the dominance of single energy channels or pathways in food webs. In intensive agro-ecosystem landscapes, for example, conventional agriculture homogenizes soil structure in ways that result in a reduction of the weak (slow) fungal pathway and a shift towards the strong (fast) bacterial pathway^{77–79}. This impact on the fungal energy channel appears to cascade upwards in the food web, impacting predator and fungivorous species within the community^{80–82}. Similarly, aquatic ecosystems have numerous examples where agriculture-derived nutrient increases and invasive species drive strong nearshore energy channel dominance^{83,84}, whereas stream–river systems have tended to lose

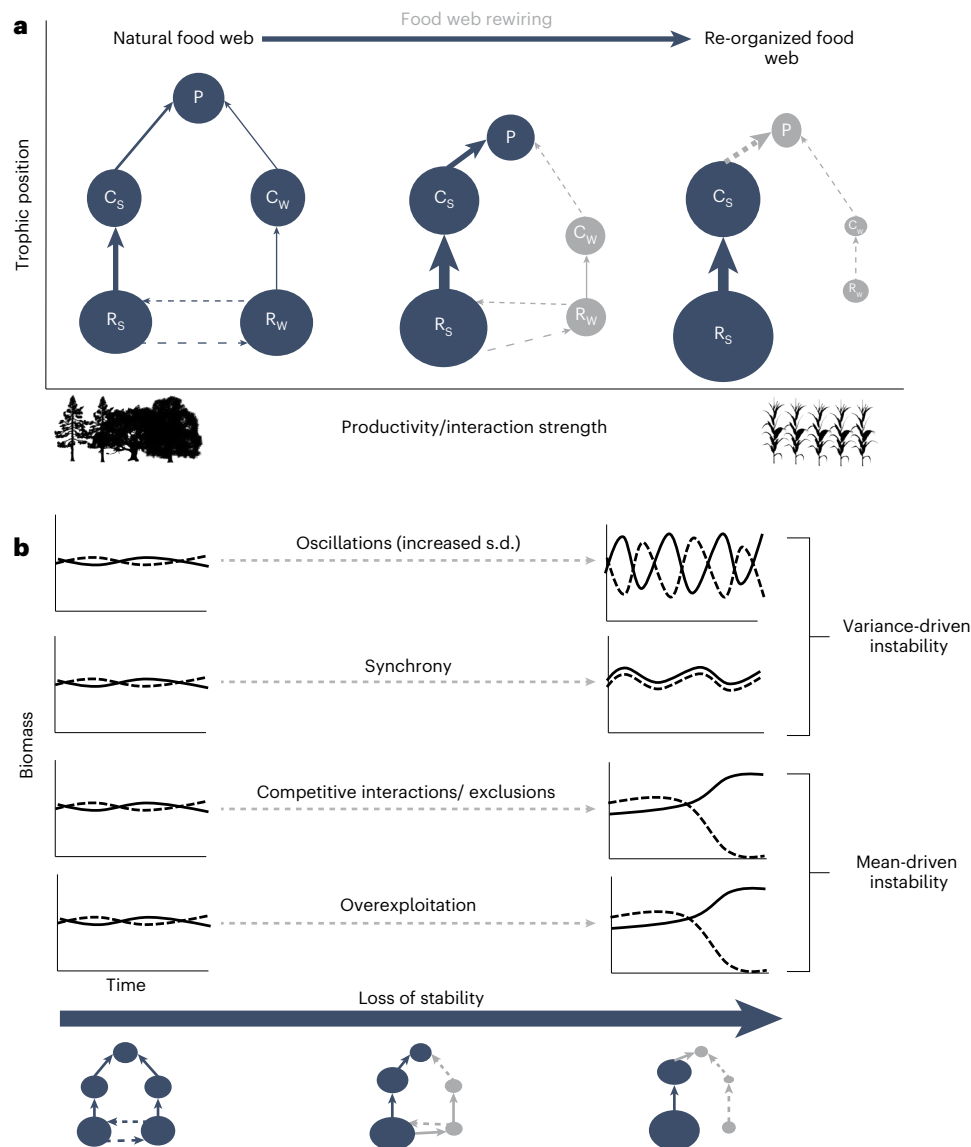


Fig. 4 | Stability responses to food web structural changes. a, Continuum of structural food web changes with increasing productivity and interaction strength as ecosystems move from natural food webs (left side of panels) to fully re-organized food webs in homogenized food systems (right). Food webs undergo topological and interaction strength rewiring towards truncated, single energy channels with strong interactions through the decline of weak energy channel species (consumer C_W and resource R_W) and predators (P). Here, size of circles represent relative differences in population/community biomass within each trophic/spatial/energy compartment; grey colour represents substantial decline/loss of species; and weight of arrows represent interaction strengths

for which thick, solid arrows depict strong interactions and thin, dashed arrows depict very weak to lost interactions. **b**, Predicted dynamic behaviours of food webs associated with continuum of structural changes. Theory shows that shifts toward truncated, single energy channels with strong interactions lead to loss of stability through increased oscillations (s.d.), increased synchrony (loss of asynchrony), competitive interactions/competitive exclusions and overexploitation. Lines represent general interacting pair of species (for example, predator–prey and competitive interactions). Credit: Silhouettes obtained from PhyloPic under a Creative Commons [CC0 1.0 Universal](https://creativecommons.org/licenses/by/4.0/) licence.

riparian insect and leaf litter, leaving behind a predominately (fast) aquatic energy channel fuelled by nutrient run-off⁸⁵. At a food web scale, this means that webs become less compartmentalized and more reliant on highly productive single energy channels and, as discussed more in the next section, less stable^{86,87}.

In summary, changes in landscape heterogeneity and organismal body size mean that (Fig. 3):

- (1) Food webs have become dominated by a single highly productive energy channel
- (2) Food webs tend to be reduced in trophic length
- (3) Food webs have become dominated by individuals/species with smaller body size, with greater per capita consumption rates, increased interaction strengths and increased growth rates.

Theory on food production-driven rewiring and stability

On the basis of theoretical insights, we predict that this set of empirical patterns (1–3 above) driven by human impacts through food production tend to all lead towards greater instability (Fig. 4). Specifically, these structural changes suggest that our means of producing food are driving food webs towards highly productive, strong interaction strength single energy channel dominated systems. This change in structure is not necessarily immediate and can be viewed as a continuum bracketed by a complex multichannel food web and a truncated, highly productive, single energy channel dominant food web (Fig. 4a). The empirical evidence we present strongly suggests that most current food production systems exist at the unstable, high-productivity end of

this continuum. However, characterizing food web structural changes along this continuum emphasizes that losses of stability can occur through transient food web rewiring (for example, changes in structure as natural habitat is converted for food production) and because of the structure of the new re-organized food web (that is, food web after food production established). There are two related, but distinct, parts to the stability theory behind the above structural food web rewiring. Below, we review the effect of species loss and increases in both productivity and interaction strength from both modular food webs and whole food web matrix theory before we then consider the related role of space.

Food web stability from modules to matrices

Food web modules depict simple, fundamental interactions (for example, consumer–resource) that are the building blocks of the complex, whole food web network of interactions often studied with a food web matrix approach. Examining food web dynamics from both perspectives helps generate a coherent understanding of food web stability responses as food production alters the nature of these interactions⁸⁸.

First and foremost, in modular food web theory, any loss of species indicates a fundamental loss of ecosystem stability as this represents a loss of the interior equilibrium. Theory has shown how losses of single or a few species can also generate substantial additional losses of species⁸⁹. Such destabilization is enhanced under increasing productivity conditions, where increasing interaction strengths increase the likelihood of competitive exclusion^{12,75,76}. This can be exacerbated through the loss of top predators (for example, overharvesting) that can otherwise mediate competition and drive co-existence¹². The decline in mean density to local extinction because of competition or overexploitation has broadly been defined as mean-driven change in stability⁹⁰ (Box 1). Second, modular food web theory shows that increasing productivity or the strength of species interactions (per capita flows through consumer–resource interactions), are both ultimately strongly destabilizing, producing destructive consumer–resource oscillations^{11,73,74}. Increased oscillations have broadly been characterized as variance-driven instability⁹⁰ (Box 1). At a simple level, the increase of productivity leads to greater energy flows, on average, through all interactions. After a short, stabilizing effect in low productivity conditions, this increased overall flux has a destabilizing effect that excites interactions and drives overshoot dynamics, which drives the oscillations, especially when enhanced by lags that are inherent in the interactions⁹¹. Here, theory illustrates that the presence of weak interactions can stabilize the oscillatory potential of different modular webs but these effects are rapidly eroded with even modestly increased interaction strengths^{9,88,92}. From an energy flow perspective, increases in productivity and interaction strength are qualitatively similar and both together excite consumer–resource interactions into hostile dynamic overshoots that can drive the loss of either the consumer or the resource. Indeed, the recipe for chaos in single-channel food chain models is increased productivity (K) and increased interaction strengths^{93,94}. The simple modular food web theory reviewed above, is mirrored in the whole food web matrix literature that has largely found that strong interactions are inherently destabilizing^{86,88,95}.

Spatial heterogeneity and food web stability

The above-described theoretical literature frequently ignores the role of space, although modular spatially implicit food web theory has generally found that the reduction of spatial compartments, when associated with different food web energy channels, is destabilizing^{96–98}. This is especially true if the reduction in compartments occurs in tandem with the increasing productivity of the remaining energy channel as the empirical evidence suggests. With several compartments, different energy channels can operate to stabilize webs by producing portfolio effects that mobile consumers, foraging from both pathways, can average over^{8,99,100}. Further, asymmetric spatial compartmental structure can also induce ‘switching’ behaviours in predators that are known to

be potent stabilizing factors where interaction strengths reduce when needed⁹⁹. This stabilizing effect is magnified when there is competition between pathways since competition can heighten asynchronous pathway dynamics and provide a stronger portfolio effect that buffers the top predator against low resource availability⁹⁹. The loss of large-bodied top predators (loss of trophic compartment) can remove the stabilizing ‘switching’ mechanism and biotic homogenization in general tends to erode differential responses and portfolio effects across landscapes (through, for example, loss of specialists)⁵⁵. Portfolio effects are known to be potent players in the stability of communities to meta-ecosystems^{101–104}.

When we consider the role of space in general on whole ecosystem dynamics, theory has found that in high-productivity systems, spatial homogenization is destabilizing¹⁰⁵. Frequently, in spatially explicit models, increased movement rates synchronize local dynamic habitats to produce coherent regional resource pools that act in a manner consistent with unstable homogenized models^{106,107}. These results are mirrored in microcosm experiments with highly connected patches showing destructive oscillations and instability¹⁰⁸. Subsidies also play a strong role in structuring ecosystem dynamics in space. Theory suggests that constant, high inputs of subsidies (for example, high fertilizer inputs) ought to be destabilizing and lead to the decoupling of food chains, increased interaction strengths, strong trophic cascades and resultant species loss^{109–111}. However, if subsidy input varies across time such that subsidy inputs occur when local productivity is low, or additional mitigation strategies such as pest control work to suppress trophic cascades, subsidies may act to locally stabilize recipient ecosystems¹¹². Subsidies can also spatially link ecosystems such that instabilities can manifest in distant ecosystems (for example, excess nutrients on land can cascade to impact water quality and fisheries hundreds of kilometres away^{90,113}) presenting potential trade-offs between local stabilization and distant destabilization. Collectively, theory suggests that food production has increased productivity, growth rates and interaction strengths, homogenized spatial structure, eroded portfolio effects and probably greatly destabilized food webs (Fig. 4).

Empirical results of instability in food production ecosystems

We now turn to empirical data and end by exploring the literature to synthesize examples of research on food webs and ecosystems that show evidence of the productivity–stability trade-off. We do this by examining empirical research papers that have documented food production-driven ecosystem stability loss across large spatiotemporal scales and across ecosystem types and taxa (59 examples; Supplementary Table 1). Following our definitions of stability loss (Box 1), for each example we synthesized the type of food production, evidence of stability loss and the noted change in biostructure associated with the loss in stability. A full description of methods used for the literature synthesis are provided in the Methods.

The results of the synthesis demonstrate that both terrestrial (aboveground and belowground) and aquatic (marine and freshwater) environments show strong evidence of anthropogenic food production-driven stability loss. Across ecosystem types and taxa, we see evidence of loss of ecosystem stability due to increasing agricultural intensity and fishing pressure (Supplementary Table 1). Such losses of stability are a result of changes in ecosystem biostructure, where food production tends to reduce functional compartments (for example, loss of specialists and increase in generalists), reduce body size (for example, shift towards faster life histories), shorten food chains (for example, loss of top predators) and shift to dominance of single energy channels (for example, shift to dominance of fast, bacterial energy channel in soil food webs). These changes in biostructure rewire how energy flows through food webs and destabilizes ecosystems through species loss, increasing oscillatory dynamics and increasing synchrony (see Supplementary Table 1 for examples and citations).

These examples of large-scale ecosystem destabilization can feedback to affect the stability and magnitude of the food resources themselves (crops and fish) and often require increased inputs such as fertilizers, pesticides and fish stocking to maintain yields. For example, increased rates of selective fishing have led to overexploitation and collapse of important fish stocks (for example, large-bodied predators)^{30,67} and resulted in increases in smaller, faster growing fish species whose populations are more variable through time, directly affecting yield magnitude and stability^{29,114,115}. In agricultural systems, erosion of ecosystem stability has contributed to loss of essential ecosystem services (for example, soil quality and biological pest control) that has increased disease and pest outbreaks, increased crop susceptibility to drought and resulted in yield declines^{116,117}, collectively threatening the stability and resilience of crops¹¹⁸. Research has also demonstrated that increasing crop yield productivity comes at the cost of increasing yield instability¹¹⁹. While the feedbacks between ecosystem and yield instability are not fully explored here, these examples highlight the importance of considering this productivity–stability trade-off in discussions around global food security and working to mitigate such losses.

Towards mitigation of food production-driven stability loss

The broad suggestions for mitigating food production-driven stability losses in Supplementary Table 1 centre around limiting and/or reversing the shifts in ecosystem biostructure that lead to such stability loss in the first place. For example, in terrestrial agricultural systems, we suggest increasing habitat heterogeneity across spatial and temporal scales using a multiscale integrated heterogeneity management approach that uses methods such as intercropping, perennial polycultures, crop rotations and marginal land restoration (for example, planting native prairies/hedgerows, wooded ‘islands’, riparian buffers and wetlands)^{120–123}. While broad, such mitigation strategies help generate heterogeneity across scales in ways that mimic natural ecosystems and provide the fabric to support the natural, resilient structure of food webs^{124,125}. Indeed, research has shown that agricultural systems with higher landscape heterogeneity and crop diversity can increase yield magnitude and stability through mechanisms such as increasing ecosystem services (for example, pollination^{126–128}, soil carbon and nitrogen cycling^{129,130}) and buffering environmental variation^{131–133}, indicating that such mutually beneficial management approaches are possible. Similarly, in aquatic systems, changing harvesting strategies and using ecosystem-based management (EBM) approaches could reduce fishing pressure on large-bodied fish, weakening selectivity towards smaller-bodied species with high growth rates and thus reducing average interaction strengths which theory predicts will increase the resilience of fishery yields^{23,134}. Emerging empirical research suggests that such EBM approaches can be effective in maintaining fishery yields under future climate change, yet uncertainties exist in long-term effectiveness, highlighting the need for more empirical research to understand the effects of EBM on maintaining fishery yield stability in a variable world¹³⁵. While specific recommendations and applications of these management approaches are complex and beyond the scope of this paper, we hope to motivate future work to establish specific guidelines and frameworks to implement such management types, as it is evident that a comprehensive approach must be adopted to identify, protect and restore stabilizing structures and processes in nature.

A potentially interesting counter example may be found in regions across the global south where governments have embraced agro-ecological and regenerative practices that prioritize reduced (or no) chemical inputs in the name of creating more natural and resilient food systems. A notable recent example is the government of Sri Lanka’s ban on synthetic fertilizers in an effort to encourage organic farming. Evidence suggests that this policy led to widespread instability, yield losses and greater food insecurity¹³⁶. Such examples highlight

the complexity of this issue and demonstrate that arguments such as the ones presented in this paper should not be seen as any sort of antitechnological rejection of modern agrichemical inputs. Indeed, many farming regions across Africa confront substantial yield gaps—the disparity between current food production levels and potential outputs if optimal technologies and practices were used¹³⁷. Addressing these yield gaps is critically important. However, this paper argues that attempting to close these gaps with conventional industrial agricultural methods might lead to unintended consequences, affecting both yield and system stability. This argument is made from the perspective of ecosystem services, yet ref. 138 makes a very similar case using a political economy lens by showing how the same industrial agricultural practices that lead to homogenous-yet-productive landscapes also create highly homogenous political economic landscapes that are highly vulnerable to global disruption¹³⁸.

Indigenous communities have a long history of sustainable management of food production systems and we stress the importance of weaving indigenous knowledge systems with Western scientific approaches in developing effective strategies for sustainable food production^{139–142}. This integration of systems holds the potential to unravel the intricacies of sustainable food production and ecosystem protection. This synergy not only enriches our understanding of the effects of food production strategies on ecosystems but also aligns inherently with the principles embedded in the UN Declaration on the Rights of Indigenous Peoples (UNDRIP)¹⁴³ and SDGs²⁶. By weaving indigenous traditional ecological knowledge, accumulated over generations, with contemporary scientific insights, a comprehensive framework emerges for addressing the challenges of ensuring food security and safeguarding biodiversity¹³⁹. Ultimately, the fusion of these knowledge systems offers a pathway that not only supports the aspirations of indigenous communities but also contributes substantively to the global pursuit of a sustainable and just future.

Mitigation of stability loss is essential, as the management of highly unstable systems to maintain food security comes at considerable costs. Loss of pollinators, for example, necessitates the expansion of agricultural footprints to maintain yields¹⁴⁴ and rising pest issues are associated with increased per capita demand in pesticides^{144,145}. In what might be considered an economic externality, the loss of soil nutrients drives increased nutrient applications^{1,118,145} that increase distant nutrient instabilities in water (for example, dead zones and harmful algal blooms)⁹⁰, altering fisheries production and water quality¹⁴⁶. Concurrently, the loss of organic matter in the soil results in greater vulnerability to the impacts of droughts, floods, erosion and soil degradation¹⁴⁷. All these are effectively signatures of loss of ecosystem function (forms of stability loss), bringing with them substantial management costs. These hidden instabilities highlight the inextricable link among the structural, functional and dynamic properties of systems and are a critical area of management that has yet to be fully acknowledged. As discussed above, emerging evidence has shown that lower intensity agricultural methods such as polycultures and perennial cropping systems (many of which are used by indigenous communities), which can help maintain ecosystem stability, can also maintain yield stability and reduce costs^{124,128,129,148}, suggesting that improving ecological resilience can increase overall resilience of food production systems in an increasingly uncertain future. Taken together, this highlights the importance of sustainable food production which acts to increase ecosystem stability in ways that may help offset these large costs and reduce risk of potential collapses.

Conclusions

In this paper, we have shown that management of terrestrial and aquatic ecosystems for food has tended to homogenize ecosystems, reduce body sizes and truncate food web lengths. Typically, this results in fast-growing, productive, ecosystems with inherently strong interaction strengths. While these changes boost productivity

and drive higher average yields of small, fast-growing species (thus feeding many people), empirical data and theory suggest it does so by simultaneously reducing the biodiversity and associated stability of the systems on which we depend for food production. Additionally, theory suggests that these inherent instabilities ought to manifest in simplified crop–pest interactions, requiring more pesticide and fertilizer to regulate the potential instability, which represents an underestimated economic cost of managing these highly productive but unstable food systems.

Through this paper we aim to illuminate the seldom considered trade-off between increasing productivity and the loss of stability in adjacent habitats in efforts to catalyse research on and development of sustainable food production approaches that work to reduce ecosystem-wide stability losses and maintain food security, indeed a non-trivial endeavour. We have largely focused on stability trade-offs in surrounding and adjacent ecosystems ('off the field'), yet future work is urgently needed to determine feedbacks between ecosystem stability loss and crop and fish yield stability ('on the field') to identify potential solutions that satisfy these seemingly contradictory but in reality complementary objectives. Additionally, whereas here we have considered two broad forms of stability loss, mean-driven instability and variance-driven instability, there are numerous other dimensions of stability that can in themselves exhibit trade-offs and encourage future work to examine food production trade-offs with other measures of stability to develop a more holistic understanding of stability responses^{149,150}.

Food production systems include not only the land or water where food is produced but also the economic and governance systems that regulate food supply chains. The economic and governance system components of food systems have undergone changes that parallel those of ecosystems—transitions from small-scale, local producers to homogenized large-scale global food systems that are largely controlled by few, large corporations who outcompete small-scale operations and ultimately simplify and strongly connect food distribution networks. The effect of this industry concentration, which may be considered analogous to a loss of functional diversity from a political economy perspective, has been studied extensively by social scientists^{35,151}. Another study¹³⁸ argues that this process of industrial homogenization and concentration has created major new vulnerabilities within the global food system¹³⁸. Hence, in this article, we present data showing empirically how this vulnerability maps onto ecological theory. Such parallel changes open interesting opportunities to apply the structure–stability relationships used here within the context of ecosystems more broadly to understand the stability and resilience of whole food systems. Additionally, economic and regulatory systems can feedback to provide incentives and compensations to support food production approaches that mitigate ecosystem-level effects, collectively working towards a more sustainable food system ecologically, socially and economically.

Food web theory predicts that the combined impacts of homogenization of habitats and the loss of large mobile predators from high trophic levels is seriously threatening Nature's balance^{8,99,100,152}. This theory argues that the variation in species occupying lower levels in food webs allows an ecosystem to elicit a range of responses to a variable world. The mobile larger organisms interact with this landscape of species variability in a way that prevents any single species from monopolizing space and energy. In other words, the large organisms promote the balance and maintenance of a diverse and variable assemblage of organisms and this in turn creates buffers against an ever-changing world.

According to this theory, Nature is an intricate balance of bottom-up (driven by habitat heterogeneity) and top-down (driven by predators) forces⁸. By homogenizing habitats and truncating higher-order predators, we increase interaction strengths and the erosion of critical landscape-scale portfolio effects that can cascade through food webs in a destabilizing manner. Restoration of habitat

heterogeneity and mobile top predators are critical to the maintenance of biodiversity and stability in a high food demand world⁸.

As the world calls for responses to climate change and the simultaneous maintenance of biodiversity (COP15), in addition to preserving large tracts of land (30% by 2030), it is critical to recognize that key areas of natural land productivity often act both to feed a growing human population and as biodiversity hotspots¹⁵³. Food production often occurs in areas where naturally rich nutrients and soil meet with streams and transition to large coastal ecosystems that frequently also foster productive fisheries⁹⁰. Although not explored here, instabilities from productive agricultural systems can materialize in highly coupled (telecoupling) distant ecosystems^{90,154–156}. Given that instability due to food production can manifest in distant ecosystems⁹⁰, then it becomes critical that we manage biodiversity at the meta-ecosystem scale. Unfortunately, given the known connectivity of ecosystems, this nexus of several ecosystems impacted by food production is seldom, if ever, co-managed.

The SDGs highlight the need for ending hunger (goal 2) while simultaneously ensuring sustainable consumption and production methods (goal 12). Towards attaining sustainable food production, we argue that it is critical to recognize the fundamental trade-off between productivity and stability. Drawing from decades of research on the relationship between biodiversity and stability¹⁵⁷, we argue that perhaps the simplest management approach should be to increase heterogeneity across spatial and temporal scales. The potential to manage food production systems in ways that increase ecological stability while also stabilizing yields, is growing^{129,148,158}, with grassroots farmer movements operating to add heterogeneity to the landscape¹⁵⁹ (for example, Alternative Land Use Services Canada). Further, more formal, management treatments are critical to ensure both the sustainability and security of food production for humanity.

Methods

Historical pollen dynamics analysis

Historical land-use data and pollen records from Europe were used to detect evidence of early human-driven landscape homogenization towards smaller, faster growing species and subsequent stability loss. First, we used data from ref. 5 to depict the average proportion of arable land used in Europe over the last 3,000 years (Supplementary Fig. 1). In their study, the authors developed and applied a deforestation model to simulate fine-scale spatiotemporal changes in forest cover in arable lands across Europe and neighbouring areas from 1000 BC to AD 1850. Using a combination of a database of human population densities, maps of relative land suitability and relationships between population density and amount of cleared land, they were able to estimate the percentage of arable land that was covered in forest across 51 regions for the last 3,000 years. In all 51 regions, by 1000 BC agriculture was well-established, and thus this change in land use occurred as a result of the rapid expansion of land clearance for cropland, pasture, construction materials and wood as a source of fuel⁵. We extracted data from supplementary table 3 in Kaplan et al.⁵, to generate Supplementary Fig. 1. We selected regions that were only within Europe (41 regions) and calculated the mean proportion of arable land used for each region ((100% forest cover on arable land)/100) over time.

The high-resolution pollen analysis was conducted using a dataset of pollen records compiled by ref. 160. We discuss the methods used to compile the data briefly below (see ref. 160 for more details), before discussing the specific analysis conducted here to detect changes in pollen dynamics. To produce the dataset, historical pollen records were extracted from the European Pollen Database. For this study, 180 pollen records from sediment cores with radiocarbon dated pollen counts across Europe were used (Supplementary Fig. 2). Radiocarbon dates were calibrated to calendar year using classic age–depth models, in which calibrated pollen ages were either part of the downloaded record (that is, already calibrated) or were calibrated using non-Bayesian

classical age–depth models with the clam R package^{161,162}. Pollen counts for 37 plant taxa, organized into six groups (trees, *Cerealia*, *Poaceae*, *Cyperaceae*, cultivated pollen types and other herbaceous plants), were used for this study as they represent common plant species occurring throughout historical European plant communities^{163–166} (see Supplementary Table 2 for list of taxa in each category). Counts of unidentified plant species, non-terrestrial plant species (for example, algal pollen) and non-pollen indicators (for example, charcoal) were removed from the data and pollen counts were converted to proportions before further analysis.

Regime-shift detection analysis was conducted to estimate the inception of agricultural development in each pollen record and thus allow for comparison of pre- and post-agricultural development pollen dynamics. *Cerealia*-type pollen (cereal species such as wheat and barley) were used as the sole regime-shift indicator as they are cultivated species and can be differentiated from other wild grasses, making them an accurate indicator of the presence or absence of agricultural development in the region surrounding the pollen basin^{166,167}. The regime-shift detection analysis was conducted with Shift Detection (v.3.2), which uses a sequential *t*-test analysis of regime shifts (STARS) method (cut-off = 10, $\alpha = 0.05$)^{168–170}. This approach conducts *t*-tests between each sequential temporal observation within a pollen record to determine if the proportion of *Cerealia* pollen in the next time step is significantly different from the previous time step. The point in time where the proportion of *Cerealia* pollen significantly increased from 0 was determined to be the onset of agricultural development and all pollen ages were then converted relative to their respective year 0. This allowed for direct comparison of pollen dynamics pre- and post-agricultural development despite regional differences in timing of agricultural development. Lastly, pollen proportions for all taxa were standardized to the nearest 100th year interval using linear approximations to standardize differences in calendar years, and allow for more direct comparisons between pollen records. In cases where several pollen assemblages occurred within a given 100 year interval, linear regression equations from the line of best fit were used to standardize to 100th year.

To determine the influence of agricultural development on pollen dynamics we compared the proportion and variability of tree and crop pollen before and after onset of agriculture (Fig. 2). First, to compare temporal trends in tree and crop pollen, we calculated the mean proportion of pollen at each 100 year time point for trees (consisted of 22 families) and crops (*Cerealia* and cultivated pollen types) for the 3,000 years before and after the onset of agricultural development (Fig. 2a and Supplementary Table 2). Second, to compare temporal variability in pollen dynamics pre- and post-agriculture in tree and crop species we calculated s.d. across a five time step (500 year) moving window across the time series. Mean tree and crop pollen s.d. were then calculated for the period before agriculture and after the onset of agriculture to investigate how the variability (s.d., stability) of tree and crop pollen has changed since the inception of agricultural practices in Europe (Fig. 2b). To determine if the onset of agricultural development led to significant increases in pollen variability within plant type, two-sample two-sided *t*-tests were conducted on distinct s.d. samples from pre- and post-agricultural development for each plant group ($n_{\text{pre}} = 26$, $n_{\text{post}} = 30$ for each plant group). To satisfy normality and homogeneity of variance assumptions of two-sample *t*-tests, s.d. was log transformed. As the results are qualitatively the same using untransformed and transformed s.d., we present untransformed results in the main text for clearer interpretation and include the statistical results from log-transformed data in Supplementary Table 3. To ensure that differences in available pollen records across the time series did not influence s.d. results, a sensitivity analysis was conducted. The minimum number of pollen records available within a given 100 year time point (that is, 12) were randomly selected for each 100 year time point and the mean proportion and then s.d. across a 500 year moving window was calculated. This process was iterated 1,000 times and then mean

s.d. pre- and post-agriculture were calculated and compared with a two-sample *t*-test for each group. The results were qualitatively similar, therefore we included the results using all available pollen records in the main manuscript and have provided the results from the sensitivity analysis in the supplement (Supplementary Fig. 4). Lastly, we repeated the analyses above for the other three pollen groups (*Cyperaceae*, *Poaceae* and other herbaceous plants) to see if agricultural development also influenced non-cultivated, small fast-growing plant species and if there was evidence for more plant community-wide responses.

All statistical analyses were conducted using R (v.4.3.2). All animal and plant silhouettes were obtained using the rphylopic package¹⁷¹. Data are available on Zenodo (<https://doi.org/10.5281/zenodo.12702274>)¹⁷² and code is available at https://github.com/mariegutgesell/Productivity_Stability.

Literature synthesis

For the literature synthesis, we first conducted a literature search using Web of Science (accessed 7 July 2023). The aim of the literature synthesis was to obtain examples from natural food production systems that have explored stability responses of ecosystems and ultimately found evidence of stability loss. We developed two sets of keywords to capture as many relevant papers as possible. The general structure of our keywords for these searches were food production, stability, levels of biological organization (for example, food webs and ecosystem) and then empirical/natural experiment or diversity/biotic homogenization. For each of these categories we included several words as they can be discussed in the literature in different ways (for example, farming versus agriculture). The complete keyword equations used for the literature search are listed below.

Search 1:

((AB=(agricultur* OR farming OR fishing OR 'land-use intensity' OR fisher* OR 'food production' OR aquaculture)) AND AB=('temporal variability' OR stability OR asynchrony OR synchrony)) AND AB=(empirical OR 'natural experiment' OR 'ecological experiment' OR 'long-term experiment')) AND AB=('food web*' OR ecosystem* OR population* OR communit* OR species)

Search 2:

((AB=(agricultur* OR farming OR fishing OR 'land-use intensity' OR fisher* OR 'food production' OR aquaculture)) AND AB=('temporal variability' OR stability OR asynchrony OR synchrony)) AND AB=('food web*' OR ecosystem* OR population* OR communit* OR species)) AND AB=(diversity OR 'biotic homogenization')

Combined, these searches produced 948 papers. We reduced this set of references to those that aligned with our aim according to the contents of the abstract of each reference using the initial criteria in a decision flow chart in Supplementary Fig. 3. On the basis of these abstracts, we identified 186 papers as potential candidates for which the full text was scrutinized further on the basis of our decision flow chart. If a paper fit the initial criteria, the relevant information was extracted from the paper and added to the table. This generated a total of 64 papers on the topic of food production systems that included an assessment of stability. We then imposed the final criteria determining whether the studies indicate stability loss or not. Nine studies (14%) did not show evidence of stability loss (that is, no loss of species or changes in population means or variance) and these studies were excluded leaving 55 studies in the final table (details are provided in Supplementary Table 4). Lastly, we supplemented these examples with a few (four) known examples from ecosystems where few/no examples were identified in primary search (for example, freshwater lakes and streams).

From each of the final 59 papers, we tracked the type of food production, evidence of stability loss, the taxa impacted and the noted change in biostructure associated with the loss in stability. We identified the following five metrics of stability loss: (1) loss of species

(indicates local extinctions), (2) loss of functional groups (implicit loss of species), (3) substantial declines in population densities (collapses or losses >70% of population), (4) increasing temporal or spatial variability (loss of asynchrony, increased CV) and (5) shift towards single dominant energy channels/interactions (for example, using stable isotopes and network analysis). We then categorized stability loss as mean-driven (substantial decline in populations, change in CV attributed to mean), variance-driven (change in CV attributed to s.d. or asynchrony) or undefined when the mechanism driving local extinction or change in CV was unable to be determined from available data. In the six papers in which CV was reported but not partitioned into mean and s.d., raw data were available for two of these papers and we were largely able to reproduce CV results from one of the papers¹¹⁵. McClanahan et al. showed increasing CV of catch per unit effort (CPUE) with increasing fishing pressure¹¹⁵; here we examined changes in mean CPUE and s.d. of CPUE across the gradient of fishing pressure and found that mean CPUE significantly declined whereas s.d. had no change with increasing fishing pressure ($R^2 = 0.4478, P < 0.001$; $R^2 = -0.0239, P = 0.524$, respectively) indicating mean-driven stability loss (Supplementary Table 1).

The food production driver of stability loss was categorized into agricultural landscape modification, agricultural management intensity, agricultural duration and fishing pressure. See Supplementary Table 5 for how different forms of food production mechanisms were categorized. We also note that ecosystem responses can be driven by several stressors (for example, climate and fishing pressure) and where these additional stressors were evaluated and attributed to some of the resultant stability changes, we listed these following the food production mechanism in the table. The change in biostructure describes the specific stability loss evidence and subsequent changes in the system such as species composition (for example, loss of large-bodied species and increase in small), network/food web structure or population dynamics. Lastly, we identified broad mitigation strategies which were purposely kept general and aimed to alleviate the general mechanism driving stability loss (for example, habitat restoration for which loss of natural habitats was the main mechanism of stability loss).

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

Data to produce Fig. 2 and Supplementary Fig. 3 are available online at <https://doi.org/10.5281/zenodo.12702274> (ref. 172).

Code availability

Code for all pollen analysis is available online at https://github.com/mariegutgesell/Productivity_Stability.

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Author contributions

M.G., K.M., N.R., I.D., J.C.M., E.D.G.F., K.C., B.M., C.B., R.H.H., T.T., R.O. and C.W. contributed to the conceptualization of the study. M.G., K.M., R.O., W.G., Z.G. and N.R. contributed to the method design and pollen analysis. M.G., N.R., K.M., R.O., C.W., A.S. and B.P. contributed to literature investigation and analysis. M.G., R.O. and K.M. contributed to visualization and figures. K.M. and E.D.G.F. contributed funding acquisition. M.G. and K.M. led the final draft preparation and submission stages with comments from all authors being received before submissions.

Competing interests

E.D.G.F. is the co-chair of the Canadian Food Policy Advisory Council, sits on scientific advisory boards of Genome Quebec and Protein Industry Canada and is the vice-chair of the Maple Leaf Centre on Food Security. The remaining authors declare no competing interests.

Additional information

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Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

| | |
|--------------------------|--|
| Study description | The study used existing pollen record data to analyze how the onset of agricultural development influenced the temporal variance of pollen over time. Treatment factor in statistical tests was categorical, pre- and post-agricultural development, response variable was standard deviation in mean pollen proportions over time. Experimental units were the standard deviation of a rolling window over a 500 year time step (pre- and post-agriculture data spanned a total of 6000 years). |
| Research sample | The existing data used in this study was downloaded from the European Pollen Database. In total, 180 pollen records with radiocarbon dating from sediment cores were downloaded from the database. Pollen counts for 37 plant taxa belonging to 6 categories were extracted from each |
| Sampling strategy | Downloaded pollen records selected for this analysis satisfied 3 criteria. 1) The pollen record contains data within the Holocene that overlapped with agricultural development (i.e., record had evidence of agricultural development), 2) Records are radiocarbon dated, and 3) Time-step resolution was sufficient to calculate relevant statistics. This generated 180 usable pollen records. |
| Data collection | The data was downloaded from the publicly accessible European Pollen Database (https://epdweblog.org/epd_data/). |
| Timing and spatial scale | The data was extracted from the EPD in 2017. Collectively, the pollen records span 3000 years pre-agriculture to 3000 years post agriculture. The length of individual pollen records varies. |
| Data exclusions | The only data that was excluded from the analysis was counts of non-terrestrial plant pollen (e.g., algae) and non-pollen indicators (e.g., charcoal). The purpose of our study was to focus on changes in temporal dynamics of terrestrial plant communities, so these data were excluded as they were not relevant to our objective. |
| Reproducibility | To ensure reproducibility all data and code is publicly available. We had two separate researchers conduct each analysis (M. Gutgesell, and R. O'Connor) to ensure analysis results matched. Additionally, we conducted a sensitivity analysis that randomly selected pollen records within each 100-year interval, calculated the moving-window SD and compared pre- and post-agriculture mean SD. We repeated this 1000 times and found the results were qualitatively the same, we included the results of this sensitivity analysis in the supplemental materials of this paper. |
| Randomization | This is not relevant to our study. We did not assign treatments, the determination of pre- and post-agriculture, which were then the groups compared with our statistical test, were identified based on the timing of significant Cerealia pollen change appearing in the pollen record. Therefore, randomization was not necessary or part of our experimental design. |
| Blinding | The determination of group (i.e., pre- and post-agricultural development) was done through a statistical program called Shift Detection, where a regime shift detection that indicated pre- or post- agriculture was based on a significant change in the presence of Cerealia (cultivated plant species). Therefore, the determination of treatment groups that were compared was objective and not biased by researcher observations. |

Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

| n/a | Involved in the study |
|-------------------------------------|--|
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Antibodies |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Eukaryotic cell lines |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Palaeontology and archaeology |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Animals and other organisms |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Clinical data |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Dual use research of concern |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Plants |

Methods

| n/a | Involved in the study |
|-------------------------------------|---|
| <input checked="" type="checkbox"/> | <input type="checkbox"/> ChIP-seq |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Flow cytometry |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> MRI-based neuroimaging |

Plants

Seed stocks

Report on the source of all seed stocks or other plant material used. If applicable, state the seed stock centre and catalogue number. If plant specimens were collected from the field, describe the collection location, date and sampling procedures.

Novel plant genotypes

Describe the methods by which all novel plant genotypes were produced. This includes those generated by transgenic approaches, gene editing, chemical/radiation-based mutagenesis and hybridization. For transgenic lines, describe the transformation method, the number of independent lines analyzed and the generation upon which experiments were performed. For gene-edited lines, describe the editor used, the endogenous sequence targeted for editing, the targeting guide RNA sequence (if applicable) and how the editor was applied.

Authentication

Describe any authentication procedures for each seed stock used or novel genotype generated. Describe any experiments used to assess the effect of a mutation and, where applicable, how potential secondary effects (e.g. second site T-DNA insertions, mosaicism, off-target gene editing) were examined.