Future shock: forecasting a grim fate for the Earth

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In recent years, much attention has focused on the potential environmental effects of global climate change, but other anthropogenic impacts might be even more important. A new study by Tilman *et al.* highlights the threat posed to natural ecosystems worldwide by increasing agricultural development. Over the next 50 years, model projections suggest that rates of habitat destruction, water consumption and emission of agricultural pollutants will increase drastically. Such changes will be greatest in developing nations, which sustain a disproportionately large fraction of the Earth's biological diversity.

What sort of world will our children inherit? A recent article by Tilman *et al.*[1] suggests that it will be far more crowded and less habitable than the world that we occupy today.

During the last century, the world changed profoundly as a result of dramatic improvements in technology, medicine and agricultural methods, leading to an even more dramatic growth of the human population. In 1900, there were only 1.6 billion people on Earth, but this had nearly quadrupled by the end of the century[2]. The global population is still rocketing upward (Fig. 1), driven largely by the rapid growth in developing nations, and it is expected to reach 7.5 billion by the year 2020 and ~9 billion by 2050 (Ref. 3).

In addition to having an expanding population, humans are consuming ever more resources and energy. Average consumption, as measured by per-capita Gross Domestic Product (GDP), rose by an astonishing 460% over the last century[4]. Current values are projected to increase by 240% by the year 2050, as ever-larger segments of the population of the world adopt the consumptive lifestyles of industrial nations[5]. If this occurs, per-capita GDP will have jumped 11-fold since the year 1900.

Because of a burgeoning populace and rising wealth, human impacts on the global ecosystem are increasing exponentially. Humans currently appropriate 40% of terrestrial productivity[6], exploit half of the useable freshwater on Earth[1], and have destroyed or degraded vast expanses of natural habitat. Global biogeochemical cycles of carbon[7], nitrogen[8] and phosphorus[9] have been fundamentally altered, leading to widespread anthropogenic impacts on climate and natural ecosystems. Exotic species are being introduced to new ecosystems so rapidly that some biologists refer to the present era as the 'Homogeocene'[10]. These myriad changes are driving a mass-extinction event that could ultimately rival the most catastrophic episodes in the geological history of the Earth[11,12].

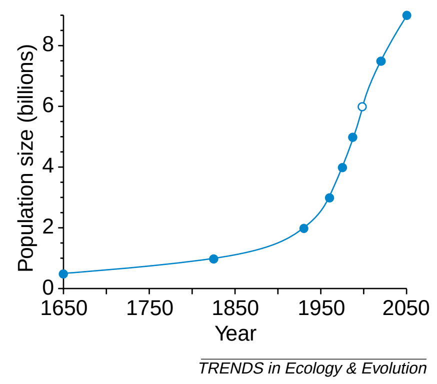

Fig. 1. Rapid growth of the human population from 1650 to 2050 (data taken from Ref. 2). The curve was fitted by a cubic spline function. The current population is indicated by the open circle.

Forecasting the future

The dramatic rise in population and in affluence means that demand for food will increase sharply over the next 50 years. According to Tilman *et al.*, meeting this demand will require an effort that is comparable to the Green Revolution, during which low-yield, labor-intensive farming systems in developing countries were replaced by Western industrialized agriculture based on new 'miracle crops' that required large inputs of fertilizer, irrigation and pesticides. Although the environmental costs of the Green Revolution were exceedingly high (Box 1), global grain production grew by 250% between 1950 and the early 1990s (Ref. 2).

Box 1. Major environmental impacts of modern agriculture[a–d]

- Nitrogen (N) and phosphorus (P) from synthetic fertilizers enter surface and groundwaters (either through leaching or via untreated livestock or human wastes), and N is also volatilized to the atmosphere and deposited regionally. P pollution causes eutrophication of freshwater streams and lakes, whereas N causes eutrophication of estuaries and coastal seas, biodiversity losses in terrestrial and aquatic systems, groundwater pollution, increases in the greenhouse gas nitrous oxide, which also destroys trophospheric ozone, and acidification of sensitive soils and freshwaters.
- Irrigation increases salt and nutrient loading to downstream aquatic ecosystems, can cause salinization of soils and has impacts via damming of rivers and water harvesting. Many areas have insufficient water to meet projected demands.
- Pesticides (insecticides and herbicides) can cause environmental degradation or affect human health. Some pesticides, such as chlorinated hydrocarbons, persist for long periods and bioaccumulate in food chains and surface waters. Many insect pests and some weeds have evolved pesticide resistance.
- Habitat conversion for agriculture is a key driver of species extinctions and is also the leading cause of habitat fragmentation. Interactions among habitat loss, fragmentation and other simultaneous environmental changes will undoubtedly lead to many future extinctions.

References

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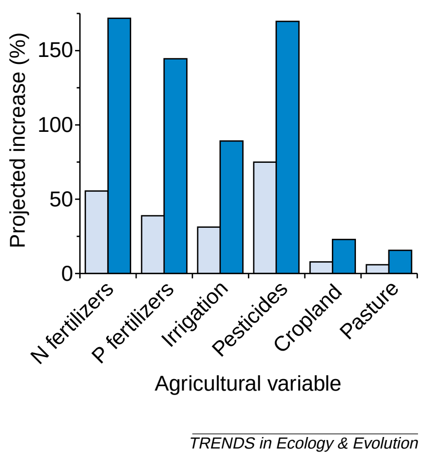

Fig. 2. Projected increases in nitrogen (N) and phosphorus (P) fertilizers, irrigated land, pesticide use, and total areas under crops and pastures by the years 2020 (light-blue bars) and 2050 (dark-blue bars; data taken from Ref. 1).

Tilman *et al.* used projected global trends in population and GDP to forecast future changes in major agricultural parameters. A key assumption of their approach was that agricultural expansion would continue along the same trajectory as during the past 35 years. Throughout this period, global use of fertilizers, pesticides and irrigation, and the total area under crops and pasturelands, all rose rapidly and in a nearly linear fashion. Moreover, during this interval, these agricultural variables were strongly and linearly related to both GDP and population size ($R^2 > 95\%$ in most cases)[1]. Because the trends were linear, Tilman *et al.* used simple linear regressions to extrapolate agricultural trends into the future using time and projected increases in global population and GDP as predictors. Multiple regressions were also employed to assess the combined effects of all three predictors. Results from the various regression models were then merged into a single average forecast for each agricultural variable.

Tilman *et al.* made separate forecasts for the years 2020 and 2050 (Fig. 2). Largely as a result of synthetic fertilizers, humans already release as much nitrogen and phosphorus to the environment as all natural sources combined[2,8]. Yet by 2050, global nitrogen fertilization is projected to rise by 270% whereas phosphorus use increases by 240%. Agricultural demands for irrigation water are expected to grow by 190% over the same period. Global pesticide production has risen at least tenfold over the past 40 years[1,2], and is expected to increase by 270% over current levels by the year 2050 (Ref. 1).

Land conversion for agriculture is also projected to rise sharply over the next 50 years (Fig. 2). The net area of pasture and cropland are expected to increase by 540 and 350 million ha, respectively, in spite of a predicted loss of 140 million ha of agricultural land in industrial nations (these lands will be converted to urban or suburban uses, reforested, abandoned, or used in other ways). This implies that, during the next 50 years, approximately one billion ha of natural ecosystems will be converted to agricultural land in developing nations.

It must be noted that many of the projections by Tilman *et al.* have relatively high variances, in the sense that different regression models and predictors (time, population, GDP, or all three combined) produced varying results[1]. Even the most optimistic projections, however, suggest that agricultural pressures on natural ecosystems will increase drastically in the future.

Alarming implications

To many, the projections of Tilman *et al.* are more than sobering – they are just plain frightening. So much attention has focused on global warming in recent years that it has been easy to forget at times that other human impacts could pose even greater threats to environmental quality. The conversion of one billion ha of land to agricultural use in developing nations would cause a worldwide loss of natural ecosystems of an area larger than that of the USA (Ref. 1). Absolute habitat destruction will be greatest in Latin America and sub-Saharan Africa[1,2,13], with large proportional declines in Asia[14], and could lead to the loss of approximately one third of all remaining natural tropical and temperate ecosystems, as well as many of the environmental services that they provide[1].

The threats to biodiversity will be unprecedented, in part because projected population increases will be greatest in species-rich tropical areas with high proportions of endemic taxa. Of 25 identified biodiversity 'hotspots' worldwide[15] (e.g. Madagascar and the Indonesian Archipelago), 19 have populations that are growing more rapidly than that of the Earth as a whole, and at least 16 have large numbers of people suffering extreme hunger and malnutrition[16]. Already, 45% of the major nature reserves of the world are being used heavily for agriculture[17], and many more are being isolated by encroaching agricultural lands. Such pressures will only rise in the future.

It is important to emphasize, moreover, that natural ecosystems and species are being threatened not only by habitat destruction, but also by the combined effects of many simultaneous environmental changes that often interact additively or synergistically[17]. The collective effects of habitat loss, fragmentation and biological invasions will pose critical threats for many species. Global climate change will threaten those species that are unable to migrate across hostile landscapes to reach new areas with appropriate climates and soils. Fundamental changes in biogeochemical cycles, water availability and pesticide release will further damage ecosystem functioning.

Studies such as that of Tilman *et al.* should be a call to arms for scientists and other aware citizens. Unless serious actions are taken quickly to slow population growth and reduce its burgeoning environmental impacts, the net result will be an unstable, biologically depauperate world, more hostile for humans and the other denizens of the Earth alike.

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The point of love

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During the final stages of courtship, helicid land snails pierce each other with calcareous 'love darts'. This bizarre sexual device has been claimed to be a nuptial gift or an indicator of the readiness of a 'shooter' to mate. However, these explanations are not supported by new work, which shows instead that mucus introduced with darts paralyses the female reproductive tract, allowing sperm to avoid female digestion and so make it in greater numbers to the sperm storage sacs. Love darts increasingly look like male instruments that are designed to manipulate females, although a role in mate choice cannot be excluded.

Hermaphrodite helicid land snails, such as the garden snail *Helix aspersa*, are known for their elaborate courtship. In spite of the slime, this seems almost human, involving circling, touching, kissing (lip–lip and lip–genital), biting and sequential eversion of the genital apparatus. After 30 min of these courtship preliminaries, one snail pushes against the other, everts its dart sac and shoots a sharp and pointed dart into its partner, an event that is usually soon reciprocated by the partner. Shooting is a misnomer, as the dart is really forced into the body of the recipient. Full penis eversion by both individuals (which then engage in simultaneous intromission) takes place only after both shootings have occurred.

Dart shooting and penetration are not necessary for copulation to proceed[1,2]. Virgins lack darts altogether but still mate, as do snails that fail to hit the target. Poor shots abound, with ~33% of darts missing or failing to penetrate (Fig. 1). Darts are not re-used and the process of regeneration takes several days; some individuals are therefore unable to shoot because their dart sacs are empty[2].

Darts increase sperm storage

The adaptive function of the love dart to the shooter and recipient has attracted much discussion, but remains a long-standing mystery. New experimental studies[3–6] have now gone a long way in clarifying the shooter's function. The experiments demonstrate how darts increase male reproductive success by promoting sperm survival in the hostile environment of the reproductive tract of the female.

In many species, sperm are deposited in their millions but only survive in their thousands[7]. *Helix aspersa* is no exception because it transfers a spermatophore with between one and ten million sperm in each copulation, but only 0.025% survive[3]. Most sperm are diverted away from the sperm storage organs into a blind sac, the bursa copulatrix (Fig. 2)[5], within which they quickly become immobilized and digested by secretions[8].

To test whether darts affect sperm storage, Rogers and Chase mated virgins to mature snails that had been isolated for several days[3]. Pairs (virgin–mature) were isolated and categorized into those where the dart of the mature snail penetrated deeply into the virgin, and those in which the dart missed. Cases of ambiguous dart success, for example when the dart penetrated but quickly fell out, were excluded from further analysis. Dissection of the sperm storage organ of the virgin a week later revealed that successful dart shooters doubled the number of sperm reaching the sperm storage organs.

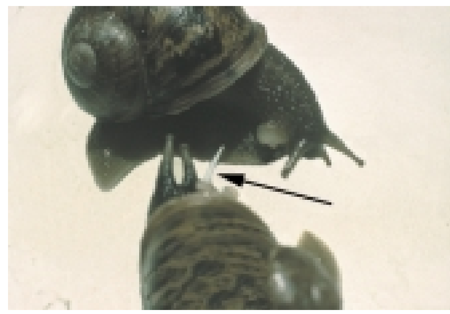

Fig. 1. Two courting *Helix aspersa* snails. The dart (arrow) is being retracted by the shooter. Reproduced, with permission, from Michael Landolfa.

The mechanistic basis of the dart appears to lie in a physiological effect that it causes on the female genital tract. When the dart is shot, it is covered by mucus derived from the digitiform glands of the donor[1]. When digitiform gland extracts are placed on the female reproductive organs, they cause a reconfiguration of the copulatory canal[5]. This opens up the tract leading to the sperm storage organ and closes off the bursa copulatrix (Fig. 2). In addition, the extracts cause an increase in peristaltic movements of the sperm storage organ, presumably leading to a greater movement of sperm into storage.

These results suggest that the dart itself is not the proximate cause of greater sperm storage. Rather, they support the idea that the dart is a means of injecting digitiform gland mucus into a mating partner. The effectiveness of dart shooting presumably varies with the ability of the shooter to hit and penetrate deeply into the body of its partner, and so to deliver higher concentrations of mucus. This remains to be tested, but there is some indication of a quantitative response. In the virgin–mature mating experiment[3],

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