

Assessing the risks associated with new agricultural practices

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One key challenge for the twenty-first century is how to produce the food we need, yet ensure the landscape we want. Genetically modified crops have focused our attention on how to answer this question for one part of agriculture. The same principles could be applied to assess environmental impacts of future land-use change in a much broader context.

he improvement of crop varieties through plant breeding has greatly increased yields over the past few decades. This in turn has reduced the area of land that would otherwise have been dedicated to agriculture as a result of an increasing world population¹. But these new crop varieties have been accompanied by changes in agronomic practice, which have included increased use of fertilizers, pesticides and irrigation. Many of these changes have been to the detriment of wildlife². Change has therefore brought both benefits and costs, and the future of food is linked inextricably with the future of the environment.

In this context, biotechnology offers new possibilities for the twenty-first century. Will the introduction of genetically modified (GM) crops exacerbate current trends or offer new avenues for environmental management? The debate presents regulators and scientists with a significant challenge — how to define and assess impact against a backdrop of constantly shifting land-management practices and resultant biodiversity. The approaches being developed in response to this debate are of generic value. Ecological science has much to offer in providing objective evidence of potential impacts of land-management practices. With sufficient resources, future changes in land management could be directed towards specific environmental goals. Solutions, however, will require an integration of science, policy and regulation.

One important issue is the proportion of wildlife that is dependent upon the management of agricultural land. In the United States and Canada, large areas are dominated by farming, but large areas are also set aside for recreation and conservation. In contrast, in Europe, agriculture and the countryside are intimately intertwined, with around 70% of land area classified as agricultural land (Fig. 1). Europeans effectively live inside their national parks. This may explain some differences in perspective towards the role of agriculture in delivering wildlife, and why the potential introduction of GM plants has raised some complex issues in Europe.

Risk assessment of GM plants has been divided traditionally into direct and indirect impacts. Direct impacts arise from the presence of the transgenic plant itself, or the consequences of transfer of the transgene into wild relatives. Indirect impacts arise from the management practices associated with the transgenic crop. Ecological theory has an important role to play in assessing such impacts.

Assessing the direct impact of GM crops

The potential direct impacts of a GM plant include any changes in ecological fitness which may make the crop plant

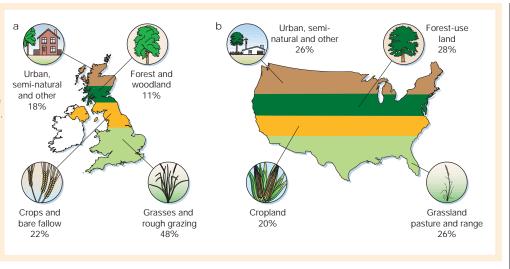
or any crop plant/wild relative hybrids more invasive (see ref. 3 for a definition of ecological fitness). Invasive species represent one of the greatest threats to biodiversity^{4–6}. Most non-native species are harmless, but a few become invasive and detrimental to indigenous ecosystems. Japanese knotweed (*Fallopia*) and rhododendron (*Rhododendron ponticum*) are notable examples in the United Kingdom, while yellow star thistle (*Centaurea solstitalis*) and European purple loosestrife (*Lythrum salicaria*) are particularly disruptive examples in the United States. Most of these invasive species originate from horticulture, and so far there is no evidence that any GM crop plant is significantly more invasive than its conventional counterpart⁷.

Nevertheless, the possibility exists that certain transgenic plants could pose a direct threat through enhanced ecological fitness. In particular, transgenes that confer enduring resistance to pathogens could cause ecological release in wild relatives if populations are regulated by those same pathogens. Indeed, the ethos behind biological control relies on this principle, in that it assumes that some plants become weeds because they have escaped their natural enemies, and seeks to reduce populations by the introduction of a suitable pathogen or herbivore. Wild plant populations contain a variety of resistance genes that have evolved in response to the presence of pathogens. But genetic modification greatly widens the pool of potential resistance genes, allowing the use of new pathogenresistance mechanisms. The use of viral coat protein genes to provide resistance against the same viral strains is a case in point⁸. Such resistance mechanisms may prove to be more enduring than those produced by conventional plant breeding. Although this is good news for agriculture, the potential for causing ecological release in wild populations should be considered.

Attempting to predict which plants will prove to be invasive in advance of their release still involves a great deal of uncertainty, and there is nothing to compare with addressing this issue through focussed field experiments, comparing ecological fitness between transgenics and their conventional counterparts^{7,9,10}. The design can involve manipulation to greatly widen the range of ecological conditions, and should be conducted over several years to encompass a range of abiotic conditions. This direct approach can draw on ecological theory to focus on those genotypes most likely to invade, and on those habitats that are most likely to be vulnerable to invasion¹¹. This should provide a good indication of potentially invasive plants, but as with all such predictions, there will always remain a

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Figure 1 Land use by agriculture and other uses. a, Land use for the United Kingdom in 2000. The total area classified as agricultural land is 70%, including both cropland and grassland/rough grazing. Source: ref. 50. b, Principal uses of land in the United States in 1997. Source: ref. 51.



degree of uncertainty. The uncertainty we are prepared to accept in the introduction of GM crop plants should not be out of all proportion to that we accept for conventional crop plants, let alone imported exotics⁵. The approaches developed to answer such questions for GM plants could be profitably applied to imported plant species.

Assessing the indirect impacts of GM crops

The much more challenging question is how do we assess the potential impacts of changing agricultural practice? This article will focus on GMHT (genetically modified, herbicide tolerant) crops as a case study, for which any impacts are most likely to be through changes in the efficiency of weed management.

GMHT crops are resistant to broad-spectrum herbicides such as glyphosate or glufosinate. Consequently, these herbicides may be applied after crop germination without harming the GM crop itself. But because these herbicides have a broad range of action, their use may reduce weed and invertebrate populations, on which birds and other wildlife depend. If herbicide application is instead delayed until later in the growing season, just before the point where weed populations would start to compete with the crop, a greater diversity and biomass of in-field vegetation would occur early in the season, during nesting time for many birds. However, fewer plants may survive to set seed after herbicide application, so this may reduce the abundance and diversity of seedlings the following year.

ACRE, the UK government's Advisory Committee on Releases to the Environment, has developed guidelines on how to assess the indirect impacts of a GM crop ¹². They require a comparison between the management of the GM crop and the equivalent non-GM crop, with an assessment of the potential impact on key indicator species typical of arable farmland. Such comparisons can be meaningfully made only through large-scale field experiments, and in fact these guidelines build on the experience of the farm-scale evaluations (FSEs), set up in the United Kingdom in 1999. The FSEs are designed to investigate the potential indirect impacts of four GMHT crops (spring and winter oilseed rape, maize and sugar beet). They are funded by the UK government, executed by a consortium of research institutes, and overseen by an independent scientific steering committee¹³. The design of these trials is outlined in Box 1, and the first set of results will be published in 2003.

These ecological experiments have provoked considerable interest from the public, and initially were presented as providing the final word in the risk assessment of these particular crops¹⁴. It is now more widely recognized that they will inform the debate, but that our options are considerably more complex than a simple pass or fail for this technology¹⁴. The trials will provide valuable data on the impact of the management of both GM and conventional crops

on key indicator species, and large-scale manipulative experiments represent the most direct and reliable method of obtaining this information. In this context, the trials are pioneering in their attempt to link a proposed change in land management with potential changes in biodiversity (number of species), prior to its introduction.

Such trials should become a cornerstone of our strategy if we aim to use ecological science to inform future agricultural and environmental strategy. But as with many good experiments, they will raise as many issues as they solve. The interpretation of the data is unlikely to be clear and straightforward — biodiversity indicators may be enhanced during certain parts of the year, and reduced at other times. Some species will become more abundant, while others will be reduced. Do we value some species over others (skylarks over earthworms for example)? And how do we extrapolate from changes in abundance of weeds and invertebrates at different times of year to potential changes in bird and mammal populations?

Mathematical models provide one means of scaling up our predictions, both spatially and temporally. Watkinson *et al.*¹⁵ provide an elegant example of this, with a model that extrapolates from data on weed numbers in conventional and GMHT crops, to calculate the impact of herbicide use on farmland bird numbers. Such models may be used to investigate the potential impacts of a range of management scenarios, and could aid the design of management guidelines ¹⁶. Data could then be gathered in such a way that could test any predictions, in the early stages of commercialization. The long-term monitoring that would be required post-commercialization under European Union legislation could be designed for precisely this purpose.

Developing protocols for risk assessment

There has been some debate in the literature about how to manage the world's ecosystems as capital assets, which is highly pertinent to the debate on the future of agriculture^{17,18}. In looking forward to the coming decades, we can continue to develop the more proactive approach of the FSEs to consider land-use change more broadly. The first step would be to specify our goals. For example, do we intend to farm for biodiversity as well as food? This requires decisions to be made about which species or habitats we wish to preserve within the agro-ecosystem (as opposed to nature reserves)¹⁹, and the extent to which we are prepared to pay for the 'non-food' component of agriculture²⁰. Clearly these biodiversity goals need to be integrated with the goal of affordable, safely produced, high-quality food.

Perhaps most important, agro-ecosystem biodiversity is only one piece of the jigsaw. In organic and many conventional systems, weeds are controlled by ploughing before planting the crop. GMHT crops could support a reduction in tillage through direct drilling into a weedy field, which may be beneficial to soil organisms. The glyphosate

Box 1 The farm-scale evaluations

The farm-scale evaluations are a series of experiments conducted over three years to determine the potential impact of GMHT (genetically modified, herbicide tolerant) crops on the agro-ecosystem.

The null hypothesis

There are no statistically significant differences in the abundance and diversity of farmland wildlife associated with the management of GMHT crops compared with the management of equivalent non-GM crops.

A number of sensitive indicator species have been chosen to represent 'wildlife' from the following groups: all plants, soil surface active arthropods, plant arthropods and gastropods, bees, butterflies and the soil seed bank. The emphasis is very much on species at the lower end of the food chain, as treatments applied at the field scale are unlikely to have much impact on mobile species such as birds and mammals, and with the anticipation that knock-on effects to larger organisms that rely on these species for food can be deduced through models 15.16.

The design

Preliminary data suggested that a split-field design would be more powerful and

appropriate than a paired-field design. Consequently, each experimental field (ranging in size from 3–12 hectares) is divided into two, and the GMHT crop is grown in one half (chosen at random), with an equivalent conventional crop grown in the other half. This minimizes any differences in biodiversity at the start of the experiment.

The management of the GM crop follows guidelines laid down by SCIMAC (Supply Chain Initiative on Modified Arable Crops), an industry body that advises on cost-effective weed control in the GM crop (subsequently audited by the scientists).

Sampling takes place throughout the year in the crop, headland and field margins. Power analysis is used to determine the size of the experiment (the number of farms needed to participate), to ensure with high probability that a 50% change in abundance of any one of the common species would be detected

By the close of the experiment, around 60 farms will have taken part across the United Kingdom for each of the four crops, chosen to represent the range of regional geographical differences and current farming methods.



The funding and management

These trials are funded by the UK government, undertaken by a consortium of research institutes, and overseen by an independent scientific steering committee. The results will be available in 2003. For more information see:

www.defra.gov.uk/environment/fse/ index.html/.

or glufosinate herbicides used with these crops are less persistent than many conventional herbicides such as atrazine, and may lead to a reduction in the costs of removing agrochemicals from watercourses. Moving from herbicide-tolerant to insect-protected GM varieties, the potential to reduce pesticide use is even greater²¹. Fewer herbicide or pesticide treatments will also mean reduced consumption of fossil fuels driving agricultural machinery and a significant reduction in atmospheric carbon dioxide emissions²¹. A true comparison of environmental impact would require all externalities to be included²², encompassing ecological, social and economic considerations.

The second step is to evaluate all possible routes to achieve our goals. This should include all ways in which GM crops could be managed to minimize environmental impact, as well as all alternative agricultural systems. In the context of GM crops, the FSEs are designed to answer the question 'What will be the potential impact of the management of GMHT crops on key biodiversity indicators, compared with the equivalent conventional herbicide-tolerant crop?' This question informs us about impact in the context of current agricultural practice. However, an equally valid question might be 'In what ways can GMHT crops be managed to maximize biodiversity without reducing yield?' Other field trials are currently addressing some of these issues in the United Kingdom²³, and illustrate the importance of the framing of the question.

It would be illogical to focus on one particular technology, such as GM crops, if our aim is to deliver wildlife as well as food. The potential exists to reduce pesticide use in a variety of ways, including enhancing beneficial insects and birds, inducing the plant's own innate defences against pests or diseases through chemical signals, using pheromone traps to interfere with mate-finding, and resorting to chemicals only when specific thresholds are reached. The philosophy of integrated pest management has been evident for the past few decades, and is

promoted through a variety of organizations (for example, the UK charity Linking Environment And Farming or $LEAF^{24}$), but needs to become mainstream policy to maximize its contribution to sustainable change. Technological advances such as precision agriculture, in which fertilizer applications rates are adjusted across fields according to crop needs, could contribute to this process 25 .

The third step would be an evaluation of the status quo. One signal is clear — biodiversity is in decline. This is a global trend, and many of these changes may be ascribed to agriculture (for example, changes in the floral diversity of grasslands and arable field margins resulting from overgrazing or fertilizer input^{26,27}, loss of critical habitats through eutrophication and conversion to agriculture²⁸, and loss of species diversity within the agro-ecosystem through changes in management²⁹). Restoration ecology is the science of restoring species diversity through focused management strategies, and considerable success has been achieved in the restoration of some habitats, such as species-rich grasslands. Yet not all such losses may be restored. Abiotic constraints (for example, the degree of eutrophication and acidification) and biotic constraints (for example, an impoverished seed bank) may make restoration unfeasible²⁷.

Farmland birds rely on seeds and invertebrates, and so are considered good indicators of farmland biodiversity more widely 15, but there are practical difficulties in studying biodiversity changes for such species at higher trophic levels. Being highly mobile, they respond to land-use changes at much greater spatial scales. Nevertheless, taking Europe as an example, correlative studies illustrate that conservationally valued farmland birds are in decline, and this seems to be associated with an intensification of agriculture in the latter part of the 20th century 30-33. One hypothesis is that declines may be associated with changes in frequency of those arable plants that are important food resources for farmland birds 34.35. Countryside

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surveys, conducted across the United Kingdom over the past 25 years support this hypothesis, concluding that arable field centres are a much poorer source of food plants for farmland birds now than they were in 1978^{36-38} .

Such simple temporal correlations may be misleading, and more detailed knowledge of the life history of a bird species is required to link cause and effect. Ecological studies have provided this in some cases. The switch from growing spring- to autumn-sown crops deprives many species of feeding sites in stubble fields overwinter^{39–41}. Grass margins around arable fields and weedy winter stubbles, enhanced with countryside stewardship schemes, have greatly benefited the threatened cirl bunting⁴². Skylarks breed more successfully in spring cereals and set-aside than in winter cereals, as a result of the impact of vegetation height during the latter part of the breeding season⁴³.

There is clearly an ecological cost to remaining with the status quo, and there are considerable pressures for changes in agricultural policy to address these costs⁴⁴. The fourth and final step will be to direct changes in land use towards our environmental goals. This will require both financial incentives, and up-to-date information on the best options available. Both government and environmental organizations favour shifts in subsidies towards environmental targets⁴⁵. However, resources are needed for research to find the optimal solutions that address the local conditions, and for government-sponsored extension agents to communicate the best available options to the farmer as they come on-line.

Conclusions

The challenge is to produce the food we need for the future while minimizing the environmental impact. This future vision of agriculture involves the farmer as a steward of the countryside⁴⁶. If we put aside the ideological boundaries that are often set up between different agricultural systems (organic, conventional and GM), the objectivity of ecological science can be used to pick the best elements of all systems. It is equally vital that stewardship schemes are designed with scientific input if goals are to be reached^{19,47}. Currently about e1.7 billion (\$US1.7 billion) are spent annually in Europe on agri-environment schemes, yet there are very little data on the effectiveness of these programmes⁴⁸. Long-term monitoring of key elements of biodiversity should be carefully designed, with the validation of these schemes in mind. Without long-term data we cannot direct subsidies to the most effective schemes, detect trends, or assess future changes in biodiversity.

We should promote an experimental approach to elucidate the consequences of specific changes in land management. The FSEs provide a good example of a 'proactive experiment', a product of science-based risk-assessment protocols, the aim of which is to ensure that any future change is in a better direction. This will be most effectively developed in the future if we throw off the constraints of our focus on GM technology, and use the approach to address other land-management issues. Such experiments need to be designed and resourced at the appropriate scale, so that we can adequately address these major practical questions⁴⁹.

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- Conway, G. & Toenniessen, G. Feeding the world in the twenty-first century. Nature 402, C55–C58 (1999).
- Krebs, J. R., Wilson, J. D., Bradbury, R. B. & Sirwardena, G. M. The second Silent Spring? Nature 400, 611–612 (1999)
- 611–612 (1999).
 3. Crawley, M. J., Hails, R. S., Rees, M., Kohn, D. & Buxton, J. The ecology of transgenic oilseed rape in natural habitats. *Nature* 363, 620–623 (1993).
- 4. Sala, O. E. et al. Global biodiversity scenarios for the Year 2100. Science 287, 1770–1774 (2000).
- 5. Trewavas, A. J. & Leaver, C. J. Is opposition to GM crops science or politics? EMBO Rep. 2, 1–5 (2001).
- Pimentel, D., Lach, L., Zuniga, R. & Morrison, D. Environmental and economic costs of nonindigenous species in the United States. *Bioscience* 50, 53 (2000).
- Crawley, M. J., Brown, S. L., Hails, R. S., Kohn, D. & Rees, M. The performance of transgenic crops in natural habitats: a 10-year perspective. Nature 409, 682–683 (2001).
- Cooper, J. I. in Commercialisation of Transgenic Crops: Risk, Benefit and Trade Considerations (eds McLean, G. D. et al.) 115–124 (Bureau of Resource Sciences, Kingston, ACT, 1997).
- 9. Crawley, M. J. Bollworms, genes and ecologists. Nature 400, 501–502 (1999).

- 10. Hails, R. S. Genetically modified organisms—the debate continues. Trends Ecol. Evol. 15, 14-18 (2000).
- Shea, K. & Chesson, P. What can community theory tell us about biological invasions? Trends Ecol. Evol. 17, 170–176 (2002).
- 12. Advisory Committee on Releases to the Environment (ACRE) Sub-group on Wider Biodiversity Issues. Guidance on the Assessment of the Impact on Wider Biodiversity from Proposed Cultivation of GM Crops http://www.defra.gov.uk/environment/acre/biodiversity/guidance/index.htm (31 July 2001).
- 13. Firbank, L. G. et al. Farm-scale evaluation of GM crops explained. Nature 399, 727–728 (1999).
 14. Agriculture and Environment Biotechnology Commission. Crops on Trial (DTI, London, 2001)
- Watkinson, A. R., Freckleton, R. P., Robinson, R. A. & Sutherland, W. J. Predicting biodiversity responses to GM herbicide tolerant crops. Science 289, 1554–1556 (2000).
- Firbank, L. G. & Forcella, F. Genetically modified crops and farmland biodiversity. Science 289, 1481–1482 (2000).
- 17. Daily, G. C. et al. The value of Nature and the nature of value. Science 289, 395-396 (2000).
- Tilman, D. et al. Forecasting agriculturally driven global environmental change. Science 292, 281–284 (2001).
- $19. \, Sutherland, \, W. \, J. \, \, Restoring \, a \, sustainable \, countryside. \, \, \textit{Trends Ecol. Evol.} \, \, \textbf{17}, \, 148-150 \, \, (2002). \, \, d. \, \, (2002)$
- 20. Beringer, J. E. Farming for biodiversity with GMOs? Outlook Agric. 30, 7–9 (2001).
- 21. Phipps, R. H. & Park, J. R. Environmental benefits of genetically modified crops: global and European perspectives on their ability to reduce pesticide use. J. Anim. Feed Sci. 11, 1–18 (2002).
- Pretty, J. N. et al. An assessment of the total external costs of UK agriculture. Agric. Syst. 65, 113–136 (2000).
- Pidgeon, J. D., Dewar, A. M. & May, M. J. in Proc. BCPC-Weeds 2001, 373–380 (BCPC Publications, Bracknell, 2001).
- Marsh, J. Integrated Farm Management—A Farm Strategy for the 21st Century (LEAF, The National Agricultural Centre, Stoneleigh, 2000).
- 25. Tilman, D. The greening of the green revolution. Nature 396, 211-212 (1998).
- Wilson, P. J. in Field Margins: Integrating Agriculture and Conservation (ed. Boatman, N.) BCPC Monogr. No. 58, 253–258 (BCPC Publications, Bracknell, 1994).
- Bakker, J. P. & Berendse, F. Constraints in the restoration of ecological diversity in grassland and heathland communities. *Trends Ecol. Evol.* 14, 63–68 (1999).
- 28. Bobbink, R., Hornung, M. & Roelofs, J. G. M. in Manual on Methodologies and Criteria for Mapping Critical Loads/Levels (UN ECE Convention on Long-range Transboundary Air Pollution), 71–96, III-i-III-54 (Federal Environmental Agency, Berlin, 1996).
- Perfecto, I., Rice, R. A., Greenberg, R. & Van der Voort, M. E. Shade coffee: a disappearing refuge for biodiversity. Bioscience 46. 598–608 (1996).
- Chamberlain, D. E., Fuller, R. J., Bunce, J. C., Duckworth, J. C. & Shrubb, M. Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. J. Appl. Ecol. 37, 771–788 (2000).
- Chamberlain, D. E. & Fuller, R. J. Local extinctions and changes in species richness of lowland farmland birds in England and Wales in relation to recent changes in agricultural land-use. Agric. Ecosyst. Environ. 78. 1–17 (2000).
- Gates, S. & Donald, P. F. Local extinction of British farmland birds and the prediction of further loss J. Appl. Ecol. 37, 806–820 (2000).
- Donald, P. F., Green, R. E. & Heath, M. F. Agricultural intensification and the collapse of Europe's farmland bird populations. Proc. R. Soc. Lond. B 268, 25–29 (2001).
- Campbell, L. H. et al. A Review of the Indirect Effect of Pesticides on Birds JNCC Report No. 227 (Joint Nature Conservation Committee, Peterborough, 1997).
- Wilson, J. D., Morris, A. J., Arroyo, B. E., Clark, S. C. & Bradbury, R. B. A review of the abundance and diversity of invertebrate and plant foods of granivorous birds in northern Europe in relation to agricultural change. *Agric. Ecosyst. Environ.* 75, 13–30 (1999).
- Haines-Young, R. H. et al. Accounting for Nature: Assessing Habitats in the UK Countryside (Department of the Environment, Transport and the Regions, London, 2000).
- Smart, S. M., Firbank, L. G., Bunce, R. G. H. & Watkins, J. W. Quantifying changes in abundance of food plants for butterfly larvae and farmland birds. J. Appl. Ecol. 37, 398–414 (2000).
- 38. Firbank, L. & Smart, S. in Aspects of Applied Biology, Birds and Agriculture (eds Boatman, N. D. et al.) 165–170 (Association of Applied Biologists, Wellesbourne, 2002).
- Hald, A. B. The impact of changing the season in which cereals are sown on the diversity of the weed flora in rotational fields in Denmark. J. Appl. Ecol. 36, 24–32 (1999).
- Siriwardena, G. M., Baille, S. R. & Wilson, J. D. Variation in the survival rates of some British
 passerines with respect to their population trends on farmland. *Bird Study* 45, 276–292 (1998)
- Siriwardena, G. M., Baille, S. R. & Wilson, J. D. Temporal variation in the annual survival rates of six granivorous birds with contrasting population trends. *Ibis* 141, 621–636 (1999).
- Peach, W. J., Lovett, L. J., Wotton, S. R. & Jeffs, C. Countryside stewardship delivers cirl buntings (Emberiza cirlus) in Devon, UK. Biol. Conserv. 101, 361–373 (2001).
- Chamberlain, D. E., Wilson, A. M., Browne, S. J. & Vickery, J. A. Effects of habitat type and management on the abundance of skylarks in the breeding season. J. Appl. Ecol. 36, 856–870 (1999).
- Robinson, R. A. & Sutherland, W. J. Post-war changes in a rable farming and biodiversity in Great Britain. J. Appl. Ecol. 39, 157–176 (2002).
- Falconer, K. & Ward, N. Using modulation to green the CAP: the UK case. Land Use Policy 17, 269–277 (2000).
- 46. Policy Commission on the Future of Farming and Food. Farming and Food—A Sustainable Future http://www.cabinet-office.gov.uk/farming/index/CommissionReport.htm (January 2002).
- Kleijn, D., Berendse, F., Smit, R. & Gilissen, N. Agri-environment schemes do not effectively protect biodiversity in Dutch agricultural landscapes. *Nature* 413, 723–725 (2001).
- 48. Whit field, J. Birds fly in the face of 'green' farming incentive scheme. Nature 413, 659 (2001).
- Lawton, J. H. Community Ecology in a Changing World Excellence in Ecology no. 11 (International Ecology Institute, Oldendorf/Luhe, 2000).
- 50. Department for Environment, Food and Rural Affairs. Digest of Environmental Statistics <www.defra.gov.uk/environment/statistics/des/index.htm> (November 2001).
- 51. Vesterby, M. & Krupa, K. S. Major Uses of Land in the US, 1997 ERS Statistical Bulletin No. 973 http://www.ers.usda.gov/publications/sb973/> (September 2001).

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