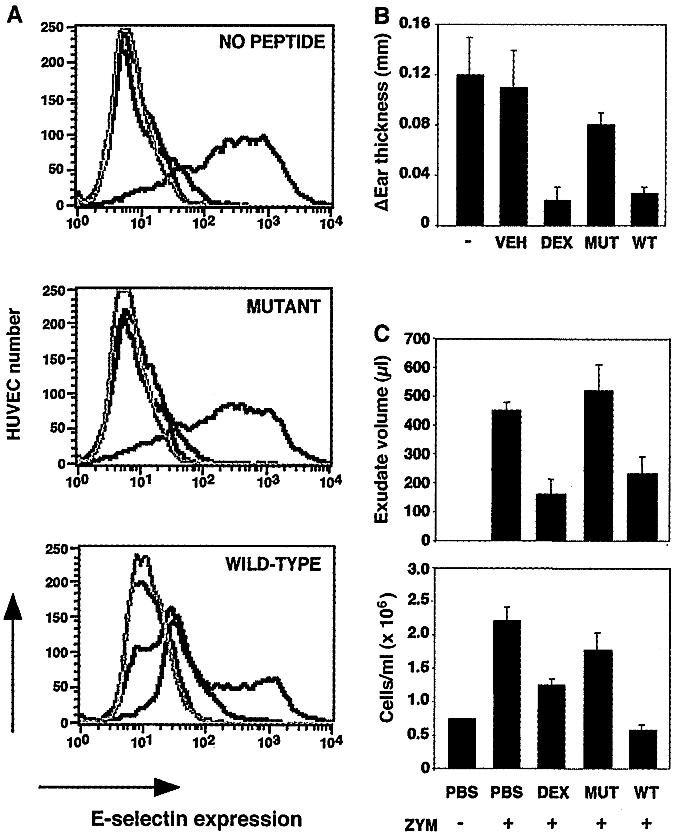

Fig. 5. The wild-type NBD peptide inhibits NF-κB–induced gene expression and experimentally induced inflammation. (**A**) Human umbilical vein endothelial cells were incubated for 2 hours with mutant (middle) or wild-type (bottom) NBD peptides (100 μM) then stimulated with TNF-α (10 ng/ml) for 6 hours. Control cells (top) received no peptide. Cells were stained with either anti–E-selectin (H4/18) or a nonbinding, isotype-matched control antibody (K16/16) and expression was measured by FACS [FACSort, Becton Dickinson, Paramus, NJ (*27*)]. The profiles show E-selectin staining in the absence (black) and presence (red) of TNF-α and control antibody staining under the same conditions (blue, no TNF-α; green, +TNF-α). (**B**) PMA-induced ear edema in mice topically treated with vehicle (VEH), dexamethasone (DEX) or NBD peptides was measured as described (*20, 21*). (**C**) The effects of the NBD peptides and dexamethasone (DEX) on Zymosan (ZYM)-induced peritonitis in mice were determined as described (*22*). Control mice were injected with phosphate-buffered saline (PBS).

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20. Ear edema was induced in replicate groups of mice (C57BL/6NCR) as described previously (*21*). Briefly, 20 μl of either NBD peptide (200 μg/ear), dexamethasone (40 μg/ear) or vehicle (DMSO:ethanol, 25:75 v/v) was applied to the right ear of mice 30 min before and 15 min after the application of 20 μl of PMA (5 μg/ear) dissolved in ethanol. Swelling was measured 6 hours after PMA application by using a microgauge (Mitutoyo America, Aurora, IL) and expressed as the mean difference in thickness between the treated and untreated ears.
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25 May 2000; accepted 29 June 2000

Predictions of Biodiversity Response to Genetically Modified Herbicide-Tolerant Crops

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W. J. Sutherland[1]

We simulated the effects of the introduction of genetically modified herbicide-tolerant (GMHT) crops on weed populations and the consequences for seed-eating birds. We predict that weed populations might be reduced to low levels or practically eradicated, depending on the exact form of management. Consequent effects on the local use of fields by birds might be severe, because such reductions represent a major loss of food resources. The regional impacts of GMHT crops are shown to depend on whether the adoption of GMHT crops by farmers covaries with current weed levels.

There is a growing research interest in the potential effects of the release of genetically modified (GM) crops (*1*) on biodiversity. This is prompted by concerns relating to the direct impact of GM crops on target organisms and the indirect effects on the wider environment. The environmental debate has to be set within a biodiversity landscape that is already affected by the intensification of agriculture (*2*). Although, in some senses, the introduction of GM crops may be no different than the introduction of any other technology that leads to the further intensification of agriculture, this new technology might offer a uniquely rapid increase in intensification.

We modeled the effects of the introduction of a herbicide-resistant sugar beet (a spring-sown crop grown throughout Europe and North America) on the population dynamics of an annual weed, *Chenopodium album*. This weed occurs worldwide, and its seeds are an important source of food for farmland birds (*3, 4*). We asked two questions: How do weed populations respond to changing the efficiency and mode of weed control, and what impact will the introduction of GMHT crops have on biodiversity and, specifically, a seed-eating bird, the skylark (*Alauda arvensis*)?

We based our analysis on a model of the population dynamics of *C. album* in the sugar beet that predicts the change in plant and seed bank numbers from one sugar beet crop to the next (*5*) (Table 1). We modeled a five-course rotation where sugar beet is grown every fifth year, with winter cereals grown in the other 4 years. *C. album* can establish only every fifth year, when sugar beet is grown. Between sugar beet crops, populations of *C. album* persist in the form of a dormant seed pool. Seeds germinate in the spring, and survival from germination to flowering in the autumn is determined by herbicidal and mechanical control. In conventional systems, this control is modeled through a parameter q, defined as the proportion of plants that survive control (all plants survive control when $q = 1$, and none survive when $q = 0$). Seed production is a function of competition for resources during growth between individual weed plants (density dependence) and the crop.

We modified the model as follows to simulate the introduction of GMHT crops on weed populations. (i) The efficiency of weed removal in the GMHT crop is modeled by multiplying the control parameter for conventional crops q by a parameter h. When $h = 1$, control in the GMHT crop is the same as in the conventional crop, whereas values of <1 indicate increasingly more effective control in the GMHT crop; net control of weeds in a GMHT crop is consequently hq, and the increased mortality of plants, or efficiency of control in the GMHT crop, can be defined as $\gamma = 1 - h$. (ii) In the conventional crop, we assumed that the average density of emerging weeds was N^* seedlings per square meter. This density was varied within a wide range from 0.1 to 1000 m^{-2} by manipulating q; typical densities of emerging seedlings are $\sim 100\ \mathrm{m}^{-2}$. (iii) We modeled control in two ways. First, we assumed that a constant proportion of weeds was killed within a season, irrespective of the number of weeds emerging. Second, we employed a threshold form of control, whereby control was applied only when the weed density exceeded a level of N^+ seedlings per square meter.

For GMHT sugar beets, trials have suggested that close to 100% of weeds may be killed by a single herbicide application (*6–8*); that is, γ is close to 1. Increasing weed mortality from that in the conventional crop ($\gamma = 0$) to such levels leads to dramatic reductions in weed densities (Fig. 1). This reduction depends, however, on the way in which control is implemented. When a constant proportion of the population is killed, the weed population may be eradicated if the control efficiency γ reaches a critical value, such that the lower the equilibrium weed density before the introduction of GMHT crops, the lower the value of γ (Fig. 1A).

In contrast, if spraying occurs only when a threshold density is exceeded, weeds may persist even when weed control in the GMHT crop is very effective (Fig. 1B). The predictions of the threshold model are complex. For values of γ that are lower than the point of eradication under conventional management, densities are the same for both forms of control; this is because spraying occurs every year. As γ increases beyond this value, the population increases, as a result of seed production in years when numbers fall below the threshold for spraying. Further increases in γ lead to a relatively constant population density. This level is, however, typically <10% of the original density and represents a major decline in weed numbers. The behavior of the model is basically unaffected by the introduction of increased stochasticity (Fig. 1C), indicating that populations are highly resilient.

Skylarks aggregate locally during the winter in response to weed seed density (*9*). Figure 2A illustrates a sample of data on the aggregation of birds within fields in Norfolk, UK; the fitted equation is $y = 0.14 + 0.0002x$, where y is the density of birds per hectare and x is the weed seed density per square meter near the soil surface. The positive intercept of the relation represents components of local field use (e.g., movements between fields and feeding on grain) that are not explained by weed seed availability.

Table 1. Summary of mean parameter values for modeling the population dynamics of *C. album* (*5*).

Parameter	Definition	Mean value
s_m	Seed production of an isolated individual	230,000
a	Density response parameter (m^2)	0.10
g	Per annum probability of seed emergence	0.10
m	Per annum probability of seed mortality and loss of seed to emergence in cereals	0.20
ε	Competitive equivalence coefficient	1
B	Density of sugar beets (m^{-2})	11.11
q	Proportion of seedlings surviving control	Varied

Given that birds aggregate in direct response to weed seed abundance, the effects of GMHT crops on field use by birds will depend critically on the degree to which high-density patches of weeds are affected. In an attempt to explore such impacts, we extended our model for the population dynamics of the weed to simulate the effects of changes in farming practice and weed control on field use by birds (*10*). The model assumes the following. (i) There is a

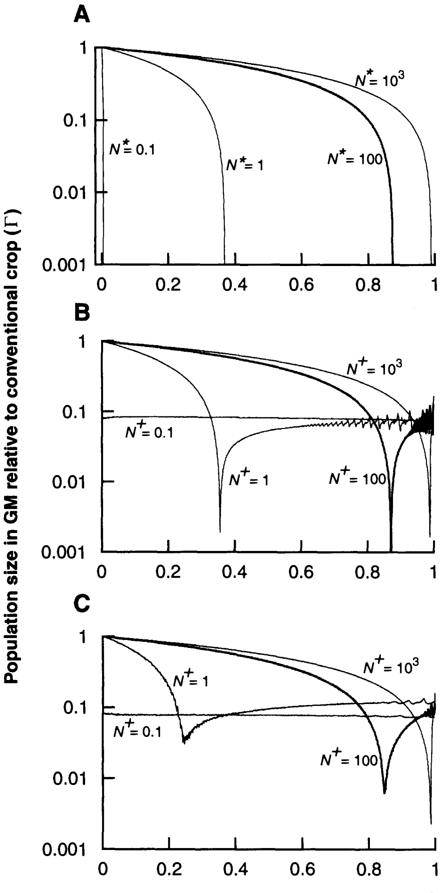

Fig. 1. Changes in weed seedling abundance (Γ, the density in the GMHT system relative to the equilibrium density in the conventional system) as a function of control efficiency γ in the GMHT crop. (**A**) The density of weeds where a constant proportion of plants are killed for a range of initial weed populations N^*. (**B** and **C**) The density of weeds under threshold management as the threshold for control, N^+, is varied. Low (B) and high (C) stochastic variations are modeled. The density of emerging seedlings in the conventional crop (N^*) was set equal to N^+.

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leptokurtic distribution of mean seed densities across farms before the introduction of GMHT technology (*11*) (i.e., most farms have a relatively low density of weed seeds, with fewer having very high densities), with a mean seed density of 1000 m^{-2}. (ii) The impacts of the introduction of GM technology are approximated by a parameter Γ, the proportion by which the seed bank is reduced when GMHT crops are introduced. Fig. 1 indicates that this value of Γ is likely to be low (<0.1). (iii) The probability of a farmer adopting GMHT crops is related to seed bank density through a parameter ρ. Positive values of ρ mean that farmers are more likely to adopt the new technology where seed densities are currently high and there is the potential to reduce yield losses to weeds; negative values indicate that farmers are more likely to adopt the new technology where seed densities are currently low, perhaps because a history of effective weed control is correlated with a willingness to adopt new technology. Therefore, ρ crudely models the socioeconomic response to the introduction of the new technology.

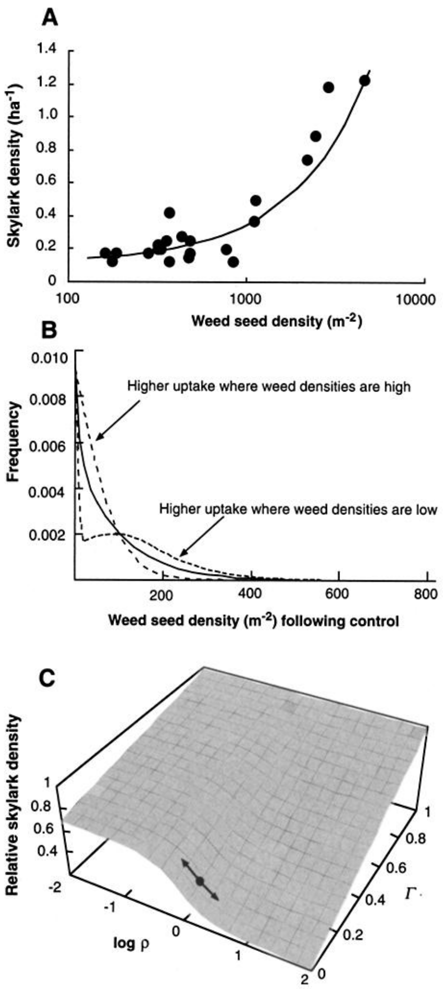

Fig. 2. Scaling up from local to regional impacts of the introduction of GMHT crops. (**A**) Relation used to predict field use by skylarks in response to weed seed density, data reanalyzed from (*9*). (**B**) Effects on the distribution of weed seed population size across farms through variation of the selective uptake of GMHT technology by farmers differing in their current levels of weed control. (**C**) Impacts on winter field use by skylarks (zero: field use at zero weed density; unity: field use before the introduction of GMHT crops) as a function of the association between weed density and uptake of GMHT crops (ρ) and the approximate reduction in weed seed bank density owing to the introduction of GMHT crops (Γ).

Figure 2B shows an example of the effect of varying the uptake of GMHT crops on the frequency distribution of seeds across farms. A higher uptake on farms where weed densities are currently high ($\rho > 0$) leads to an increase in the relative abundance of low-density fields. In contrast, the frequency of these fields is depressed when intensively managed farms ($\rho < 0$) preferentially adopt the new technology, as these already have low densities.

The relation between the uptake of GM technology and current levels of weed infestation (ρ) is as important to bird populations as the direct impact of the new technology on weed abundance (Γ) (Fig. 2C). Depending on the value of ρ, the impacts on bird populations range from severe to negligible. Most important, Fig. 2C indicates that the assumption that the uptake of the GMHT crops is uncorrelated with current weed infestations ($\rho = 0$) is unsatisfactory and misleading for predicting impacts on bird numbers, because small positive or negative values of ρ give rather different predictions in the region of parameter space (i.e., $\Gamma < 0.1$) that we expect the system to occupy.

Figure 2, B and C, highlights the fact that the effects of GMHT crops on weed abundance, and hence on bird populations, will depend on the socioeconomic reaction to the new technology as much as on any possible improvement in weed control. Accurate temporally and spatially replicated estimates of γ across a range of farm types are essential (*12*) if we are to predict the impacts of GM technology on weed and bird numbers. In terms of bird populations, the degree to which these predicted impacts on winter field use translate into changes in overall population size will depend on the relative levels of density dependence in summer and winter (*13*). However, Fig. 2C shows that the regional-scale consequences of farm-level decisions might be the key to predicting the impacts of GMHT crops on biodiversity. Our ability to predict the impact of GM technology on biodiversity therefore depends critically not only on an understanding of how the ecological system will respond to technological change at a local scale, but also on how the farming community will respond. Although the model that we have developed is very simple, we think that it is generic for weeds, seed-eating birds, and, indeed, for any technological innovation.

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$$\begin{aligned} N_{t+5} &= g(1-m)^{4.5} s_m q N_t f(qN_t) \\ &\quad + g(1-m)^5 S_t \qquad (1a) \\ S_{t+5} &= (1-m)^5(1-g)S_t \\ &\quad + (1-m)^{4.5}(1-g) s_m q N_t f(qN_t) \qquad (1b) \end{aligned}$$

Populations are censused at 5-year intervals. The dynamics of seeds are determined by the emergence fraction g, and the per annum probability of seed mortality m, which is used to account for the mortality of seeds through the entire rotation (5 years for seeds in the seed bank, and 4.5 years for seeds produced at time t). Mature plants produce s_m seeds per plant, at maximum. Competition acts to reduce the mean seed production per plant, and this effect is modeled through the function $f(N) = [1 + a(N + \varepsilon B)]^{-1}$, where a models the effect of intraspecific competition and ε and B model the effect of competition with the crop. Control is modeled through varying q, the proportion of plants that survive to maturity. Stochastic variation was included in the model by randomly drawing the emergence rate g from a lognormal distribution with log mean equal to 0 and log variance of either 0.05 (low variance) or 0.5 (high variance). The mean parameter values employed are summarized in Table 1.
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10. We used a simple phenomenological model to examine the impacts of the introduction of GMHT crops and their uptake by farmers on seed-eating birds. The basis for the model is an exponential distribution of weed seed population sizes S across farms

$$f(s) = \frac{1}{\theta}\exp\left(\frac{S}{\theta}\right) \qquad (2)$$

where θ is the mean weed seed population size. The results were highly robust when the value of θ was varied, and we therefore employed a constant value of 1000 m^{-2}. We assumed that the probability a farmer switches from conventional to GM technology is related (either positively or negatively) to the current weed infestation through a logistic function

$$p_{GM}(S) = \left[1 + \rho\exp\left(-\frac{\log\rho}{\theta}S\right)\right]^{-1} \qquad (3)$$

For values of $\rho > 1$, the probability that a farmer sows a GMHT crop is positively related to weed density; for $0 < \rho < 1$, this probability is negatively related to density; and for $\rho = 1$, the probability is unrelated to density. For convenience, Eq. 2 is set such that, at $S = \theta$, $p_{GM}(S) = 0.5$; this implies that 50% of farms with the average weed density grow GM crops, i.e., that uptake of the new technology is reasonably high. Overall, the mean density of seeds, following the introduction of GMHT crops, is given by solving

$$\hat{S} = \int_0^\infty S\{f(S)\Gamma P_{GM}(S) + f(S)[1 - P_{GM}(S)]\}dS \qquad (4)$$

Equation 4 calculates the mean density of seeds by summing the densities of seeds within the fields that are sown with GMHT crops (in which the density of seeds is reduced to a level Γ of that in the conventional crops) as well as that in the conventionally managed crops. Finally, because bird density is linearly related to weed seed density, we can calculate average bird density directly from average seed density.

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18 February 2000; accepted 7 July 2000

Relation Between Population Density and Body Size in Stream Communities

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The existence of a general relation between population density and body size in animal assemblages has been debated because of known biases and ambiguities in the published data and data handling. Using new comprehensive data sets from two geographically separated stream communities that encompass 448 and 260 invertebrate taxa with a wide range of body sizes, we show that an inverse proportionality between density and body size is a consistent feature in these communities. The scaling across taxa is not statistically different between the two systems, indicating a convergent pattern of communities. Variation in the regression slope among different taxonomic groups indicates that these communities are not governed universally by a single ecological or energetic rule.

Body size influences an organism's energetic requirements, its potential resource exploitation, and its susceptibility to predation. Dimensional analysis of the relation between population density (D) and body size (mass, W) for some published data yielded linear relations on logarithmic scales ($\log D = \alpha + \beta \log W$), where the slope β is around -0.75 when the ordinary least squares (OLS) regression is used (*1–3*) or is close to -1 when the reduced major axis (RMA) regression is used (*4–7*). However, several studies have shown that density-body size relations take a peaked or polygonal pattern with intermediate-sized species having the highest density, resulting in a nonsignificant or weak regression with a shallow slope (*8*, *9*). These contrasting results are derived from data collected through different sampling procedures and are subjected to different regression methods (*8–10*). It has also been argued that data compiled from the literature result in "constructed" density versus body size relations of assemblages that may be greatly affected by sampling bias against small and rare species, which are usually not well represented in ecological studies (*10*). Underestimation of the densities of rarer species is likely to result in a shallower slope and a less significant, more scattered relation (*11*). Furthermore, analyses taking this approach mainly involved terrestrial assemblages, with a bias toward taxonomically related species. Few studies have considered aspects of scaling across many taxonomic groups in an ecosystem (*12*, *13*).

We used data from two geographically separate communities of benthic stream invertebrates to assess the generality of density–body size relation in stream systems. The data encompassed species of wide ranges of taxonomy and body size and allowed us to achieve a high taxonomic resolution. Also, population densities of all the species in an assemblage were estimated with reference to the same habitat area.

We sampled riffle/pool sections of the gravel streams Oberer Seebach in Austria and Afon Mynach in Wales (*14*). The two streams were similar in mean annual water discharge and fractal dimension of habitat, but different in grain-size composition (*15*). Population density and body size (*16*) of the species included in the analysis were evaluated for each of the two streams. 448 and 260 invertebrate species occurred in the streambed sediments of the Oberer Seebach and Afon Mynach, respectively (*17*, *18*).

In both communities, abundance declined in a broad band with increasing body mass without showing a peaked pattern (Fig. 1). Body weight explained a significant amount of variation observed in the population density of both communities [$F(1,446) = 380.42$, $F(1,258) = 269.70$; $P < 0.001$]. As well as the OLS regression, we used the OLS-bisector regression (OLS_{BIS}) to estimate the relation between population density and body mass (*19*, *20*). The OLS_{BIS} regression gave a slope of -1.03 for both streams, which was not significantly different from -1 but differed from -0.8 (Table 1). In contrast, the slopes of the OLS regression were significantly different from -1 but not from -0.75 (Table 1) and did

Table 1. Regression slopes for the relation between body size (μg of dry mass) and population density (individuals per m^2) in benthic invertebrate communities of the streams Oberer Seebach and Afon Mynach. n, number of species; r^2, variance explained by the correlation of body size with densities of all species (AS), detritivorous species (D), and predatory/omnivorous species (P/O), respectively; b_{OLS}, ordinary least squares regression [OLS(y|x)] slope; and b_{BIS}, slope of the ordinary least squares–bisector regression (OLS_{BIS}) (*19*), separately calculated across all species, detritivorous, and predatory/omnivorous species in the community. Bootstrap confidence limits (95%) are given in parentheses for b of OLS and OLS_{BIS}.

Data set	n	r^2	b_{OLS}	b_{BIS}
		Oberer Seebach		
AS	448	0.460	−0.702† (−0.773, −0.631)	−1.032* (−1.091, −0.974)
D	362	0.425	−0.702† (−0.787, −0.618)	−1.070* (−1.139, −1.002)
P/O	86	0.586	−0.721† (−0.851, −0.591)	−0.940* (−1.053, −0.827)
		Afon Mynach		
AS	260	0.508	−0.733† (−0.821, −0.645)	−1.025* (−1.099, −0.951)
D	210	0.450	−0.691† (−0.796, −0.587)	−1.028* (−1.118, −0.939)
P/O	50	0.614	−0.794† (−0.977, −0.611)	−1.002* (−1.152, −0.852)

*OLS and OLS_{BIS} b values significantly departing from −0.75 and −0.8, respectively. †OLS and OLS_{BIS} regression coefficients significantly departing from −1.0 (t tests, $P < 0.05$).

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