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Crop domestication and the disruption of species interactions

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Abstract

The process of crop domestication involves artificial selection for beneficial traits in plants, such as yield, standard development times for ease of harvest, and pest and disease resistance. This process has greatly improved crop performance and can allow farmers to produce viable harvests in previously un-profitable circumstances. However, there is growing evidence that domestication may impact species interactions perhaps through the amplification of effects across spatial scales and so have a pervasive influence on the functioning and sustainability of agro-ecosystems. This can occur directly, through unintentional alteration to crop traits that disrupt the host-finding ability of natural enemies; or indirectly through alterations to within-plant nutritional quality that impacts herbivore size and density and then ramifies throughout food chains. At the field level, the low variability in traits between individual plants means that particular weed and invertebrate communities are associated with each crop type. At the landscape level, the use of one or a few varieties across wide spatial scales, planted and harvested relatively synchronously, further reduces diversity. This process acting across multiple spatial scales represents a considerable selection pressure that may result in feedback-loops which favour the occurrence of particular traits within the community (e.g. resistance to pesticides). In order to properly balance the ‘pros and cons’ of the widespread adoption of new varieties, for the future, we must consider how particular traits influence interactions within the wider ecological community, and how these effects amplify across spatial scales. Here we argue that the process of domestication (with the primary goal of yield increases) and the widespread use of a few varieties has led to potentially detrimental impacts on species interactions, and suggest possible strategies for mitigating some of these negative impacts in the future.

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Zusammenfassung

Der Prozess der Züchtung von Feldfrüchten umfasst die künstliche Selektion von günstigen Eigenschaften der Pflanzen wie Ertrag, standardisierte Entwicklungszeiten für eine einfachere Ernte sowie Schädlings- und Krankheitstoleranz. Dieser Prozess hat die Feldfruchtnutzung deutlich verbessert und ermöglicht den Landwirten den Anbau mit ertragreichen Ernten unter zuvor nicht lohnenden Bedingungen. Dennoch gibt es in zunehmendem Maße Hinweise darauf, dass die Züchtung einen Einfluss auf die Interaktionen zwischen den Arten haben kann, vielleicht durch eine Verstärkung der Effekte auf räumlichen Skalen, und so einen deutlichen Einfluss auf die Funktionalität und die Nachhaltigkeit der Agrarökosysteme haben kann. Dies kann direkt geschehen, indem unbeabsichtigte Veränderungen der Pflanzeigenschaften die Wirtsfindungsfähigkeit von natürlichen Gegenspielern

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stören, oder indirekt durch Veränderung der Nahrungsqualität innerhalb der Pflanzen, die einen Einfluss auf die Größe und Dichte der Herbivoren ausübt und sich dann in der Nahrungskette fortsetzt. Auf der Ebene der Felder bedeutet die geringe Variation der Eigenschaften zwischen den einzelnen Pflanzen, dass bestimmte Unkraut- und Invertebraten-Gemeinschaften mit jedem Feldfruchttyp verbunden sind. Auf der Ebene der Landschaften reduziert der großflächige Gebrauch einer oder weniger Varietäten, die relativ synchron gepflanzt und geerntet werden, die Diversität zusätzlich. Dieser Prozess, der sich auf vielfältigen räumlichen Skalen auswirkt, stellt einen beachtlichen Selektionsdruck dar, der sich in Rückkopplungseffekten auswirken wird, die das Auftreten besonderer Eigenschaften in den Gemeinschaften (z. B. Resistenz gegenüber Pestiziden) fördern. Um in Zukunft die Vor- und Nachteile der verbreiteten Einführung neuer Varietäten auszugleichen, müssen wir berücksichtigen, wie bestimmte Eigenschaften die Interaktion in der weiteren ökologischen Gemeinschaft beeinflussen und wie sich diese Effekte über die räumlichen Skalen verstärken. An dieser Stelle diskutieren wir, wie der Prozess der Züchtung (mit dem primären Ziel der Ertragserhöhung) und der verbreitete Einsatz nur weniger Varietäten zu potenziell negativen Auswirkungen auf die Arteninteraktionen geführt hat, und schlagen mögliche Strategien vor, wie einige dieser negativen Auswirkungen in Zukunft vermieden werden können. © 2010 Gesellschaft für Ökologie. Published by Elsevier GmbH. All rights reserved.

Keywords: Agroecosystems; Parasitoids; Predators; Biodiversity; Ecosystem function; Pest control; Species interactions

Introduction

Lack of security in food supply has led to marked increases, and fluctuations, in food prices and significant social unrest in many developing countries during 2007/8. With future predictions of world population being 50% higher than the current level by 2050 (UN, 2004) it is clear that food security will only be assured through greatly increased farmland productivity and yield (OECD-FAO, 2008). There is much evidence that a drive towards productivity should make use of, and foster, farmland biodiversity. Ecosystem services, which result from species interactions, directly support crop productivity and yield (Kremen, Williams & Thorp, 2002); examples include services of pollination, natural enemy predation of crop pests and nutrient recycling by detritivores. However, approaches to developing new domesticated crop types/varieties and how these are grown across farmland landscapes are now known to disrupt beneficial species interactions. Here we collate evidence that domestication and the widespread use of a few varieties has led to unintended and potentially detrimental impacts on species interactions. We consider the effects of disruption of species interactions at the plant-, field- and landscape-level, and community-levels of ecosystem organisation. We argue that modern agricultural landscapes can be productive and sustainable if proper consideration is given to preserving interactions between species. A greater understanding of the potential community-level impacts of new crop varieties and their role in agricultural landscapes is key. We conclude that a greater emphasis on increasing crop trait heterogeneity, and adopting an appropriate landscape 'model' or description, to build-up heterogeneity across multiple spatial scales, will help deliver food security and greater farmland biodiversity in the future.

Domestication in agro-ecosystems

Domestication is the process of artificial selection that leads to a plant population becoming suited to a particular set of conditions and cultivated successfully (Evans, 1993). Current estimates suggest that there are approximately 35,000 species of cultivated plants, representing 14% of the higher plant species in the world (Khoshbakht & Hammer, 2008). From the 18th to early 20th century 'landraces', of geographically and ecologically distinct plant populations managed by local farmer-breeders (Cleveland, Soleri & Smith, 1994), were the primary source of crop varieties. Since then, technology has dramatically changed what and how we farm. First, the development and widespread uptake of hybrid maize varieties in the United States led to large increases in yield. Then, crop varieties coming out of the 'green revolution' produced much higher yields than their predecessors, but with a requirement for fertilizers and pesticides. Finally, molecular genetic technologies have transformed plant breeding. These technological advances have occurred against the backdrop of increasing mechanization that has resulted in fewer, larger farms. The current farming landscape offers a stark contrast to the great variation in cultivated plants and animals that captivated Darwin, detailed in the first chapter of *On the Origin of Species*, entitled "*Variation under domestication*", in 1859. Traditional varieties have been replaced by less diverse modern cultivars and hybrids (Hoisington, Khairallah, Reeves, Ribaut, Skovmand et al., 1999) that display consistent traits over many plant individuals and are grown in monocultures over large areas with only a few varieties being planted widely each season (Lin, Perfecto & Vandermeer, 2008). For example, just four crop types (maize, wheat, soybeans, cotton) are grown on two thirds of arable land in the United States and this has implications for

the spread of pests and disease (Margosian, Garrett, Hutchinson & With, 2009). Crops, and their associated weeds, are then subject to strong selection pressures, such as the repeated and synchronised use of pesticides. These factors result in changes to interactions between species that may build-up across spatial scales. Successful plant breeding efforts have led to a large and sustained increase in crop yields and this has been important for meeting the food demands of a growing human population. Recently, yield increases of the major cereal crops have slowed (Hoisington, Khairallah, Reeves, Ribaut, Skovmand et al., 1999) despite an ever-increasing number of varieties being released. Greater emphasis on how the effects of homogeneity of crop traits scale-up to the whole landscape may provide new opportunities for increasing productivity in a sustainable manner.

Changes across spatial scales

Here we collate research on how crop-traits and the management of modern crop varieties leads to unintended changes to species interactions at the plant, field and landscape scale. It seems likely that some effects will amplify across spatial scales even though they have been studied independently. It is this amplification that has the potential to further limit our ability to maintain biodiversity within agricultural landscapes and may work against us when trying to improve the provision of ecosystem services in farmland.

Comparisons between wild and cultivated varieties or cultivated varieties of the same crop show that domestication can affect species interactions at the plant level (Table 1; Fig. 1: “C”). Chen and Welter (2007) found that herbivorous caterpillars were more likely to be parasitised on wild than on agricultural sunflowers. This was not due to changes in parasitoid foraging behaviour, but to the creation of structural refuges in the seed layer of cultivated sunflowers, at the time when the larvae are vulnerable to attack. This effect scaled to the ecosystem level, with parasitism being 6–10 times higher in native sunflower habitats than agricultural habitats (Chen & Welter, 2002). On tomato cultivars enemy-free space is created by glandular trichomes on the leaf surface that have no effect on larval establishment of the potato tuber moth (*Phthorimaea operculella*) but did have an adverse effect on its parasitoid biocontrol agent (*Diadegma pulchripes*) (Mulatu, Applebaum & Coll, 2006). The caterpillars do not acquire defensive traits from the tomato foliage that inhibited larval parasitoid development, rather the tomato foliage hampered host-searching by the parasitoids. Bukovinszky, van Veen, Jongema and Dicke (2008) observed nutritional differences between wild and domesticated *Brassica* plants that resulted in

differences in aphid body size and density. The wild *Brassic*as were a better host for aphids and, indirectly, primary and secondary parasitoids than the domestic varieties due to both size- and density-mediated effects. Amongst domesticated *Brassica napus oleifera* (oilseed rape, canola) Bohan, Hawes, Haughton, Denholm, Champion et al. (2007) found that the number of parasitoids and the parasitoid to herbivore ratio was much higher on varieties developed to be sown in the spring than on varieties developed for sowing in the autumn, even though the numbers of herbivores were similar on the two crop types. These differences were best explained by the comparatively shorter and open structure of spring sown varieties, making herbivores more apparent. Further examples of subtle (e.g. nutritional differences) and gross (e.g. plant growth and habit) changes in crop traits that impact on species interactions are shown in Table 1.

Technological advances have led to monoculture fields where the crop variety chosen by the farmer partially dictates the management package employed (Fig. 1: “B”). Therefore, both individual crop traits and management variations may be remarkably consistent across large spatial scales. Analysis of large-scale farmland data-sets have shown that weed species and functional compositions within arable fields are structured by the crop being grown (Smith, Bohan, Clark, Haughton, Bell et al., 2008; Hawes, Haughton, Bohan & Squire, 2009). Interestingly, differences between fields of particular crops were relatively small, despite large distances. Indeed, for the crops tested, it could be inferred that the weed composition in a field of one crop in the south of the UK was more similar to the weed composition in a field of the crop in the north, than to the compositions of adjacent fields of different crops. Arguably, this effect occurred because modern crop varieties share similar traits, wherever they are grown, and the way they are grown in terms of planting and harvesting times, nutrition, and pest management, is consistent.

As each crop type largely determines the weed species that reach maturity in the field and, in combination, the crop and the weeds select for the observed compositions of invertebrates, it follows that scaling up to the landscape (Fig. 1: “A”), the community present will be strongly related to the crop make-up of the landscape. Reduction in the diversity of crops and crop traits leads to reduced habitat-diversity across space and time and this process has been blamed for impacts on biodiversity in general. A large-scale shift towards monocultures and from spring-sown to autumn-sown cereals across Europe has been implicated in the declines in arable biodiversity across a range of taxa (Fox, 2004; Robinson & Sutherland, 2002), and have prompted the development of policy directed primarily at the non-cropped areas of farmland landscapes to increase habitat

Table 1. Examples of the process of domestication and alterations to plant traits disrupting species interactions in some way (impact can be positive, negative, neutral or unknown in terms of pest control). Ordered by year of publication.

Reference	Plant(s)	Herbivore(s)	Interaction
Mbata and Brewster (2009)	Six cowpea varieties <i>Vigna unguiculata</i> (walp.) (2 bruchid resistant varieties, 4 susceptible varieties)	<i>Callosobruchus maculatus</i> (F.) cowpea weevil	In comparison to susceptible cowpea varieties the resistant varieties supported fewer weevil progeny and showed greater suppression of the weevil by the larval parasitoid <i>Pteromalus cerealellae</i> (Olivier).
Wang et al. (2009)	Wild and cultivated olive <i>Olea europaea</i> L.	<i>Bactrocera oleae</i> (Rossi) olive fruit fly	Cultivated olives have larger fruit than wild olives and so provide a better food resource for the herbivore and more enemy-free space, because the parasitoid <i>Psytalia lounsburyi</i> (Silvestri) has a relatively short ovipositor that cannot penetrate the larger fruit.
Gols et al. (2008)	Three wild <i>Brassica oleracea</i> populations and cultivated <i>B. oleracea</i> , gemmifera (brussel sprouts) cv. Cyrus	<i>Pieris rapae</i> (specialist) and <i>Mamestra brassicae</i> (generalist)	Herbivore performance and the development of endoparasitoids (<i>Cotesia rubecula</i> and <i>Microplitis mediator</i>) was affected by the plant population on which they were reared through the expression of defensive compounds.
Sarfraz, Dosdall, and Keddie (2008)	Eight Brassicaceae: <i>Brassica napus</i> (3 varieties), <i>B. rapa</i> , <i>B. juncea</i> , <i>B. carinata</i> , <i>B. oleracea</i> , and <i>Sinapis alba</i> L.	<i>Plutella xylostella</i> (L.) diamond-back moth	Survival and parasitism by the parasitoid <i>Diadegma insulare</i> (Cresson) varied among the tested plant genotypes on which host larvae were reared. Survival of <i>P. xylostella</i> did not differ between the genotypes.
Bukovinszky et al. (2008)	Wild and cultivated <i>Brassica oleracea</i> L. (Brussel sprouts cv. <i>gemmifera</i>)	Aphid community	Differences in plant traits effect aphids and their primary and secondary parasitoids through size mediated and density mediated processes.
Chen and Welter (2007)	Domesticated sunflowers a <i>Helianthus annuus</i> var. <i>macrocarpa</i> L. and wild sunflowers <i>Helianthus annuus</i> L.	Sunflower moth <i>Homoeosoma electellum</i> Hulst	Domestication created a refuge for the sunflower moth from attack by its major larval parasitoid <i>Dolichogenidea homoeosomae</i> Muesebeck. More larvae fed in seeds on the domesticated plants which were too hard for the parasitoid ovipositors to penetrate.
Rudgers and Whitney (2006)	Two distinct architectural morphs (prostrate or erect) of <i>Baccharis pilularis</i> a perennial shrub	<i>Rhopalomyia californica</i> gall-forming midge and <i>Gnorimoschema baccharisella</i> moth galls.	The composition of the herbivore assemblage varied strongly with plant architectural morph. Architectural traits were correlated with herbivory levels.
Mulatu et al. (2006)	Cultivated tomato	<i>Phthorimaea operculella</i> (Zeller) potato tuber moth	The glandular trichomes on the tomato plant had an adverse effect on the larval parasitoid <i>Diadegma pulchripes</i> through disrupting oviposition ability.
Chen and Welter (2002)	Native and agricultural sunflower habitats	Sunflower moth <i>Homoeosoma electellum</i> Hulst	Adult and larval sunflower moths were more abundant in agricultural habitats, and parasitism by its major larval parasitoid <i>Dolichogenidea homoeosomae</i> Muesebeck was higher in the native habitats. See Chen & Welter (2007) above.
Massei and Hartley (2000)	Wild and cultivated olive <i>Olea europaea</i>	<i>Ungulates</i>	The domesticated olive seems to have been selected for faster growth at the expense of allocation to secondary compounds that reduce ungulate browsing.
Rosenthal and Dirzo (1997)	<i>Zea</i> sp. maizes and teosintes: wild perennial, wild annual, landrace cultivar and modern cultivar	<i>Diatraea grandiosella</i> pyralid stemborer and other naturally occurring folivorous insects	The wild perennial was most defended by attack from herbivores followed by the wild annual, the landrace cultivar and the modern variety was least defended. The process of domestication may have resulted in the reallocation of resources from defense against herbivores into growth and reproduction.

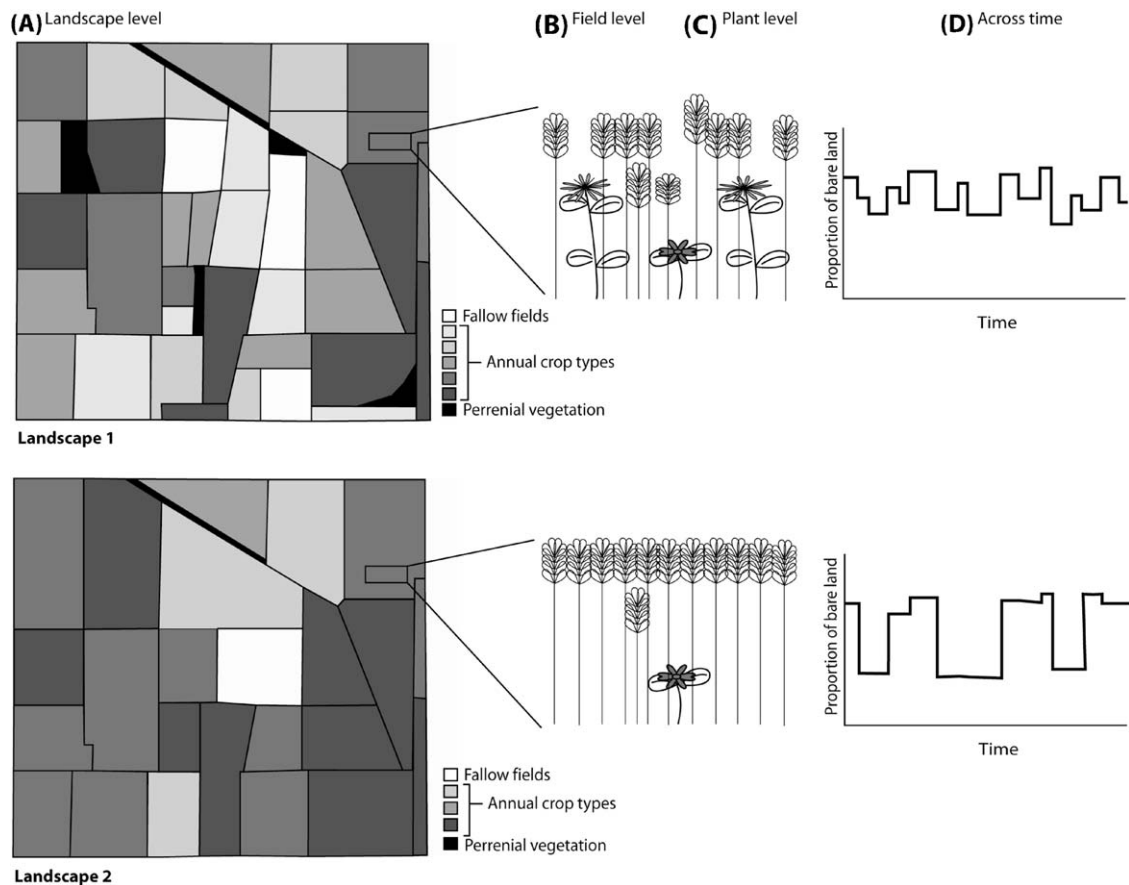


Fig. 1. A schematic figure for the multiple levels of heterogeneity possible in agricultural landscapes. Less diversity is seen at the landscape (A), field (B), and plant (C) level in landscape 1 than in landscape 2. Across time (D) landscape 2 displays less variation in the proportion of bare land at any one point in time.

heterogeneity (Benton, Vickery & Wilson, 2003) for biodiversity. However, scientific evaluation of these policies suggests that their value may be limited (Butler, Vickery, & Norris, 2007; Kleijn, Baquero, Clough, Díaz, De Esteban et al., 2006). Recently, there have been instances where consideration of landscape or higher-scale factors in the introduction of a new crop has led to clear benefit. Conservative resistance management of Bt transgenic cotton in Australia has prolonged the life of this technology, by initially restricting the area grown to 30% of the cotton cropping area per farm to provide refuges for susceptible pests (Downes, Mahon & Olsen, 2007). Similarly, loss of yield due to fungal rusts in short rotation coppice willow grown for energy, is partly managed by planting mixtures of high yielding and resistant varieties at the field and landscape scale (Dawson, McCracken & Carlisle, 2005).

Large, homogeneous farmland landscapes present a strong selection pressure. For species that can adapt, these landscapes represent a considerable opportunity. Corn rootworms (*Diabrotica* spp.) are serious pests of maize in North America. During the late 1940's farmers began growing maize continuously, where previously it

had been grown in rotation with small grains, hay, clover or alfalfa. This continuity of host plants allowed pest populations to expand (Levine & Oloumisadeghi, 1991). A move back to a mixed rotation was successful in controlling corn rootworm damage. However, since the mid 1990's this cultural control practice has been unable to prevent damage to first-year maize (Rondon & Gray, 2004; Schroeder, Ratcliffe & Gray, 2005) because a new variant of western corn rootworm can oviposit onto a variety of crops. A similar practice of growing maize in monoculture has also allowed the rapid spread of the western corn rootworm throughout parts of Europe (Modic, Knapic & Urek, 2008). Certain spider species ('agrobionts') are often dominant in arable fields (Samu & Szinetar, 2002). For the agrobiont species there was little between field and regional variation in the species assemblage, and their life cycle was synchronized with the crop-growing season. Schmidt & Tschardtke (2005) suggested that the dominance of agrobiont species is an artefact of the low densities of other species and not due to their actual higher abundance. Whatever the explanation, this dominance of a sub-set of species is likely to impact on the potential interactions between

species and to possibly result in decreased functional diversity. This appears similar to the ‘biotic homogenisation’ of disturbed tropical forests described by Lewis (2009), where the community consists of a restricted pool of species, with habitat-specialists and endemic species most likely to be lost.

From species to the community

Ecosystem-genetic approaches are leading to a greater understanding of the community-level consequences of heritable traits (Whitham, DiFazio, Schweitzer, Shuster, Allan et al., 2008). The expression of a plant phenotype results from the combination of plant genotype and the environment in which the plant grows. Although it is not clear whether heritable traits, in a single species, have predictable effects on community structure, intra-specific variation in traits is known to shape the composition of herbivore assemblages (Rudgers & Whitney, 2006) and affect the structure of entire food webs (Bukovinszky et al., 2008). So, are agricultural landscapes that are homogeneous in terms of crop genetic diversity selecting only for a restricted sub-set of species? This question becomes particularly relevant when we consider that globally c. 34% of ice-free land surface has been covered by cultivated crops (12%) and grazed land (22%) (Ramankutty, Evan, Monfreda & Foley, 2008).

Analyses of the invertebrates in arable fields suggest that each crop might have a significantly different invertebrate composition (Smith, Bohan, Clark, Haughton, Bell et al., 2008; Hawes et al., 2009), partly explained by the composition of weeds. Outside the field, adjacent vegetation can provide source areas for invertebrate pests and predators which can then move into the adjacent crop fields (Schellhorn, Bellati, Paull & Maratos, 2008). The impact these movement and spillover events have on both the provision of ecosystem services and genetic exchange is still unclear. Vialatte, Dedryver, Simon, Galman & Plantegenest (2005) demonstrated that there can be limited exchange of individuals of a species between cultivated and uncultivated parts of the agroecosystem. High levels of genetic differentiation were found between aphid populations on host plants in cereal fields and uncultivated margins. Aphid populations on the cereals were more genetically homogeneous than populations on uncultivated plant hosts, perhaps due to highly synchronized obligate host shifts in the cultivated system following crop succession. If this pattern is the same for other species we could be unwittingly reducing genetic diversity by selecting for a reduced sub-set of genotypes. This may result in feedback-loops that could speed up the occurrence of pesticide resistance in weed or insect species. Indeed, the environmental heterogeneity of genotypes in space and

time has been shown to be crucial for delaying herbicide resistance (Roux, Paris & Reboud, 2008). Genetic diversity is also required for rapid phenotypic and ecological diversification that can lead to the emergence of multiple species (Gavrilets & Vose, 2005). In the short-term it is phenotypic diversity, resulting from underlying heritable genetic variation, which establishes the variety of environmental niches for species to occupy. In the longer-term, genetic diversity will maintain, and potentially generate, increased biodiversity in agro-ecosystems.

Planning for the future

How do we mitigate the negative impacts of domestication in the future? The current model for temperate farmland in developed countries consists of a landscape that is relatively simple, composed of isolated fragments of remnant vegetation embedded in monoculture crop fields. We believe we can increase biodiversity in this system. To date, most attention has been paid to strategies aimed at increasing biodiversity in the small non-cropped components of the landscape. Implicit, in most agri-environment schemes, is a belief that increases in biodiversity here will offset losses of biodiversity within the crop areas; an expectation that has not been explicitly tested. We would argue that greater benefit could be achieved by slightly improving the large areas of low-diversity crop. Clearly, non-crop areas have received the most attention to date because altering diversity within these areas “leaves the field for the farmer to manage” and so is attractive to landholders and policy makers. However, introducing diversity by maximising crop trait diversity might not have to come at an unbearable cost and could provide enormous benefit in the long-term. We have known for some time that introducing within-field vegetation diversity by inter-cropping or strip-cropping can lead to positive changes in species populations and communities (Andow, 1991). Pests may be reduced in intercrop systems through a variety of mechanisms (see Vandermeer, 1990), yet intercropping is not widely practiced. The challenge is to find the optimum between the ecosystem benefits of plant-level trait heterogeneity and production cost.

While emphasis has been placed on encouraging landscape diversity and low-intensity farm management, mainly through the introduction of agri-environment schemes, the genetic diversity of a landscape has been relatively ignored. Hughes, Inouye, Johnson, Underwood and Vellend (2008) suggest that for ecosystems dominated by a few species, such as in modern cropping landscapes, genetic diversity may be used by the community in a similar way to species diversity. The use of varietal mixtures is the norm for subsistence

farmers, but their use in modern agriculture is rare (Smithson & Lenne, 1996). This is not to say it cannot be done. For example mixes are widely used in coffee-agroforestry systems in tropical countries, and genetically diversified rice crops were planted across large areas of China resulting in yield gains by minimizing pathogen damage (Zhu, Chen, Fan, Wang, Li et al., 2000). While there are a number of obstacles to be overcome we believe that farmers could be encouraged to plant sections of fields with alternative varieties or crop types (as with GM crop buffers), supported by existing agri-environment schemes.

Conservation of crop genetic resources is critical for delivering new varieties in the future that are well suited to local conditions. Certainly there is a large focus on the conservation of genetic resources that underpin breeding programs mainly through *ex situ* seed banks, genebanks and germplasm collections. The FAO estimates that there are globally 6 million accessions stored in *ex situ* collections (FAO, 1996) in what are sometimes called “gene morgues” (Hoisington, Khairallah, Reeves, Ribaut, Skovmand et al., 1999). While genetic conservation is important, the greatest value is realised when they are used to create landscapes with a range of crop varieties that contain enough genetic diversity to support functioning communities. In many areas of the world farmers practice *in situ* conservation by using varietal mixtures and landraces as part of their farming system and this allows the process of natural selection and artificial selection by farmers to continue (Villa, Maxted, Scholten & Ford-Lloyd, 2005). Farmers that utilise varietal mixtures experience reduced insect and disease damage, a greater stability of production, a reduction in risk and in some instances increases in yield (Smithson & Lenne, 1996). A greater emphasis on *in situ* conservation and the use of a greater range of crop types and varieties in all agricultural landscapes may be essential for biodiversity conservation.

The choice of domestication traits and crop varieties is made for good, productivity-orientated reasoning, and this is unlikely to change in the future. An extension to this process, which incorporates alternative goals besides a simple increase in yield, might have profound benefits. This shift is already occurring with the development of drought-resistant, fertilizer responsive and disease resistant crop varieties that are better able to cope with local conditions (Takeda & Matsuoka, 2008). There are steps being taken towards systems-level approaches, such as adopting perennial grain crops that are longer lived and develop deep root systems (Cox, Glover, Van Tassel, Cox & DeHaan, 2006). These plants are particularly valuable resources during times of the year when annual crops have been harvested and fields are essentially bare (Fig. 1: “D”). Improving the provision of ecosystem services in existing agricultural lands through practices which maintain species interac-

tions must be seen as an important component of strategies aimed at increasing productivity. Whilst inputs such as pesticides can be effective at replacing naturally available pest control services (at least in the short-term), resistance is increasingly threatening current pesticide management practice and by harnessing these essentially ‘free’ services you may be more likely to achieve sustainable farming systems in the long-term.

Future research needs

To fully understand, manage and exploit biodiversity in agroecosystems, we must first understand the changes to the underlying structure of communities that result from the interactions between species and how these changes affect overall productivity. Here we have identified the process of domestication and widespread use of a few crop varieties as one pathway that may lead to alterations in community structure at multiple spatial scales. Whilst these effects are usually studied at the different spatial scales independently, the amplification of effect across spatial scales is likely to occur. Modeling approaches are a tractable way we can start to artificially manipulate landscapes to examine this amplification across spatial scales (Schellhorn, Macfadyen, Bianchi, Williams & Zalucki, 2008). Combining these approaches with experimental manipulations that use a combination of species-based and trait-based descriptors might prove practical for explaining how crop domestication influences ecosystem function across spatial scales (Bell, Mead, Skirvin, Sunderland, Fenlon et al., 2008). Modeling approaches can also be used to look at how a functionally-based farmland ecosystem, in which the crop is treated as a component of biodiversity, is affected by variation of management and of environmental conditions (Caron-Lormier, Bohan, Hawes, Raybould, Haughton et al., 2009), allowing optimization. The application of high-throughput sequencing technologies to agroecosystem studies may be one way of examining emergent properties of these different farming systems. Recent developments in eco-genomics allow us to explore complex communities at the system level (Valentini, Pompanon & Taberlet, 2009). This rapid form of biodiversity assessment may prove useful for examining alterations to community composition in large-scale studies that compare different agricultural landscapes.

At this stage it is still unclear whether genetic diversity can substitute for species diversity across spatial scales. If we encourage farmers to plant different varieties of the same crop species on their farm will this lead to the same biodiversity benefits as encouraging them to plant different crop species? If the different crop varieties chosen show dramatic differences in growth habit or seasonality this might suffice, however, the varieties

chosen by the farmer are usually those that fit within the agronomic constraints of the farm. There may not be much choice but to plant one particular variety, in which case crop species diversity may be needed. Again a combination of modeling approaches and empirical studies could be used to start to examine these trade-offs in agricultural landscapes. Furthermore, information from a large amount of earlier research on introducing within-field vegetation diversity by inter-cropping or strip-cropping is available but has only occasionally been put into practice (Vandermeer, 1990) in western cropping systems. Understanding how these techniques can be incorporated into today's farm management and in what contexts they will be most useful is a limiting knowledge gap.

There is evidence that important ecosystem services such as plant pollination (Biesmeijer, Roberts, Reemer, Ohlemuller, Edwards et al., 2006) and natural pest control (Landis, Gardiner, van der Werf & Swinton, 2008) are impoverished. Food security issues mean that it is now even more important that we make biodiversity work for us and it seems that heterogeneity at multiple spatial scales is essential (Tylianakis, Rand, Kahmen, Klein, Buchmann et al., 2008). Solely focusing on crop yield and performance has done little to solve inequalities in food supply around the world. However, expanding the goals of crop domestication to exploit trait variation that supports community-level functions may go some way to improving this situation.

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