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Human Health Outcomes of a Restored Ecological Balance in African Agro-landscapes

Abstract

Biodiversity loss and invasive species are exacting negative economic, environmental and societal impacts. While the monetary aspects of species invasion have been well-assessed, their impacts on human and social livelihood outcomes routinely remain obscure. Here, we empirically demonstrate several important human health and demographic consequences of a 1970s invasive pest species of cassava across sub-Saharan Africa. Pest-induced crop loss in 18 African countries relying heavily on cassava as a staple inflicted cascading effects on human birth rate (-6%) and adult mortality (+4%) over the span of a decade. The 1981 deliberate release of the specialist parasitic wasp *Anagyrus lopezi* restored cassava yields, thus reconstituting food security in these agricultural systems and enabling parallel improvements in human health indices. Our analysis shows how agricultural performance can influence health and demographic outcomes, and accentuates how deliberate efforts to safeguard agro-ecological functions and resilience could be important during times of global environmental change.

Keywords: social-ecological systems; sustainable intensification; tele-coupling; agri-environment schemes; biological control; biodiversity conservation; agroecology

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Introduction

The UN Sustainable Development Goals (SDGs) set out targets for global alleviation of malnutrition and poverty, improved human well-being and a stabilization of the Earth's life-support systems (Griggs et al., 2013). Biodiversity lies at the core of many SDGs, and in addition to high intrinsic value underpins the delivery of several ecosystem services (Wood et al., 2018). However, many efforts to meet dietary requirements of a growing global population combined with changes in consumption patterns have negatively impacted upon biodiversity and the public goods supplied by natural capital (Godfray et al., 2010; Fischer et al., 2017). Land conversion, ecosystem mismanagement and externalities of agricultural development continue to negatively affect the world's biodiversity (Maxwell et al., 2016; Isbell et al., 2017; Pretty et al., 2018). These human-mediated processes risk destabilizing both terrestrial and marine ecosystems and exert a pervasive influence on "safe operating spaces" for the world's social and economic development (Cardinale et al., 2012; Steffen et al., 2015).

Invasive species can exacerbate environmental pressures, often constraining the production of food and agricultural commodities, and disrupting ecosystem functioning (Bradshaw et al., 2016; Paini et al., 2016). Regularly tied to the global trade in agricultural produce, invasive species inflict substantial economic losses globally (Pimentel et al., 2001; Bradshaw et al., 2016) and place a disproportionate burden on developing economies and biodiversity-rich tropical settings (Early et al., 2016). Though the ecological effects of invasive species have been well-studied, with some impacts calculated in economic terms, their broader (long-term) effects on human well-being and livelihoods have received considerably less attention (Jones, 2017; Shackleton et al., 2019).

Ecosystem alteration, loss of ecological resilience and the appearance of invasive species impact human health in several ways (Myers et al., 2013; Sandifer et al., 2015). Plant pathogen invasion in genetically-uniform crops can trigger famine and human migration, as illustrated by the role of fungal blight in the 1845 Irish Potato famine (Cox, 1978). Non-native human pathogens, animal disease or vector mosquitoes pose further public health risks (Phoofolo, 2003; Ricciardi et al., 2011; Medlock et al., 2012), which can be exacerbated by land-use change or environmental pollution (Myers et al., 2013). In agri-food systems, (human-mediated) biodiversity decline can degrade resilience to invasive pest establishment, proliferation or impact. It can further compromise food provisioning, downgrade nutritional value of harvested produce or impact welfare (Potts, 2010), while persistent anthropogenic pressure on ecosystem services can even derail entire civilizations (Mottesharrei et al., 2014). Such non-monetary assessments point to the contribution of nature to societal well-being (Daily et al., 2009) and indicate how losses may shape livelihood and social vulnerability. Yet, the social or human health repercussions of pest invasion or biodiversity loss are rarely measured.

One notorious invasive species is the cassava mealybug, *Phenacoccus manihoti* (Hemiptera: Pseudococcidae), a sap-feeding insect that arrived in Africa during the mid-1970s. Native to the Neotropics, *P. manihoti* adopts clonal (asexual) reproduction and relies upon different (natural, anthropogenic) means to disperse within and between cassava fields. Sustaining year-round viable populations and rapidly spreading across Africa's cassava belt (Herren and Neuenschwander, 1991; Blackburn et al., 2011), *P. manihoti* caused yield reductions of up to 80% on farms and across regions, sometimes leading to total crop loss (Supplementary Fig. 1). Cassava, *Manihot esculenta* (Euphorbiaceae), is a major food staple and vital source of carbohydrates for many farm families and urban people. At the time of the *P. manihoti* invasion, cassava constituted a basic energy for large parts of Africa's population, with an estimated 50 million people drawing over 500 kcal/day from cassava consumption (Cock, 1982). Though *P. manihoti* compromised food security at a continental scale, there were only a few published accounts of mealybug-induced famine e.g., in northwestern Zambia (Hansen, 1994). The populations of this invasive pest were then suppressed by the 1981 introduction of a host-specific parasitic wasp *Anagyrus lopezi* (Hymenoptera: Encyrtidae) from Paraguay (South America). This biological control (BC) project resulted in a yield recovery and generated Africa-wide economic benefits worth US $120 billion over approx. 30 years (Herren and Neuenschwander, 1991; Zeddies et al., 2001; Raitzer and Kelley, 2008). There have, however, been no comprehensive evaluations of how this agro-ecological imbalance (i.e., *P. manihoti* invasion) and its subsequent ecological restoration affected human health and livelihoods across Africa.

We draw upon historical invasion records, crop production statistics and human population data to quantify the extent to which invasive species and its ensuing BC impact food availability and human wellbeing in a subset of 18 mealybug-invaded countries of sub-Saharan Africa. These countries experienced comparable long-term precipitation deficits, remained unaffected by marked rainfall anomalies and did not suffer any drought-induced famine (Devereux, 2000), yet are typified by a pronounced deceleration in human population growth (Supplementary Fig. 2). The study region is further characterized by relatively even rates of contraceptive prevalence (Tsui et al., 2017) and remained outside the area impacted by 1986-1992 locust outbreaks, i.e., the Red Sea coastal plains of Sudan, Eritrea and the western Sahel (Showler et al., 2008). Using demographic metrics as proxies for wellbeing, we empirically assess 1) how mealybug-induced food system collapse in the mealybug-affected countries triggers a reduction in birth rate (i.e. post-invasion impacts); 2) how the *A. lopezi* release alleviated nutritional deprivation and its effects on livelihood and human health (i.e. post-introduction impacts); and 3) how upsets in biodiversity-mediated ecosystem services (i.e., natural biological control) have protracted effects on key livelihood assets. Our analysis uncovers the extent to which agro-ecological imbalance can influence human well-being over extensive geographical areas and prolonged time periods, and how a restored agro-ecosystem balance benefits human health.

Materials and Methods

Data

Invasion history for *P. manihoti* and associated country-level introductions of *A. lopezi* -as conducted during 1981-1995- were obtained from Zeddies et al. (2001), Neuenschwander (2001) and Herren et al. (1987). Country-specific patterns of cassava production (harvested area, ha; tonnes) and fresh root yield (tonnes/ha) were obtained for all mealybug-invaded countries through the FAO STAT database (http://www.fao.org/faostat/). Historical country-level records for a range of human demographic parameters were accessed through the World Bank Open Data portal (https://data.worldbank.org/). More specifically, country-specific data-sets were obtained for birth rate, death rate, fertility rate, rate of natural increase (RNI), infant mortality and adult mortality.

Analyses centered upon a total of 18 different African countries that were affected in the early stages of the mealybug invasion, primarily including countries in West and Central Africa (Herren et al., 1987). These constitute a sub-set of the 27 African nations that were impacted by *P. manihoti* (Zeddies et al., 2001). Our country selection was based upon Herren et al. (1987), thus excluding the following 9 countries - Burundi, Guinea Bissau, Guinea Conakry, Kenya, Mozambique, Niger, Tanzania, Uganda and Zambia. Here, some countries (Guinea Bissau, Guinea Conakry, Kenya, Mozambique, Tanzania, Zambia) were heavily impacted by *P. manihoti* but studied only at a period outside the one considered in this study. In others (e.g., Niger), only a fraction of the national territory is impacted by *P. manihoti*, or there was a concurrent arrival of *P. manihoti* and its introduced parasitoid (at later stages of the mealybug invasion, e.g., in 1992 for Uganda; Zeddies et al.,2001). Furthermore, for some (omitted) countries either no early assessment was made of mealybug presence or follow-up assessments of *A. lopezi* establishment and impact were impossible due to anomalies in public security (e.g., civil unrest, war or genocide in Burundi), politics and local research collaboration.

Temporal trends in cassava production

To assess changes in cassava production following the *P. manihoti* invasion and the *A. lopezi* introduction, we examined temporal shifts in country-level root yield and aggregate production. More specifically, we contrasted yield and production trends over three different time periods: a 5-year pre-invasion period, a post-invasion period of variable duration, and a post-introduction period that followed the first in-country detection of the parasitoid (Zeddies et al., 2001). We assume that *P. manihoti* gradually colonized cassava fields and inflicted yield loss following its initial in-country detection. During the initial phase of the biological control campaign, our experience revealed how *A. lopezi* successfully established in 70% fields of a given country over a three-year period and its biological control impacts became well-apparent five years following its first release, covering virtually all mealybug-infected fields (Herren et al., 1987; Neuenschwander et al., 1989; Zeddies et al., 2001).

Statistical analysis

We employed time series analysis to detect country-by-country, year-by-year effects of both post-invasion and post-introduction phases. First, in order to elucidate an unbiased global relationship between RNI, yield and birthrate between 1961 and 1995, independent of ecological conditions (i.e., post-invasion or post-introduction phase), time series data of each variable (i.e. RNI, yield and birthrate) were averaged across all severely impacted countries. On the averaged time series data, cross-correlation analysis was conducted between RNI and yield, and birthrate and yield, to understand the relationship between yield and the respective demographic variables without condition specifications. Correlation analysis was performed using the cross-correlation function (ccf) in base R (v 3.4.1). Time series were scaled using the scale function in timeSeries package (Wuertz et al., 2017) in R (v3.4.1). Each time series was differenced until stationarity was obtained, as assessed using the augmented dickey fuller test in R (v 3.4.1) package tseries (Trapletti and Hornik, 2018). R package ggplot2 (Wickham, 2016) was used to plot the time series using the area (geom_area) based metric. Structural changes in individual time series were assessed using the strucchange package (Zeileis et al., 2003) in R (v 3.4.1). Structural changes with respect to the number of breakpoints, and their respective confidence intervals, were selected based on the lowest Bayesian information criterion (BIC) and residual sum of squares values.

In order to elucidate multi-country impacts of yield shifts, we conducted a generalized additive regression model, using year-by-year shift values for cassava root yield, birth rate and RNI. For post-invasion regression analysis (i.e., to quantify impacts of *P. manihoti* attack), root yield, RNI and birth rate shifts corresponded to differenced values, between 5-year averaged values pre-invasion, with year-by-year value post invasion, prior to *A. lopezi* introduction. A dummy variable 'time-step' was constructed, that reflected the number of years since the *P. manihoti* invasion. To quantify impacts of biological control, a regression analysis was performed on proportional shifts in root yield, RNI and birth rate, as calculated by differencing their respective yearly post-invasion and post-introduction values with (5-year averaged) pre-invasion values. In this post-introduction regression analysis, a dummy variable representing the condition of 'biotic stress' was used to represent in-country mealybug and/or parasitoid presence (i.e., post-invasion and post- *A. lopezi* introduction). As the same time period was considered for all countries, and *P. manihoti* attack and *A. lopezi* introduction occurred at different country-specific time points, the number of shift value data points representing either post-invasion or post-introduction conditions for each country differed. Yet, this should not compromise the validity of the analysis, as regression analysis did not intend to capture effects within a single country but instead to quantify multi-country impacts. Sets of regression equations were computed for either RNI or birth rate as outcome variables, and time step, proportional yield shift for post-invasion analysis, and biotic stress and proportional yield shift were used as explanatory variables for the post-introduction analysis.

Due to the complex distribution of yield shift values, a Generalized Additive Model for Location, Scale and Shape (GAMLSS) approach was used for regression analysis. For each set, we compared three regression models, i.e. either using the dummy variable or yield shift as explanatory variables and a full factorial (both variables plus their respective interaction term). Goodness-of-fit of models was assessed by comparing the sets of regression equations for both the post-invasion and post-introduction phase, using the global Akaike information criterion score (AIC), CraggUhler Pseudo-R-squared metric between predicted and actual values of the demographic parameters (i.e., shifts in birth rate and RNI) as response variables. The fitDist function was used to identify the most suitable fit based on the AIC criterion, and the fit with lowest AIC score was used to fit the distribution for the response variables. For the post-introduction regression analysis, birth rate and RNI were fitted using sinh-arcsinh (SHASH) and skew type 3 (ST3) distributions, respectively. For the post-invasion regression analysis, birth rate and RNI were fitted using a Gumbel distribution (GU) and skew normal type 2 (SN2) distribution, respectively (Supplementary Fig. 3). Regression analysis was performed using the GAMLSS package in R (v 3.4.1) (Harezlak et al. 2018).

Results

Descriptive statistics

Demographic time series revealed declining trends in birth rate during 1975-1989 and a steep decline in the rate of natural increase (RNI) over 1980-1986, followed by an upward trend (Fig. 1). The above period was equally marked by two consecutive events of cassava yield reduction, with the largest yield reductions during 1978-1982 (Fig. 1). Analysis of structural changes of each time series revealed no breakpoints in yield across time, three breakpoints for birthrate (i.e., years 1974, 1978 and 1982), and three for RNI (i.e., 1976, 1980, 1984). More specifically, the 1978 and 1982 breakpoints for birthrate, and the 1980 breakpoint for RNI (with decline starting from 1978), coincided with a time period that witnessed two subsequent yield reduction events, unlike the remaining time period, wherein the trend was typified by alternating yield increases and decreases. Temporal trends in crop yield and demographic parameters thus reflected a gradually expanding mealybug distribution, from the mid-1970s onwards.

To validate whether these trends related to the mealybug invasion (i.e., post-invasion) or parasitoid release (i.e., post-introduction), we analysed data around the dates of mealybug invasion and parasitoid release for each individual country. Across sub-Saharan Africa, the mealybug invasion coincided (i.e., post-invasion) with a 18.1 ± 29.4% (average ± SD) decline in cassava root yield and a 17.6 ± 28.3% drop in aggregate production over the subsequent 1-11 years (Table 1; Supplementary Table 2). Following deliberate parasitoid releases (i.e., post-introduction) in all mealybug-invaded countries, a 28.1 ± 34.5% increase of yield and a 48.3 ± 50.7% increase in production were recorded over variable time periods. Important inter-country differences were observed between the successive time periods (i.e., pre-invasion, post-invasion and post-introduction), for both root yield and aggregate production (Table 1; Supplementary Table 2). Maximum pest-induced shocks in yield and production were recorded for Rwanda (-84.3%) and Senegal (-86.7%), respectively. Following the *A. lopezi* introduction, the largest recovery in cassava yield and production occurred in Togo (+ 113.5%) and Senegal (+ 208.0%), respectively.

Across all 18 African countries, the post-invasion phase was equally typified by declines in birth rate, natural rate of increase (RNI), fertility rate and increases in adult mortality rate (Fig. 2; Table 2). The largest drops in birth rate were recorded for Ghana (9.6%), Togo (10.1%), Rwanda (11.6%) and Senegal (12.30%) (Supplementary Table 1). An annual reduction of 377,943 births and a deceleration of RNI by 156,493 was estimated across all 18 African countries affected by early *P. manihoti* invasions. Over the 10.0 ± 3.6 year-long period of *P. manihoti* invasion, this was equivalent to a net loss of 3.26 million births regionally.

Conversely, following the *A. lopezi* introduction, several of the above demographic parameters were restored. More specifically, infant and adult mortality rate decreased by a respective 6.4% and 11.4%, life expectancy grew with 6.7 years and birth rate rose by 5.6% as compared to the post invasion period (Fig. 2, Table 2). In countries such as Ghana, Togo, Senegal or Côte d'Ivoire, birth rate increased by 9.1-12.1% between the post-invasion and post-introduction phase (Supplementary Table 1).

Human demographic impacts of pest invasion and biological control

We examined year-by-year impacts of yield changes and in-country presence of biotic stressors (i.e., the invasive *P. manihoti* and its antagonist *A. lopezi*) on demographic parameters for two specific events (i.e., post-invasion, post-introduction), using generalized additive regression modelling. During the post-invasion phase, full-factorial models (i.e., Interaction model; Table 3) with a time-step and yield shift provided the best goodness-of-fit with respect to Akaike

Information Criterion (AIC; AIC = 190.84 and 179.99 for shifts in birth rate and RNI respectively), and Pseudo R-squared values (0.13 and 0.15 for shifts in birth rate and RNI respectively), as compared to other models that had either time step or yield shifts separately as predictors (Table 3). Interaction models yielded significant negative impacts of the interaction term, i.e., yield-shift x time-step (Estimate: -0.21 and -0.19 for shifts in birth rate and RNI; Table 3) on both demographic parameters.

During the post-introduction phase, full-factorial models with the interaction term of biotic stress x yield-shift provided the best fit (AIC = 497.54 and 216.93, Pseudo R^2 values of 0.29 and 0.60 for shifts in birth rate and RNI, respectively) as compared to other models (Table 3). Similar to the post-invasion phase, interaction models revealed a significant impact of the interaction term on shift values of both demographic parameters (Estimate: -0.32 and -0.20 for shifts in birth rate and RNI; Table 3).

Discussion

Invasive terrestrial invertebrates cause major economic impacts, with insects inflicting US $70 billion per year globally in direct costs (Bradshaw et al., 2016). Such monetary analyses do not fully capture the long-term adverse effects on biodiversity-mediated ecosystem services, e.g., the US $400 billion annual service of natural biological control (BC) (Costanza et al., 1997), and only reveal a part of their broad societal impacts. Here, we demonstrate how a crop-damaging insect pest contributed to multi-country declines of birth rate and fertility rate, compounded by elevated adult mortality. By inducing a primary productivity loss of cassava; one of Africa's main food staples and a valued source of dietary carbohydrates (Cock, 1982), *P. manihoti* plausibly triggered sequential periods of food insecurity and nutritional deprivation along its 1970-1980s invasion path. Mirrored in an elevated mortality, the mealybug conceivably caused hardship and deepened poverty for some 162 million people in the 18 African countries over a 10-year period. Though an increased availability of contraception, vaccination, female education (e.g., on family planning) and public health investment might have contributed to a slower population growth and lifted infant survival, our analyses show a close association with pest-induced cassava yield drops. The 1981 *A. lopezi* release permanently resolved continent-wide mealybug issues (Neuenschwander, 2001), contributed to a 48% (absolute) recovery of crop output and enabled parallel improvements in multiple demographic indices (e.g., 6.4-11.4% drops in infant and adult mortality, respectively; Table 1, 2). In the absence of data, birth rate is a comparatively poor indicator of human health while infant mortality captures the demographic reality of a BC-assisted recovery in cassava production. This illustrates the social and human health repercussions of ecological upsets in subsistence farming systems, providing lessons for global efforts to resolve food insecurity, mitigate invasive species and safeguard functionality and resilience of agroecosystems.

Our estimates of mealybug-induced yield loss and parasitoid-mediated yield recovery are cautious and at the lower bounds of outcomes (Zeddies et al., 2001). The use of coarse-grained government statistics conceivably under-estimated BC-mediated yield gains in various contexts, e.g., a recorded 50-97% loss reduction in the vulnerable savanna zone of Ghana (Zeddies et al., 2001; Neuenschwander et al., 1989). The parallel invasion of the spider mite *Mononvchellus tanajoa* (Yaninek et al., 1993), releases of improved cassava clones and civil wars or genocide (e.g., Rwanda) further obscure BC-related yield gains in certain countries. Though drought is a recurring feature of African agriculture and a key determinant of famine, climatic variability likely only affected cassava yield loss (or recovery) to minor extent (Jarvis et al., 2012; Supplementary Fig. 1). Typically, small countries showed clearer impacts because BC deployment resulted in a swift yield recovery registered across national territories. In large countries *P. manihoti* expanded still in some provinces, while *A. lopezi* already diminished the pest impact in others. Furthermore, our exclusion of nine countries where *P. manihoti* and *A. lopezi* either arrived simultaneously, multiple invasion instances occurred, or ground-truthing did not cover the entire country because of civil unrest precluding further surveys will have led to an underestimation of continental-scale BC benefits. Nonetheless, our work confirms earlier assessments of the agronomic impacts of *A. lopezi* for e.g., Nigeria or Ghana, and reliably captures its benefits for food security (as part of wider integrated pest management -IPM- programmes).

Diagnosing food insecurity is difficult, and food availability measures have low predictive accuracy (Sen, 1981; Barrett, 2010). Extended periods of food shortage and malnutrition regularly progress into famine and population loss (Scrimshaw, 1987). Though some records confirm mealybug-induced famine at certain locations (Hansen, 1994), our reports of lowered birth rate and increased mortality signal important population level outcomes across many countries due to deprivation (Scrimshaw, 1987; Kane, 1987). Crop failure can influence direct food entitlements amongst farmers and non-farmers, driving up food prices (Sen, 1981; Kane, 1987; Swinnen and Squicciarini, 2012). Nutritional deprivation can thus bring about social upheaval (e.g., disrupted family structure, delayed marriages, migration), leading to psychological disruption and lowered resistance of malnourished populations to disease attack (Cox, 1978; Painter et al., 2005).

Given the distinctive impacts of invasive species on livelihoods, proactive mitigation strategies will be essential so that agro-ecosystems will be able to sustain the delivery of ecosystem services under a range of external stressors (Ricciardi et al., 2011; Pretty et al., 2018; Early et al., 2016; Jones, 2017; Shackleton et al., 2019). Our food systems framework allowed fusing ecological facets of global change, such as species invasion with their social or human aspects, and thus permitted a reliable interpretation of their societal outcomes (Ericksen, 2008; Ingram, 2011). As basis for many of today's food systems, agricultural production systems seldom provide simultaneous positive outcomes for ecosystem service provisioning and human well-being (Garibaldi et al., 2017; Rasmussen et al., 2018), often allowing biotic shocks to cascade into socio-economic domains (Wyckhuys et al., 2018). Also, the synthetic pesticides that are habitually used to safeguard agri-food production from (endemic, invasive) pest attack can compromise human health either directly (i.e., occupational exposure) or indirectly (i.e., dietary intake of tainted produce). Insecticides were also tested against cassava mealybug on agricultural experiment stations, but among resource-poor African smallholders in the 1970s and 1980s there was never a wide-spread use of synthetic insecticides on cassava – i.e., a low-value staple crop. A stabilization or strengthening of the ecological foundation of food systems could thus bolster resilience, alleviate the environmental burden of pesticides and reduce other negative externalities (Cox, 1978; Fraser et al., 2005). One way to achieve this is through ecological intensification: an integrated set of interventions that harness ecosystem services, conserve crop yields and often enhance farm profit (Bommarco et al., 2013; Garbach et al., 2017). Such sustainable or ecological intensification of agriculture consistently produces 'win-win' outcomes for natural and social capital (Pretty, 2003; Rasmussen et al., 2018), asking for a targeted redesign of conventional farming systems (Pretty et al., 2018; Reganold and Wachter, 2016; Eyhorn et al., 2019). This kind of transformation is enabled by consciously prioritizing resource-conserving biodiversity-based approaches, and by integrating agro-ecological metrics in government decision-making or food crisis vulnerability diagnostics along the food value chain (Sukdev et al., 2016; Gordon et al., 2017).

As an environmentally-sound approach to pest management, biological control has enabled the long-term suppression of over 200 invasive insect species at favorable benefit:cost ratios, often surpassing 1,000:1 (Bale et al., 2007; Naranjo et al., 2015; Heimpel and Mills, 2017; Neuenschwander, 2004; Norgaard, 1988). Four other large-scale biological control projects benefitted the same African farmers who experienced *P. manihoti* biological control, generating staggering economic dividends and important (though unquantified) effects on human health (Neuenschwander, 2004). Though unintended ecological upsets resulted from mis-guided releases of vertebrates or generalist arthropod predators in the early-1900s, the science of BC has advanced greatly over the past decades. Modern biological control has centered on a careful selection of a specialized natural enemy (e.g., the monophagous parasitoid *A. lopezi*). Ensuring durable, cost-effective control of crop pests, BC can deliver improvements to human health and further economic outcomes (Bale et al., 2007; Naranjo et al., 2015), thus becoming a valuable service for resource-poor farmers. While a scientifically-guided introduction of natural enemies can restore ecological balance and diverse, extra-field habitats tend to support biological control, a field-level reliance on biodiversity-friendly practices is pivotal to the effective conservation of agro-ecosystems' natural functionality (Landis et al., 2000; Karp et al., 2018). Disruptive agrochemical-based interventions can accelerate pest proliferation and reduce biological control benefits (Losey and Vaughan, 2006; Geiger et al, 2010; Lundgren and Fausti, 2015). We have illuminated here how one example of biological control boosted on-farm functional biodiversity, increased productivity, and may have generated broad societal dividends. We equally encourage other studies to characterize these often-overlooked downstream societal impacts.

Invasive species attack, biodiversity depletion and ecosystem simplification undermine several of the UN Sustainable Development Goals (Dobson et al., 2006; Cardinale et al., 2012; Bradshaw et al., 2016; Oliver et al., 2015). This study shows how, during its 1970s-80s passage through sub-Saharan Africa, the invasive *P. manihoti* instigated food system collapse, impacted human health and compromised the well-being of millions of Africans. Though ecological and economic facets of the mealybug invasion (and its biological control) had been investigated, its human livelihood repercussions so far had been obscured. Yet, in order to meet SDG implementation targets, integrative social-ecological approaches and a deliberate recognition of inter-sectoral linkages are necessary (Brondizio et al., 2016; Stafford-Smith et al., 2017). As such, we not only reveal how biological control fortifies agro-ecosystem functionality and restores food security (Godfray et al., 2010; Stephens et al., 2018), but also generates positive spillover benefits for societal welfare (Pretty et al., 2018; Rasmussen et al., 2018). If the current combined health and biodiversity crises are indeed a warning sign of impending agro-ecological imbalance, similar nature-based approaches can prevent socio-economic hardship from becoming a recurrent feature of our uncertain future.

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Data Availability

All data underlying the analyses are made available through Dryad Digital Repository at https://datadryad.org/stash/share/fgSgfpj9o-u1wvY1y_PFkWp_Djt9RA_fTPJSGCN4csI.

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Tables and Figures

Figure 1. Scaled and stationarized time series values for cassava root yield, rate of natural increase (RNI) and birth rate across all 18 mealybug-invaded countries, over a 1960-1995 time window. Significant drops can be observed in human demographic parameters from the mid-1970s onwards, coincident with the progressive continent-wide invasion of the cassava mealybug and the associated inflated variability in root yield. The largest drops in cassava yield are recorded during 1978-1982.

Figure 2. Percentual shifts in infant mortality (/1,000 live births) during the mealybug invasion and ensuing *A. lopezi* introduction, for 18 sub-Saharan African countries. Percent annual change is computed at a country-level either between the five years pre-invasion (averaged) and the post-invasion minima, and between the former pre-invasion measure and averages for a (max. 10-year) post-introduction recovery phase. All analyses are conducted over a 1965-1995 window. Data are missing for Gabon and Angola. Population loss in Rwanda (see also Supplementary Table 1) can be partially ascribed to the country's 1990-1994 civil war and genocide.

Table 1. Temporal changes in country-level cassava fresh root yield (tonnes/ha) over a 1965-1995 time period, comprising the *P. manihoti* invasion and ensuing *A. lopezi* introduction. The (country-specific) percentage of cassava in savanna systems reflects the relative vulnerability of local cassava production systems to *P. manihoti* impact[29]. For each country, percent change in yield is computed either between averaged pre-invasion values and the respective post-invasion minima, and between the post-invasion minimum and respective averages over a parasitoid-induced recovery phase.

Table 2. Shifts in cassava production and human demographic parameters (average ± SD) following the mealybug-invasion and *A. lopezi* introduction, as averaged across 18 African countries over a 1965-1995 window. For each parameter, percent change is computed at a country level either between averaged pre-invasion values and the respective post-invasion

minima, and between the post-invasion minimum and respective averages over a parasitoid-induced recovery phase. In the recovery phase, a 5-year period is included to account for a gradual in-country establishment of *A. lopezi*. Though (region-wide) infant mortality declined during the post-invasion phase, a far steeper drop is recorded following the *A. lopezi* introduction.

Table 3. Generalized additive regression models for proportional shifts in rate of natural increase (RNI) and birth rate following the *P. manihoti* invasion (post-invasion) and *A. lopezi* introduction (post-introduction). Explanatory variables include yield shift between pre-invasion values yearly post-invasion values, and in the case of post-introduction analysis, yield shifts between pre-and post-introduction of *A. lopezi*. For post-invasion analysis, an additional variable named “time step” was included, reflecting time since mealybug invasion, while for post introduction, an additional variable ‘biotic stress’ was included, reflecting in-country mealybug or parasitoid presence. Three different regression models were contrasted, for which µ coefficient estimates and corresponding p-values are represented (additional information in the text).

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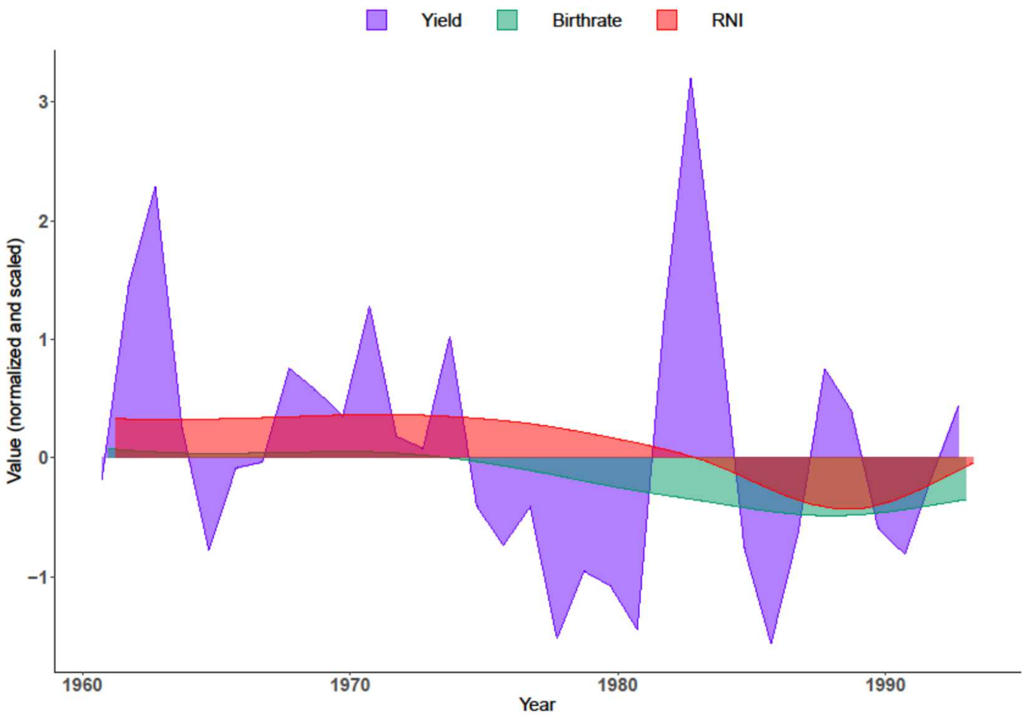

Figure 1.

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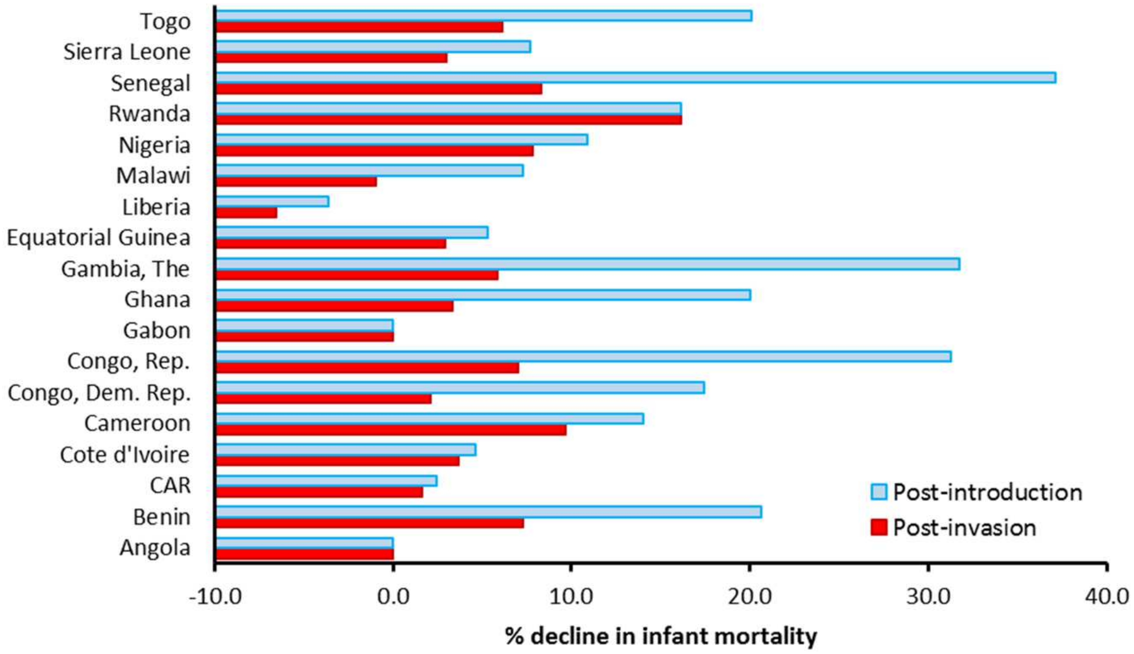

Figure 2.

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Table 1.

Country	**% cassava in savanna**	**Pest-induced shocks (% change of pre-invasion baseline)**	**Parasitoid-mediated recovery (% change of invasion baseline)**
Congo, Dem. Rep.	45	- 3.40	+ 18.81
Congo	60	+ 3.33	+ 44.09
Central African Republic	75	- 13.27	+ 11.46
Gabon	20	- 1.00	+ 0.08
Benin	95	- 12.27	+ 23.75
Angola	18	- 6.17	+ 13.31
Ghana	67	- 16.31	+ 27.72
Liberia	10	- 15.01	+ 2.82
Nigeria	15	- 10.61	+ 16.12
Togo	95	- 79.06	+ 113.49
Cameroon	29	+ 42.83	+ 12.64
Côte d'Ivoire	40	- 0.66	+ 1.88
Equatorial Guinea	0	- 14.56	+ 1.08
Rwanda	0	- 84.33	+ 106.94
Malawi	89	- 52.53	+ 24.38
Sierra Leone	60	- 20.16	+ 69.30
Senegal	100	- 30.30	+ 19.01
Gambia	-[a]	- 12.35	- 1.67
Regional average (average ± SD)		**- 18.10 ± 29.45**	**+ 28.07 ± 34.53**

[a]: No data.

Table 2.

Parameter	**Pre-invasion baseline**	**Post-invasion phase (% change of pre-invasion baseline)**	**Recovery phase (% change of invasion baseline)**
Cassava yield (tonne/ha)	6.55 ± 3.59	-18.10 ± 29.45	28.07 ± 34.53
Production ('000 tonne)	1,692 ± 3,221	-17.61 ± 28.30	48.26 ± 50.74
Birth rate (per 1000 people)	47.09 ± 4.21	-5.75 ± 3.93	-0.17 ± 0.53
Death rate (per 1000 people)	19.11 ± 3.70	1.35 ± 22.72	-12.76 ± 12.45
RNI (per 1000 people)	27.98 ± 3.99	-4.47 ± 15.41	4.66 ± 7.32
Fertility rate (per 1000 people)	6.77 ± 0.75	-5.47 ± 5.70	0.02 ± 1.86
Infant mortality rate (per 1000 people)	126.52 ± 22.55	-4.84 ± 5.02	-11.28 ± 10.27
Adult mortality rate (per 1000 people)	404.96 ± 46.72	3.73 ± 14.10	-7.66 ± 9.33
Life expectancy (years)	46.60 ± 4.62	0.08 ± 8.25	6.77 ± 7.73

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Table 3.

Response variable	**Model**	**Predictor variable**	**Estimate (µ coefficient)**	**p-value**
Post-invasion				
Birth rate	1	Time step	- 0.032	0.432
	2	Yield shift	0.328	0.005 **
	3			
		Time step	- 0.001	0.984
		Yield shift	0.831	0.001**
		Interaction	- 0.218	0.048*
RNI	1	Time step	0.098	0.007**
	2	Yield shift	- 0.009	0.942
	3			
		Time step	0.177	1.6e-05 ***
		Yield shift	0.697	0.233
		Interaction	- 0.195	0.001 ***
Post-introduction				
Birth rate	1	Biotic stress	0.504	1.10e-08***
	2	Yield shift	0.180	0.0003***
	3			
		Biotic stress	0.656	6.97e-11***
		Yield shift	0.454	8.01e-13***
		Interaction	- 0.323	0.001***
RNI	1	Biotic stress	- 0.009	0.936
	2	Yield shift	0.220	2.00e-16 ****
	3			
		Biotic stress	0.011	0.256
		Yield shift	0.396	0.005**
		Interaction	- 0.208	0.092