but had a limited effect on both the numbers of species and crop yields. Averaged over four years, there were 18.25 species over the conservation headlands compared to 15.25 species over the fully sprayed headlands. Further studies indicated greater numbers of ground beetles (predators) in conservation headlands (Cardwell *et al.*, 1994). Chiverton & Sotherton (1991) suggested that there were several effects of the beneficial arthropods of conservation headlands, especially in relation to providing food for the chicks of gamebirds (Sotherton, 1992). The striking feature of conservation headlands in the landscape is their richness in wildflowers, giving red, white or yellow stripes according to the dominant 'weed' species. The fact that they do increase biodiversity is undoubted (Dover, 1991), encouraging predators of the herbivorous ('pest') insect species in neighbouring fields (Cardwell *et al.*, 1994).

If conservation headlands have this effect, can one design structures that would favour the agriculturally beneficial invertebrates without at the same time benefiting the 'pest' species? The concept of creating habitat 'islands' concentrated on the structure of such islands, on the density and diversity of the predator communities that they could support, and on the ability of these predators to colonise neighbouring fields in the spring (Thomas et al., 1991, 1992). The majority of predators favoured in this work were beetles, and hence the term 'beetle banks' was coined for what is in effect an attempt at the biological control of crop pests. Winter survival of the beetles in grass tussocks was found to be important (Dennis et al., 1994), but 'beetle banks' have not been widely adopted. This is probably because the predators are unable to keep up with the reproductive potential of crop pest species feeding on the one plant species of the simple arable ecosystems. By slowing the rate of increase of the pest species, these predators may bring economic and environmental advantages in that less frequent pesticide applications are needed. Both methods, conservation headlands and beetle banks, have the potential to contribute significantly to the maintenance of biodiversity on agricultural land, though there are costs to farmers (Deane, 1989).

The advent of 'set-aside' has provided a focus for biodiversity in a non-equilibrium environment. If land that was maintained in production by large anthropogenic inputs is abandoned (or largely so), how do the native species respond to the changed environmental conditions? A study by Welch (1995) of 19 fields indicated that weedy grass species, e.g. annual meadow-grass (Poa annua) and black bent (Agrostis gigantea), were replaced successively with species more characteristic of permanent grassland, e.g. common bent (Agrostis capillaris), Yorkshire fog (Holcus lanatus) and cock's-foot (Dactylis glomerata). After the first year, weeds of arable land declined, but the dicotyledonous species of permanent grassland were slow to colonise. The plant species richness of setaside fields therefore declined during the five years of the study. However, in Sweden, effects were noted on the field-feeding birds, with species such as skylark (Alauda arvensis) and linnet (Carduelis cannabina) being more abundant on set-aside fields than on arable fields (Berg & Pärt, 1994). For small mammals, the demography of wood mice (Apodemus silvaticus) was different on set-aside fields than on mixed livestock fields, though this may be due more to differences in productivity of the sites rather than to the set-aside (Rogers & Gorman, 1995). In Germany, colonisation of set-aside fields by bees and wasps was studied by Gathmann et al. (1994). Body size was a good predictor of colonisation by these insects, with larger species colonising sooner; cutting the set-aside, which increased the plant species richness, doubled the number of bee species colonising.

Set-aside is still a relatively new concept, and it might only be a temporary measure. Abandoning land, however, is not a panacea for maintaining biodiversity. Many species are slow to colonise these areas, as demonstrated for vascular plants by Welch (1995) and for bees and wasps by Gathmann *et al.* (1994). Studies are still at an early stage in Europe, since the European Union's aim to reduce agricultural surpluses by set-aside only dates from 1988. The extensive American literature on old field succession indicates that much more time, perhaps 20-50 years, will be required before gains in biodiversity become apparent on set-aside land. Management options, such as seeding with species-rich mixtures and/or cutting to favour mixed species swards, will undoubtedly speed the process, as will the presence of hedges, forest edges (Berg & Pärt, 1994) and the proximity of appropriate habitat fragments. A source of propagules is very important in determining the initial colonisation and hence species richness of abandoned land.

Habitat fragments are possibly the key to the longer-term maintenance of biodiversity on agricultural land. As reviewed by Matthews (1987), they consist of ponds, wetlands, scrub, heaths, woods, and grasslands that have been traditionally managed with low inputs of fertilizers (usually dung); hedges, and both field and yard corners, are also included. There are few studies on the extent to which these can act as sources of colonists for newly created habitats or for set-aside fields. In some areas, however, it is these small fragments that provide the only habitat for some species to live, to lay their eggs, to undertake their courtship behaviour, etc. At worst they are neutral and at best they are vital in the maintenance of biodiversity in agricultural landscapes. In The Netherlands, Hermans & Vereijken (1992) indicated that ways must be found of integrating both plant and animal husbandry with the conservation of biodiversity on farms.

SPECIES

Although a number of species has been mentioned in relation to habitats, it is important to ask whether there are any species that are particularly characteristic of agricultural habitats. In grasslands, several species are associated with meadows that have not received large fertilizer or pesticide inputs. In the Pennine hay meadows, the traditional methods of dunging, cutting a hay crop and grazing in the autumn have maintained considerable botanical species richness (Smith & Jones, 1991). These include a range of grass species as well as attractive plants such as the wood crane's-bill (Geranium sylvaticum), meadow saxifrage (Saxifraga granulosa) and fragrant orchid (Gymnodenia conopsea). Although less well quantified than the botanical species richness, these hay meadows support considerable richness of invertebrate species as well as thriving populations of birds such as skylark (Alauda arvensis). It is probably true, however, that none of these species is entirely dependent upon the managed meadow habitat, as they occur, perhaps in more limited quantity, along roadside verges, near wood margins, etc.

Some species occur only, or virtually only, on arable land. Wilson (1991) discussed the flowering plants of arable fields, giving statistics for their decline from the period 1930-1960 to the latter half of the 1980s. He listed two species that had become extinct in Britain - the corncockle (*Agrostemma githago*) and thorow-wax (*Bupleurum rotundifolium*) - though populations remain in other countries. The endemic grass,

interrupted brome (*Bromus interruptus*), appears to have become extinct in the wild about 1989. Wilson's (1991) statistics for the decline of many other arable weed species indicates that many such species could become extinct. An example is the reduction in the corn buttercup (*Ranunculus arvensis*), which previously occurred in 432 10km grid squares and has declined to 22 such squares, Although these species are annuals and are associated with bare ground, where there is only limited competition from other plants, one has to ask why they have declined in the face of greater herbicide use and changing land husbandry techniques. Other species, such as barren brome (*Bromus sterilis*) or cleavers (*Galium aparine*), that at least superficially have similar ecological requirements, have apparently increased and pose problems to farmers.

There are two general points that emerge from the kind of statistics reported by Wilson (1991). First, far more of these annual, early successional species have declined than have increased, and hence there has been an overall loss of biodiversity. Secondly, many species of insects eat only one species of plant, and, unless these insects can change to another host plant (an extremely uncommon event), they will also be lost as the plant becomes scarcer and eventually becomes extinct. For example, the peacock (*Inarchis io*) and small tortoiseshell (*Aglais urticae*) butterflies rely on stinging nettles (*Urtica dioica*) in hedges and field margins as their only food plant. The nettle is not endangered, but if it were to be lost then these butterflies, and many other nettle-feeding insects, would also be lost from our farmland. The plants of arable environments, and the animals that depend on them, need to be recognised as a group of rapidly declining species (usually over 90% in the last 50 years) in need of conservation action if they are not to be lost from the UK.

This raises two particular issues. How do the different arable crops affect the plant and animal species associated with them? Would any of these associated species really be missed?

In relation to the first question, Wilson (1991) showed that crop type (barley or wheat) and date of sowing could have large effects on the weed species, most of which have a seed bank in the soil. Studies of small mammals have indicated that it is the amount of cover, i.e. an ability to avoid predators, that determines the use that voles and mice make of crop fields (e.g. FitzGibbon, 1997). It is probably the structure of the crop that most affects the abundance of ground beetles (Cárcamo & Spence, 1994), although each invertebrate species has a separate ecological requirement and generalisations cannot easily be made. It is often suggested that organically grown crops will yield a greater abundance and diversity of associated wildlife. However, working with ground beetles in Scotland, Armstrong (1995) showed that this was not necessarily true in potato crops. This supported earlier work by Dixon & McKinlay (1992) invoking the behaviour of the beetles, indicating that well-fed beetles (feeding on aphids knocked down by insecticidal treatments) may be less inclined to fall into pitfall traps than more hungry beetles actively searching for food! There is still much research needed to understand how different crop types, and different management practices of each crop type, affect and interact with the biodiversity that they can support.

The second question is more difficult to address. It relates also to the question of why there are so many species in the soil. Commenting on the fact that so few of the species that inhabit the soil have been characterised taxonomically, André *et al.* (1994) described

the soil as the 'last biotic frontier', containing 'a huge reservoir for biodiversity'. Usher (1996) put forward three hypotheses about this species richness, namely that

- H₁: all species have a distinct ecological role to play and, as each species is lost, the ecosystem loses some aspect of its function;
- H₂: there are a few 'key' species whose loss will lead to a malfunction of the ecosystem and many 'passenger' species whose loss would not affect ecosystem function; and
- H₃: there is considerable redundancy in that there are whole suites of species capable of performing each ecosystem function, and hence the ecosystem will function normally whilst at least one species from the suite survives.

Although these hypotheses are not mutually exclusive, it remains a challenge to design experiments that could determine if any one is true for agricultural systems. Lockwood & Pimm (1994) have suggested that H_1 is true, arguing that each species contributes to the stability of the ecosystem that it inhabits. The arguments, which are largely theoretical and focused on resistance to perturbations (drought, effects of disease, etc.), are now starting to move into laboratory experimentation (Lawton *et al.*, 1996), but not yet into field experimentation.

As we look at the biodiversity of agricultural land, there is a dearth of information. How many species are there in a field or hedgerow? We probably have a reasonable estimate of the numbers of species above ground. The birds and mammals are well known, as are the vascular plants. Some of the cryptogamic plants are reasonably well known, such as the mosses, liverworts and lichens, but other groups such as algae and fungi are more poorly known. Some of the invertebrates groups, such as butterflies, moths, beetles and spiders, are reasonably well known, but this is not true of the nematodes and protozoa. It is therefore below ground, where there are very large numbers of species (André *et al.*, 1994; Usher, 1996), that it is difficult, and probably impossible, to estimate the number of species in a defined area. It is this lack of information that is addressed by Georgiadis & Balmford (1992). They concluded that we must not spend too much time deciding how to measure biodiversity; the best approach to conservation is the one that works! Information that is needed to get it working, but we must make maximum use of the information that is currently available.

HOTSPOTS AND A LANDSCAPE PERSPECTIVE

A hotspot is a defined geographical area that has more species than average. Thus, Prendergast *et al.* (1993) counted the number of species of birds, butterflies, dragonflies and damselflies, freshwater macrophytes and bryophytes in the 10km squares of the National Grid, and defined 'hotspots' as being the 5 percent of squares with the largest number of species. The concept was extended to Scotland by Usher (in press), who used both 'hotspots' (10 percent of squares with the largest number of species) and 'coldspots' (10 percent of squares with the smallest number of species). In such studies each 'square' had the same land surface area (100ha), except for coastal squares, and the number of species was counted irrespective of the kinds of habitat that occurred in the square.

This approach is inappropriate in agricultural environments. This review has already indicated that there are likely to be large differences in biodiversity from one habitat type to another in agricultural environments. The crude use of equal and large areas obscures the processes that are occurring in fields of different sizes, the field boundaries, and the patches of other habitats, be they woodlands, ponds, old grasslands, thickets, etc. Agricultural land is a mosaic of large patches (e.g. fields), small patches (e.g. copses) and linear features (e.g. hedges and ditches). Rather than considering hotspots *per se*, it is better to investigate this mosaic and to ask if some mosaics support greater biodiversity than others. In other words, biodiversity on agricultural land should be viewed at a landscape scale.

Studies on three species of birds in America (Haas, 1995), using agricultural land with a sparse structure of shelterbelts, indicated that most movements were of short distance within belts. Inter-belt movement was significantly more frequent in belts joined by a woody corridor than between isolated belts. In the Netherlands, nuthatches (*Sitta europaea*) use farm woodlands, and behave as a metapopulation (Verboom *et al.*, 1991) with a dynamic distribution in space and time. Extinction in any farm woodland was dependent on the size of the woodland and the quality of the habitat; colonisation depended on the nuthatch density in surrounding patches. In East Anglia, FitzGibbon (1993) inferred that the probability of grey squirrels (*Sciurus carolinensis*) occurring in a farm woodland was dependent on the proximity of other woodlands and on the presence of hedges. There are many studies of small mammals (e.g. Zhang & Usher, 1993) that indicate that the structure of agricultural environments is important in determining the density and diversity of vertebrate species. Landscapes connected by hedges and shelterbelts tend to be more species-rich, or to have more functional metapopulations, than unconnected landscapes.

Do such generalizations also apply to invertebrates? Working on ground beetles in small woods and hedges separating meadows, Petit (1994) demonstrated that woodland species occurred in lower density and had a higher intensity of movement in hedges than in woodlands. She considered that hedges were important for connecting small populations of beetles into a metapopulation structure. Working intensively on one species of ground beetle, *Abax ater*, Petit & Burel (1993) showed that it could establish long-lasting but small populations in hedgerow nodes, thus providing sources of colonists for newly-established woods. Although there have been few studies on the use of corridors by invertebrates, it is perhaps best to assume that corridors are at worst neutral, and at best beneficial, in increasing biodiversity in agricultural environments. Acknowledging that our understanding of mosaic environments is incomplete, McIntyre (1994) considered that the landscape perspective had both observational and theoretical support.

Perhaps the main difficulty is that we understand a few species reasonably well, but there are so many species that we cannot have conservation action plans for each (Franklin, 1993). Hence, the only practical way to conserve diversity is to think of ecological processes and to focus on habitats, though the three hypotheses outlined above become important here. We probably have a less clear understanding of habitats than of species. However, more and more observations indicate that it is the mosaic of habitats, their interconnections, and the nature of the boundaries between them, that influence the diversity of large areas such as agricultural land. Compared to our knowledge of species, we know relatively little about the interactions of habitat patches in mosaic landscapes; here indeed is a potentially fruitful area for both practical and theoretical research.

DISCUSSION: WHAT DO WE VALUE?

This review has indicated that agricultural land is not without biodiversity, at the gene, species and habitat levels. Intensification of agriculture, and the wealth of agrochemicals available, have unquestionably had impacts on the biodiversity of large areas of land, yet some of that natural biodiversity remains in the non-farmed fragments, including woodlands, hedges, ditchsides and field corners. Intensification has had many influences on the environment, as reviewed by Isselstein *et al.* (1991), but the creation of agricultural surpluses has led to a variety of responses, which include set-aside, extensification, organic production and the search for modern technologies that are more environmentally benign (Anon., 1997). There are increasing opportunities for conservationists and agriculturists to work together (Hook, 1994) for biodiversity conservation; indeed, 'partnership' is the message of many campaigns (Anon., 1990).

Why do we focus on biodiversity in the 1990s? What value can it have? Is it aesthetic, or the interest of a minority who are natural historians, or a preserve of professional ecologists, or a matter for hard-nosed economists? In the 1950s, Rachel Carlson's *Silent Spring* prophesied environmental problems, as a result of using organochlorine insecticides such as DDT, that have subsequently been recognised as major economic problems. In the 1990s, is our concern about biodiversity prophesying problems that we might experience with our economies somewhere in the 21st century?

Whatever the answers to such questions, there is an increasing literature on the value of biodiversity. Methodological studies have explored the reasons why it is extremely difficult to use standard economic models for a subject that is generally poorly understood (Hanley *et al.*, 1995). Such studies tend to resort to potentially unrealistic comparisons between species (Polasky *et al.*, 1993). Does one consider the economics of a small scale, local resource (Burton *et al.*, 1992), or aim to consider biodiversity in its global context and suggest international mechanisms (Swanson, 1992) for conserving the biological diversity of this planet? The task of assessing the economics of biodiversity is new and much research still needs to be done. Can existing economic models and theories be transferred to considerations of biodiversity, or is a new series of models and theories required?

One of the greatest difficulties is knowing what to measure as an output. If a farmer plans to grow wheat as a crop, then there is one output that can be easily measured; namely wheat yield per hectare. If the farmer is choosing which crop to grow, then there are a few alternatives that need to be considered; namely maximizing the margin on growing wheat, or barley, or oil seed rape, or flax, or whatever; the number of possible outputs is really quite small. Conversely, if we are concerned with biodiversity, how do we start to measure outputs or achievements, and what does maximization mean? Do we want more species, more habitats, some particular species or some particular habitats, a greater range of genetic variability, either more or less complex mosaics in the landscape, and how do we choose between all of these?

It is little wonder that the economics of biodiversity are so poorly studied and understood. We cannot define precisely what is required, nor do we have quantitative measures of biodiversity. As a result, models and theories can hardly be developed except in very simplified cases. One can understand the more emotional analyses of authors such as Ehrlich & Ehrlich (1992). It may take decades or centuries to refine economic theories, but it is now that we need to take action. Ehrlich & Ehrlich (1992) outline four reasons for valuing biodiversity; these are

- as the dominant species on earth, humans have a stewardship responsibility for other life on this planet;
- biodiversity has an aesthetic value, as demonstrated by gardening, ecotourism, and popularity in the media;
- biodiversity provides many economically valuable products, including food, medicine and industrial raw materials; and
- biodiversity provides an array of free ecosystem services, including the maintenance of the O₂/CO₂ balance in the atmosphere and recycling nutrients from dead or waste materials.

Given this array of benefits, how can we use, increase or maximise biodiversity on agricultural land? Should we be focusing more on the natural control agents (predators, parasites, diseases) of the pests of our crop plants and domestic livestock (Altieri, 1991)? Should we be recognising that a mosaic landscape provides far more benefits, many of them non-tangible, than hectares of monoculture where pesticides have tended to eliminate most other plants, invertebrates and possibly vertebrates? The answers to these questions are bound to be subjective. If there is no acceptance of environmental responsibility (Ballantyne & Gerber, 1994), then biodiversity probably does not matter. If the concept of environmental responsibility is accepted, then biodiversity matters. Happily there is evidence that more and more people accept that they have such a responsibility. It then becomes a challenge to manage our agricultural land in a way that balances the tangible and non-tangible benefits, that retains the land's productivity, but yet maintains or enhances the land's biodiversity and aesthetic qualities, In fact our agricultural land must be a place in which we would wish to live.

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