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Abstract

 This study shows how data from very different disciplines can be combined to address questions relevant to contemporary conservation and understanding. This novel, interdisciplinary approach provides new insights into the role of economic factors as a driver of biodiversity loss in the uplands. Biodiversity levels have varied considerably over 400 years, partly as a function of land management, suggesting that establishing baselines or "natural" target levels for biodiversity is likely to be problematic. Changes in livestock grazing pressures brought about by changes in prices had statistically significant effects on estimated plant diversity, as did land abandonment. This suggests that long-term management of upland areas for the conservation of diversity should focus on grazing pressures as a key policy attribute. Another policy implication is that drastic cuts in grazing pressures – such as might occur under current reforms of the Common Agricultural Policy - can have adverse biodiversity consequences.

Introduction

It is becoming increasingly evident that current biodiversity values are influenced not just by recent or 20th century management (e.g. Anderson & Yalden 1981; Fuller & Gough 1999; Palmer 1997; Sutherland & Hill 1995, Thompson *et al*. 1995), but also by longer-term drivers (e.g. Lindbladh & Bradshaw 1995; Gustavsson, Lennartsson & Emanuelsson 2007; Willis *et al*. 2007). The importance of such historical legacies has recently been recognised as 'a rather awkward ancient spanner in modern works' (Marrs 2008). If effective policies are to be developed to conserve biodiversity, then it is clearly important to understand the determinants of biodiversity change as mediated through longer-term changes in land use. Economics has a strong influence on land-use, and thus on biodiversity, past and present (e.g. Barbier 2007; Davies & Watson 2007). Taking agricultural land use as an example, farmers respond to price signals in a predictable way overall. For example, incentives to increase production through the guaranteeing of prices for farm outputs above market-clearing rates resulted in significant increases in livestock numbers when the UK joined the European Community and became party to the Common Agricultural Policy or CAP (Bowers & Cheshire 1983). In upland areas classified as "disadvantaged", income support payments based on stocking rates amplified the desire to expand sheep and cattle numbers. Similarly, current agri-environmental measures rely on the idea that farmers can be induced to supply more environmental "goods" – such as new wetlands or native woodlands – if they are offered payments to do so. Understanding the role of economic incentives such as prices in partially explaining biodiversity change would thus appear to be important.

The principle aim of this paper is to analyse the effect that prices for farm outputs have had on an index of plant biodiversity over 11 sites in the Scottish uplands over the period 1600-2000, during which time there have been marked changes in the intensity and structure of agriculture. Other potential determinants of changes in plant species diversity, such as technological change, land ownership change and climatic variability are also included as variables in the statistical model estimated. As explained below, both economic theory and the statistical approach adopted allow us to use changes in agricultural prices as a proxy for changes

in actual grazing pressures. This means that the historical relationship between grazing pressures

and plant diversity can also be investigated, an analysis which complements and extends more

contemporary ecological studies which have focussed on the effects of shorter-term changes in

grazing pressures on biodiversity. This study also allows us to highlight the potential for historical

and interdisciplinary studies in addressing questions of current policy relevance.

Materials and Methods

SITE SELECTION

Most of the data used in this analysis was obtained from primary historical sources and

new palaeoecological analyses. The data collection sites represent a range of biogeographical

zones in the Scottish uplands (Usher & Balharry 1996). Site selection was an iterative process,

involving the identification of sites with historical potential (where there was a reasonable chance

of obtaining adequate documentary sources), alongside fieldwork to seek suitable small peat

deposits to obtain undisturbed historic pollen sequences for palaeoecological analysis. The 11

sites finally chosen are shown in Supplementary Material Fig. S1. All sites were predominantly

upland livestock farms, with very limited arable cropping during the study period.

CONSTRUCTION OF DATA SERIES ON PLANT SPECIES DIVERSITY

A diversity time series was calculated for each of our sites. We refer to this measure as

B_{it}, the estimate of plant diversity at site i in time period t. This was derived from fine-resolution

pollen data. The pollen analyses were conducted using peat cores from small bogs, rather than

large peatlands, thus ensuring that the pollen signal is sensitive to vegetation cover within a radius

of up to 1 kilometre; this allows a reconstruction of vegetation and land-use change on the scale

of fields and farmsteads. One peat core was taken from each site using a closed chamber corer to

avoid disturbance and compaction. Each core was sampled at c.20 year intervals and dated using

radiocarbon and lead-210 techniques, both with an associated error (see Davies & Watson 2007

for more details). Between 18 and 42 samples were analysed per core. The diversity estimate for

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each sample was derived by applying rarefaction analysis, so providing minimum variance

unbiased estimates of the expected number of taxa (x) in a random sample of n individuals taken

from a collection of N individuals containing X taxa (Birks & Line 1992); n was set at 300 for the

analyses presented. Rarefaction estimates incorporate both plant diversity and vegetation

evenness (equitability), but are not linearly related to either because (1) not all pollen types can be

identified to species level, (2) pollen data are influenced by differences in representation (not all

plants produce equal amounts of pollen), (3) there can be interference in pollen dispersal from

vegetation structure and (4) due to constraints on the relative representation of taxa, since pollen

data are presented as percentages (Birks & Line 1992; Odgaard 1999, 2001). Consequently,

vegetation diversity indices other than the total number of taxa (e.g. Shannon-Wiener, Shannon's

information index or Simpson's index) are not appropriate for pollen.

CONSTRUCTION OF DATA SERIES ON PRICES, AGRICULTURAL LAND USE AND

OTHER POTENTIALLY RELEVANT FACTORS.

Historical land use data was collected from estate papers (archives of material relating to

the landholdings of particular noble families generated by owners, their estate officials and

lawyers, and, less frequently, their tenant farmers) relating to each site. These are mostly held in

the National Archives of Scotland in Edinburgh. Cattle and sheep grazing was the dominant

agricultural land use at the sites investigated over the period in question, and impacts on

biodiversity are expected to depend on how intensively land was managed, and on what

technology was available and utilised (e.g. new breeds of sheep which exert different grazing

pressure than older breeds). Contemporary studies of agricultural impacts on upland plant

diversity focus on grazing pressure, defined as livestock units per hectare (ha). Unfortunately, the

historical record of livestock numbers and area grazed on individual farms is highly incomplete.

Individual estate records typically do not record either the area being grazed or the total number

of livestock at individual sites. We thus cannot use a traditional grazing intensity measure in the

statistical analysis of determinants of plant species diversity. Instead, we reconstruct a time series of prices for livestock and crops by region.

Prices for livestock (sheep and cattle) were taken from estate papers for the early period, and from secondary sources for later periods. In the former case, these prices were assembled for each region in our analysis. Despite being rather patchy and incomplete, data show that separate regional markets existed, but that regional prices closely tracked one another over the period 1580-1880. After 1880, we assume a single national price exists for sheep and for cattle, as markets became more closely integrated. Prices for a single arable crop, bere barley *Hordeum vulgare* L. (Stace 1997), were taken from the "fiars" prices available from 1626-1780 (Gibson & Smout 1995). Later figures for these prices were found in the General Records Office. Fiars prices were "declared" by regional sheriff courts each year as officially-sanctioned prices in settling a range of contracts and bargains.

Technological change is represented by creating count variables for recorded introductions of new breeds, such as Cheviot or Blackface sheep, or the advent of new agricultural techniques, such as liming or the growth of fodder crops (Table 1). Distinct changes in farm management such as enclosure were also recorded. The degree of utilization of each site through a typical farming year was recorded, from abandonment to summer-only use to year-round grazing. Data were also collected on changes in land ownership, size of holding (due to farm amalgamations, which occurred at most sites) and tenancy change.

Information was also needed on relevant environmental factors. Since no long-term time series on climate is available at even the national level for Scotland, we use English data for precipitation (Alexander & Jones 2001) and temperature (Parker, Legg & Folland 1992). However, an "extreme weather events" dummy variable was also constructed for each site, to represent weather events such as floods or droughts that were unusual enough to be recorded in historical documents.

To allow for the imprecise alignment in time of palaeoecological and historical information, and to handle the relative paucity of historical information on land use change, the

data were structured into 20-year intervals over the 400-year study period. The model thus analyses change from one twenty-year period to the next. Where multiple responses are available on a variable within a twenty-year period, a mean score (for quantitative variables) or a count (for qualitative variables) was calculated. However, the paucity of historical sources available resulted in gaps being encountered in this 20-year averaged data for some variables. Although the aim of pollen analysis was to provide a sample every 20 years, more "observations" are available in recent, near-surface sediments due to the relative lack of compaction and decay in upper peat compared with older, deeper sediments. The final dataset is therefore not balanced in terms of the number of periods and number of sites, and we are able to use a total of 119 observations in the modelling reported below.

DATA ANALYSIS

The data to be analysed have some features for which provision needed to be made from a statistical viewpoint. First, adequate data are not available to conduct either a time-series analysis of drivers of plant diversity change at any individual site, or a cross-sectional analysis across all sites in a given time period. Therefore, we need to use all the available information on variability in both biodiversity and its potential determinants across both time (that is, from 1600-2000) and space (across our sites). We thus make use of a "panel" dataset – one where we combine information on variables across sites and over time. An implication of pooling information across time and sites is that we have to allow for unobserved site-specific effects. In particular, some of the determinants of the variation in plant diversity across sites are site-specific and are not expected to change over the time period analysed. Examples include altitude, soil type, exposure and latitude. To deal with these unobserved factors (which are not the focus of our analysis), we control for them in the regression analysis by including a dummy variable for each site (Balgati, 2001; Wooldridge, 2002).

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In addition, as noted above, historical data is missing on actual livestock numbers and area grazed. From the perspective of the individual farmer, a rising price could be interpreted as being consistent with an increase in stocking rates according to a normal supply response: higher prices cause firms to wish to raise their output. In the present context, higher cattle prices would thus be a signal to farmers to increase cattle output. It is also reasonable to assume that no individual farmer has a big enough influence on the market for his decisions over how many cattle or sheep to stock to affect the market price: farmers are thus, individually, "price takers". In this case, we could use prices as a proxy for grazing pressure, the assumption being that higher prices imply higher livestock numbers and hence higher grazing pressure.

However, if a "shock" occurs which causes all farmers in a region to reduce their output (for example, an outbreak of animal disease, or civil war), then periods of high prices could coincide with periods of *low* levels of aggregate supply (low total animal numbers), and periods of low prices with periods of high aggregate supply (high total animal numbers). This introduces a problem of endogeneity to the data and implies that we cannot simply assume that higher prices are an indicator of higher livestock numbers. We deal with this concern by using *instrumental variable* (IV) methods to estimate our statistical model. The main idea behind IV methods is to find variables that are related to prices but are unrelated to the supply of livestock, other than through their effect on prices, and then use these as "instruments" for prices. Such variables are those related to the demand for livestock. The reasoning is that if, for instance, demand for livestock (i.e. for meat) increases, then prices will increase and farmers will respond by increasing herd size or output. By controlling for such demand-side effects at a first stage, we can identify supply-side effects at a second stage in the estimation (more details are given below). The Instrumental Variables used here are the English population (a measure of market demand)*;* the presence or absence of garrisons in a particular region (which increases local demand); the passing of the Act of Union between England and Scotland (this reduced trade barriers); the

advent of refrigerated transport from the New World (this reduced demand for UK meat)*; and*

grain prices, as a substitute for meat in consumption.

Ecologically, the model we are interested in estimating could be written as:

$$B_{it} = \alpha B_{i,t-1} + bQ_{it} + S_{it}\delta + c_i + u_{it}$$

eqn 1

where B_{it} is our measure of biodiversity for site i in time period t, Q_{it} is a measure of the numbers

of livestock which farmers keep and thus the preferred indicator of grazing pressure, S_{it} includes

other observed land management variables that are also thought to affect biodiversity, c_i are site-

specific (fixed) effects relating to plant diversity levels (such as soil type and elevation), u_{it} is an

error term assumed to be normally distributed and α, b and δ are parameters to be estimated.

Historic vegetation composition and land-use will influence biodiversity, and we therefore

include a lagged term for species number, $B_{i,t-1}$ as a predictor of B_{it}, since this represents past

ecological conditions.

As we note above, we cannot directly observe Q_{it} over the time period analyzed, and so

must use prices for cattle and sheep instead (denoted *pcattle* and *psheep* respectively). By using

the IV approach, the parameters estimated for *pcattle* and *psheep* can be used to infer the impacts

of changes in Q_{it} on plant diversity (more detail is given in Supplementary Material Appendix

S1). We also include as potential determinants of plant diversity change a number of management

variables, denoted S_{it} in eqn 1. These include *sizechange*, *mgtchange* and *mgtinten* (Table 1). The

first of these represents whether farm amalgamations occurred in a given time period, since we

know from the historical analysis that such amalgamations are sometimes linked to changes in

management. *Mgtchange* is a count variable which represents recorded changes such as enclosure

and large-scale draining. *Mgtinten* represents how much of the year the site was actively managed

for agriculture, from abandonment to year-round use. We also include in S_{it} the variables

andisease, *annewbreed*, *extrweather* and *extrcivil*. These represent incidents of animal disease, the introduction of new breeds, extreme weather events that were sufficiently unusual to be recorded, and extreme civil events such as civil war (which might disrupt supply chains and take labour away from farms).

Results

As an example, pollen data for one farm site in NW Scotland indicate a predominance of grassy pastures with arable fields, areas of flushed bog and a small amount of local tree cover for the period pre-c.1830 (Fig. 1), with relatively high diversity (B_{it}) (above the mean for the study period, Fig. 2) (zone GLE1). A subsequent prolonged fall in diversity from c.1830-1870 (zone GLE2a) reflects the cessation of cultivation, loss of the remaining tree growth and of many previously common grass and meadow herbs (e.g. campions *Silene vulgaris*-type, cf. daisies *Solidago virgaurea*-type, cf. yarrow *Achillea*-type and poppies *Papaver rhoeas*-type; Bennett 1995). The subsequent increase in plantain *Plantago lanceolata*, cf. dandelions *Cichorium intybus*-type and buttercups *Ranunculus acris*-type suggests intensified grazing (zone GLE2a), followed by reduced grazing and the rise to dominance of grasses, sedges and cf. tormentil *Potentilla*-type (zone GLE2b-c), indicative of poorer drainage and/or nutrient depletion. This occurred in the wake of the 1812 eviction of tenant farmers to create a sheep farm. The loss of pollen diversity is attributed to increased grazing intensity with the cessation of intensive soil management associated with occupation, as diversity does not recover following the market-led decline in sheep numbers after c.1880. These processes gave rise to the poorly drained and homogeneous grass and bog present today, with birch invading the old fields since c.1900.

Regression results are presented in Table 2. Correlation analysis showed that cattle and sheep prices are highly correlated across sites and over time, so separate models are reported using each in turn as the agricultural price which potentially determines plant diversity change. Results for a first-stage regression which uses the Instrumental Variables to predict values for *pcattle* and *psheep* are not shown for brevity. The results for models (1) and (2) show that higher

prices for either sheep or cattle imply lower levels of biodiversity on average over time and across sites, since in both cases the coefficient estimate on price is negative. Note that both effects are statistically significant at the 95% level ($P < 0.05$). Based on the IV specification used, this is equivalent to finding that higher grazing pressure from either cattle or sheep resulted in lower plant diversity, across sites and over time. This is supported by analyses of the full pollen datasets, since the strongest pollen diversity losses occur under conditions of higher grazing intensity during the 19th and 20th centuries. The only other variable that emerges as statistically significant is *mgtinten*, the degree to which sites are grazed year-round, and the results show that site abandonment reduces biodiversity ($P < 0.05$). Neither technological innovations, as measured by management changes such as enclosure, nor the introduction of new sheep breeds seem to matter to our measure of biodiversity. Finally, in accord with expectations, it can be seen that higher diversity values in preceding periods are associated with higher diversity estimates in subsequent periods ($P < 0.05$ for B_{t-1}).

To investigate whether national trends in climate might have had an effect on plant diversity on the case study sites, we extended the model by adding data for mean temperature and annual rainfall taken from English sources (we do not include these two variables in the main specification in models (1) and (2) because they are available for fewer time periods – rainfall data only starts in the 1761-80 period - so that the sample size drops to 85). The results are shown in models (3) and (4) of Table 2. As can be seen, neither of these variables is significant, and their inclusion caused no significant changes in parameter estimates for the effect of prices on biodiversity.

A quadratic relationship between Q and B was also tested for: finding such a relationship would imply that up to some point, increasing grazing pressure increased plant diversity, but that after this threshold, increased grazing pressure reduced diversity. However, results show that any such effect is not revealed in the data presented here, since the parameter estimates on squared terms for *pcattle* nor *psheep* were insignificant. However, more detailed site-specific palaeoecological analysis does show some instances when over short time periods, increased

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grazing seems to have resulted in increased diversity. This generally occurred pre-1800 and usually on improved pasture rather than summer grazing sites.

The analysis reported above used prices as a proxy for livestock numbers, due to the lack of site-specific data on stocking rates. An obvious question is whether the findings in Table 2 are robust to actual stocking levels. Data on sheep and cattle numbers does exist from 1860 onwards at the parish (local administrative) level. There are two drawbacks when using these data. First, these are available at the parish – and not the specific site – level, so that the number of animals at this larger spatial unit can only be considered as a proxy for the actual livestock number at the site where the pollen data was collected: recall that we earlier used price changes as a proxy for the changes in the number of animals an individual farmer (i.e. at any of our case study sites) would want to hold. Secondly, these data are available from 1860 onwards only, so that we cannot use the information on biodiversity for earlier periods. Despite these two shortcomings, however, the census data provide useful information for an alternative test of the hypothesis that higher livestock numbers are related to lower biodiversity.

Models 1 and 2 present results without the climatological variables, which are added in models 3 and 4 (Table 3). The main result that emerges is that higher cattle numbers are significantly related to a decrease in the biodiversity index, while the parameter on *sheep*, although negative, is not statistically significant. Indeed, this result is verified when we include both *cattle* and *sheep* in the same regression, because, as can be seen in column 5, *cattle* remains significant and *sheep* insignificant. Overall, therefore, our analysis suggests that using different proxies for grazing pressure in general associates higher grazing pressure with a decrease in plant diversity, the results being more robust for cattle than for sheep. The parish data in fact shows the biggest changes in cattle numbers, rather than sheep, over the period 1860-2000. Consequently, additional pressure from cattle in a system which was, by the 1860s, dominated by sheep, appears to have exacerbated existing grazing impacts, resulting in marked diversity losses. This argument is further supported from the results in model 6, where we have added the ratio of *cattle* over *sheep* (denoted as *cattle/sheep*) in the regression, in addition to *cattle*. In this model, the

additional affect on biodiversity from increasing the number of cattle (as given by the partial derivative of B_t with respect to *cattle*) is estimated to be (-0.004+(90.044/*sheep*)), which implies that an increase in the number of cattle has a higher adverse impact on biodiversity when the number of sheep is also large.

In addition, we see that in Table 3 a number of other variables are significant in explaining biodiversity change over this later period. An increase in the number of size changes (*sizechange)* in the farm holding, whether this was an increase in the farm size due to amalgamations, or (much more rarely in the records) a decrease due to the farm holding being split up, is associated with a fall in diversity. Site abandonment also negatively affects diversity. The number of management changes such as burning, liming or fencing (*mgtchange)* also has a significant effect on diversity, with more innovations having a positive effect. Finally, extreme weather events in this later period seem to be related to plant diversity changes in the cattle numbers model. However, the analysis in Table 3 should be viewed with care, since as noted above, we cannot be sure that the stocking changes in the parish data were reflected by changes at the sites where the pollen records were obtained, and they do not cover pre-1860 time period.

Discussion

This paper investigates the possible economic determinants of one measure of biodiversity change over a 400 year period. We constructed a panel of estimates of plant diversity across space and time using pollen analysis, and assembled a matching dataset of prices, land use change, technological improvements and changes in social conditions. An instrumental variables panel regression analysis was then used to explore relationships between the diversity estimate and these economic and social drivers. Several limitations in the analysis should be recognised. The first is simply that of missing information, in that the historical record is increasingly 'patchy' further back in time. We also note the problems in transforming historical information into a form suitable for quantitative analysis: much detail is lost from the historian in transferring this information into a usable quantitative form. The same applies in reducing complex pollen

data to a single variable. Consequently it is important to utilise the full palaeoecological and historical datasets in interpretation of particular periods and sites. We were unable to test whether the average relationship measured between prices and diversity has changed dynamically and spatially, i.e. across time periods or across sites: there are simply too few data to permit such a split-sample analysis. Despite these limitations, this study does have relevance both in developing interdisciplinary methods, as well as in furthering our understanding of the drivers and dynamics of biodiversity change.

The main conclusions that emerged were that agricultural prices exerted significant influences on biodiversity over the period 1600-2000. Rising prices brought about higher livestock numbers, which on average seem to have depressed diversity values. Robustness analysis (Table 3) which used actual livestock numbers over a shorter time period seems to partly confirm these main results. Site abandonment and site amalgamation/ enlargement also affected diversity. Both transformations may partly signal a move to more homogeneous landscapes, as farm sizes increased, larger areas were managed as single units in an extensive grazing system, and the patchwork of small fields which maintained heterogeneity on a smaller scale disappeared, since the pollen diversity estimates are influenced by vegetation evenness. No significant effects were found for climatic variables, but this may have been due to the necessity of using weather data from England. Mixed signals were found with regard to the introduction of new animal breeds, but in the full (1600-2000) model, these were not statistically significant as determinants of diversity change.

Our results might thus be seen as confirming the idea that rising grazing pressures are bad for biodiversity in upland areas. While the analytical methods applied here are novel, the results support previous documentary and palaeoecological evidence for some deterioration in the quality or diversity of the UK uplands from around 200-300 years ago, particularly from 1750-1850 (depending on whether one considers evidence from the Borders or the Highlands) (Stevenson & Thomson 1993; Smout 2000; Tipping 2000; Davies & Dixon 2008). The present evidence that site abandonment had significant negative effects on diversity also supports recent historical

inferences (Smout 2000; Dodgshon & Olsson 2006). However, while previous analyses have investigated potential direct drivers of ecological change via shifts in stocking levels and types, and the removal of nutrients and biomass (e.g. Mather 1978, 1993; Innes 1983), the present approach provides strong evidence that these ecological changes were ultimately driven by economic factors.

A non-linear relationship between agricultural intensification and diversity has been proposed (Kleijn & Sutherland 2003; Whittingham 2007), but in this study no threshold effect was found for agricultural prices, in the sense that we do not observe implied increases in stocking actually increasing plant diversity levels over some range. If one has in mind a concave relationship between diversity and stocking density, equivalent to the 'intermediate disturbance' hypothesis, then our observations would appear to lie mainly beyond (i.e. to the right of) such a turning point.

Current predictions of changes due to the "de-coupling" of agricultural support under the Common Agricultural Policy and eventual removal of the Single Farm Payment are that, on average, returns from livestock farming in the uplands may fall (Oglethorpe 2005). Declining returns for upland livestock producers can be expected to translate into reductions in grazing herds and perhaps even the abandonment of sheep and cattle farming enterprises altogether. Falling sheep and cattle numbers would be expected, according to our results, to lead to an increase in plant diversity over time, but we also note the relevance in this context of our finding on the effects of the abandonment of livestock grazing altogether, which is predicted to reduce species diversity.

Our results can also be related to current debates over the appropriate balance of sheep and cattle in the uplands from an ecological viewpoint (Rook et al. 2004). The regression model in Table 3, column 6, shows that the impacts of an increase in cattle numbers on diversity are greater, the higher the level of sheep stocking. However, we do not find evidence that a mixed system produced lower adverse impacts on diversity than a single species grazing regime. This is in contrast to results such as those presented by Evans et al. (2006), who found that upland bird

numbers were higher in a mixed grazing system at "low" overall grazing levels, compared with a single-species grazing regime. However, one should note that the nature and evolution of the upland systems considered here may yield average results (i.e. over 20 year time periods, based on sometimes patchy data) which have limited relevance for changes starting from current ecological conditions: finding that higher cattle numbers depressed plant diversity by more than higher sheep numbers over the last 140 years does not mean that this would also be the result looking forward from 2008.

SYNTHESIS AND APPLICATIONS

The results of the present study show that plant diversity over the last 400 years in the Scottish uplands has been dynamic, and closely linked to intensity of grazing driven by market prices. This is of direct relevance to the debate about how grazing should or can be used as a tool in biodiversity management (Midgley 2007; Moore 2005; Marrs 2008), and discussions on the effectiveness of agri-environment schemes (Kleijn & Sutherland 2003; Whittingham 2007). Such schemes are commonly used as a means of achieving conservation aims on farmland, but any biodiversity gain from such schemes could be 'swamped' by farmers responding to market changes and intensifying grazing. Thus the role of economics must be understood both in terms of a farmer's response to market changes, and in making agri-environment schemes a viable alternative to market-driven management.

The past dynamism of all ecosystems must be recognised, and the importance of past management in determining what we see today should not be under-estimated (Honnay *et al*. 2004). The connections between recent economics and biodiversity have been noted (Watzold *et al*. 2006; Bullock, Pywell & Walker 2007), but the present study emphasises the relevance of historical ecological and economic evidence to current biodiversity research and management. Changes in biodiversity through time also raise questions about how baseline biodiversity values or conservation targets are determined (e.g. Chambers *et al.* 2007; Foster & Motzkin 2003; Willis *et al.* 2007), since our findings show the extent to which cultural factors have shaped semi-natural

communities both before and since industrialization. This is relevant to the continuing debate on naturalness and naturalistic processes, and what levels of intervention are appropriate in conservation (Bignal & McCracken 1996; Green *et al.* 2005; Willis & Birks 2006). Only by addressing such questions though interdisciplinary work can we bring all relevant information into the debate.

References

Alexander L.V. & Jones, P.D. (2001) Updated precipitation series for the UK and discussion of latest extremes. *Atmospheric Science Letters*, **1**, (2) 142-150.

Anderson P. & Yalden D.W. (1981) Increased sheep numbers and the loss of heather moorland in the Peak District, England. *Biological Conservation*, **20**, 195-213.

Andrews D.W.K. and Stock, J.H. (2005) *Inference with weak instruments*, Cowles Foundation Discussion Paper No. 1530.

Baltagi, B. H. (2001) *Econometric Analysis of Panel Data*, 2nd edn. Wiley, London.

Bignal, E.M. & McCracken, D.I. (1996) Low-intensity farming systems in the conservation of the countryside. *Journal of Applied Ecology,* **33**, 413-424.

Birks, H.J.B. & Line, J.M. (1992) The use of rarefaction analysis for estimating palynological richness from Quaternary pollen-analytical data, *The Holocene,* **2**, 1-10.

Barbier, E.B. (2007) The economics of land conversion, open access and biodiversity loss. *Biodiversity Economics* (eds A. Kontoleon, U. Pascual and T. Swanson), pp. 59-91. . Cambridge University Press, Cambridge.

Bennett, K.D. (1995) *Pollen catalogue of the British Isles*. http://chrono.qub.ac.uk/pollen/pc-intro.html.

Bowers J.K. & Cheshire, P. (1983) *Agriculture, the Countryside and Land Use.* Methuen, London.

Bullock, J.M., Pywell, R.F. & Walker, K.J. (2007) Long-term enhancement of agricultural production by restoration of biodiversity. *Journal of Applied Ecology*, **44**, 6-12.

Chambers, F.M., Mauquoy, D., Gent, A., Pearson, F., Daniell, J.R.G. & Jones, P.S. (2007) Palaeoecology of degraded blanket mire in South Wales: data to inform conservation management. *Biological Conservation,* **137**, 197-209.

Davies, A.L. & Dixon, P. (2008) Reading the pastoral landscape: palynological and historical evidence for the impacts of long-term grazing on Wether Hill, Cheviot foothills, Northumberland. *Landscape History*, **30**, 35-45.

Davies, A.L. & Watson, F. (2007) Understanding the changing value of natural resources: an integrated palaeoecological-historical investigation into grazing-woodland interactions by Loch Awe, Western Highlands of Scotland. *Journal of Biogeography*, **34**, 1777-1791.

Dodgshon, R.A. & Olsson, G.A. (2006) Heather moorland in the Scottish Highlands: the history of a cultural landscape, 1600-1880. *Journal of Historical Geography*, **32**, 21-37.

Evans D., Redpath S., Evans S., Elston D., Gardner C., Dennis P., & Pakeman R. (2006) Low intensity, mixed livestock grazing improves abundance of a common insectivorous passerine. *Biology Letters,* **2**, 636-638.

Foster, D.R. & Motzkin, G. (2003) Interpreting and conserving the openland habitats of coastal New England: insights from landscape history. *Forest Ecology and Management,* **185**, 127-150.

Fuller W. A. (1977) Some properties of a modification of the Limited Information Estimator, *Econometrica*, 45, 939-954.

Fuller R.J. & Gough, S.J. (1999) Changes in sheep numbers in Britain: implications for bird populations. *Biological Conservation*, **91**, 73-89.

Gibson A.J. and Smout T.C. (1995) *Prices, food and wages in Scotland, 1550-1780*. Cambridge University Press, Cambridge.

Green, R. E., Cornell, S. J., Scharlemann, J. P. W. & Bamford, A. (2005). Farming and the fate of wild nature. *Science*, **307**, 550-555.

Gustavsson, E., Lennartsson, T. & Emanuelsson, M. (2007) Land use more than 200 years ago explains current grassland plant diversity in a Swedish agricultural landscape. *Biological Conservation*, **138**, 47-59.

Honnay, O, Verheyen, K, Bossuyt, B & Hermy, M (2004). What history can teach us about present and future forest biodiversity. *Forest Biodiversity: Lessons from History for Conservation* (eds O. Honnay, K. Verheyen, B. Bossuyt, & M. Hermy), pp. 1-9. CABI Publishing, Wallingford.

Innes, J.L. (1983) Landuse changes in the Scottish Highlands during the 19th century: the role of pasture degeneration. *Scottish Geographical Magazine,* **99**, 141-149.

Kleijn, D. & Sutherland, W.J. (2003) How effective are European agri-environment schemes in conserving and promoting biodiversity? *Journal of Applied Ecology*, **40**, 947-969.

Lindbladh, M. & Bradshaw, R. (1995) The development and demise of a medieval forest-meadow system at Linnaeus' birthplace in Southern Sweden - implications for conservation and forest history. *Vegetation History and Archaeobotany*, **4**, 153-160.

Marrs, R. (2008) Landscape as a palimpsest: grassland sustainability in Sweden. *Biological Conservation*, **141**, 1445-1446.

Mather, A.S. (1978) The alleged deterioration in hill grazing in the Scottish Highlands. *Biological Conservation,* **14**, 181-195.

Mather, A (1993) The environmental impact of sheep farming in the Scottish highlands. *Scotland since prehistory: natural change and human impact* (ed. T.C. Smout), pp. 79-88. Scottish Cultural Press, Aberdeen.

Midgley, A.C. (2007) The social negotiation of nature conservation policy: conserving pinewoods in the Scottish Highlands. *Biodiversity and Conservation,* **16**, 3317-3332.

Moore, P.D. (2005) Palaeoecology - Down to the Woods Yesterday. *Nature,* **433**, 588-589.

Odgaard, B.V. (1999) Fossil pollen as a record of past biodiversity. *Journal of Biogeography,* **26**, 7-17.

Odgaard, B.V. (2001) Palaeoecological perspectives on pattern and process in plant diversity and distribution adjustments: a comment on recent developments. *Diversity and Distributions,* **7**, 197-201.

Oglethorpe, D.R. (2005) Livestock production post CAP reform: implications for the environment. *Animal Science*, **81**, 189-192.

Palmer, S.C.F. (1997) Prediction of the shoot production of heather under grazing in the uplands of Great Britain. *Grass and Forage Science,* **52**, 408-424.

Parker, D.E., Legg, T.P. & Folland, C.K. (1992) A new daily central England temperature series, 1772-1991. *International Journal of Climatology*, **12**, 317-342.

Rook, A.J., Dumont, B., Isselstein, J., Osoro, K., WallisDeVries, M.F., Parente, G. & Mills, J. (2004). Matching type of livestock to desired biodiversity outcomes in pastures – a review. *Biological Conservation*, **119**, 137-150.

Smout T.C. (2000) *Nature Contested: environmental history in Scotland and Northern England since 1600.* Edinburgh University Press, Edinburgh.

Stace, C.A. (1997) *New flora of the British Isles*, 2nd ed. Cambridge University Press, Cambridge.

Sutherland W. & Hill D. (1995) *Managing Habitats for Conservation*. Cambridge University Press, Cambridge.

Stevenson, A.C. & Thompson, D.B.A. (1993) Long-term changes in the extent of heather moorland in upland Britain and Ireland: palaeoecological evidence for the importance of grazing. *The Holocene*, **3**, 70-76.

Stock, J.H. & Yogo, M. (2005): Testing for Weak Instruments in Linear IV Regression. *Identification and Inference for Econometric Models: Essays in Honor of Thomas J. Rothenber*, (eds J.H. Stock and D.W.K. Andrews), pp. 77-86. Cambridge University Press, Cambridge.

Thompson, D.B.A., Hester, A.J. & Usher, M.B., eds. (1995a) *Heaths and Moorland: cultural landscapes*, HMSO, Edinburgh.

Tipping, R. (2000) Palaeoecological approaches to historical problems: a comparison of sheep-grazing intensities in the Cheviot hills in the medieval and later periods. *Townships to Farmsteads: Rural Settlement Studies in Scotland, England and Wales* (ed. J. Atkinson, I, Banks, & G. MacGregor), pp. 130-143. British Archaeological Reports (British Series), 293.

Usher, M.B. & Balharry, D. (1996) *Biogeographical zonation of Scotland*. Scottish Natural Heritage, Perth.

Watzold, F., Drechsler, M., Armstrong, C.W., Baumgartner, S., Grimm, V., Huth., A., Perrings, C., Possingham, H.P., Shogren, J.F., Skonhoft, A., Verboom-Vasiljev, J. & Wissel, C. (2006) Ecological-economic modelling for biodiversity management: potential, pitfalls, and prospects. *Conservation Biology*, **20**, 1034-1041.

Whittingham, M.J. (2007) Will agri-environment schemes deliver substantial biodiversity gain, and if not, why not? *Journal of Applied Ecology*, **44**, 1-5.

Willis, K.J., Araujo, M.B., Bennett, K.D., Figueroa-Rangel, B., Froyd C.A. and Myers, N. (2007) How can a knowledge of the past help to conserve the future? Biodiversity conservation and the relevance of long-term ecological studies. *Philosophical Transactions of the Royal Society of London, Series B*, **362**, 175-186.

Willis, K.J. & Birks, H.J.B. (2006) What is natural? The need for a long-term perspective in biodiversity conservation. *Science* **314**, 1261-1265.

Wooldridge J. (2002) *Econometric analysis of cross section and panel data*. MIT Press, Cambridge, Ma.

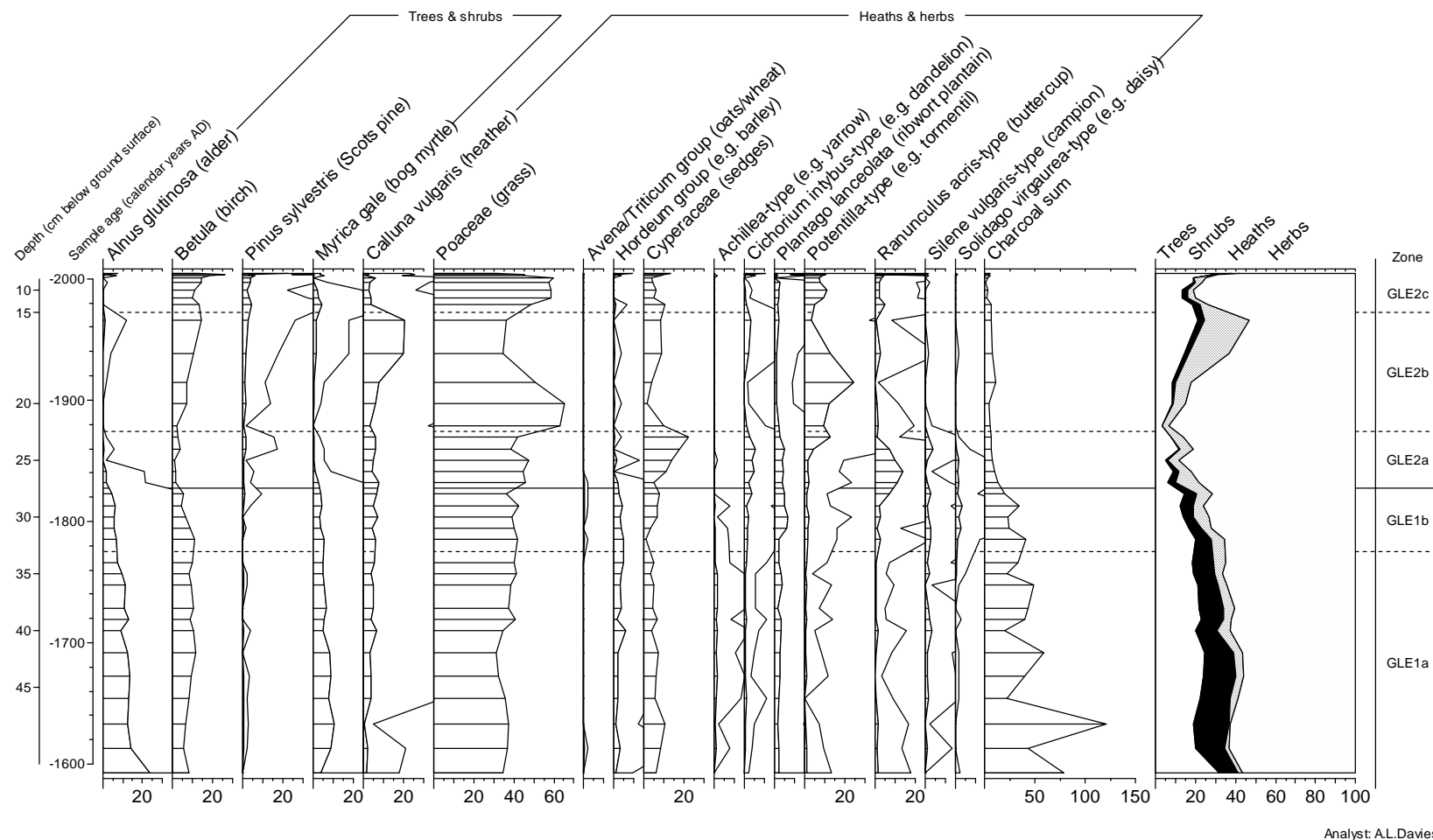Figure 1. Selected percentage pollen data for farm in far NW Scotland, c.1600 (base of Y-axes) to present (top of Y-axes). Each curve shows variations in pollen content through peat depth, expressed as % total land pollen, excluding spores, in each sample. The clear curve shows a x10 exaggeration for clarity. Horizontal lines (zones) depict periods of vegetation change (see text for explanation).

(a)

(b)

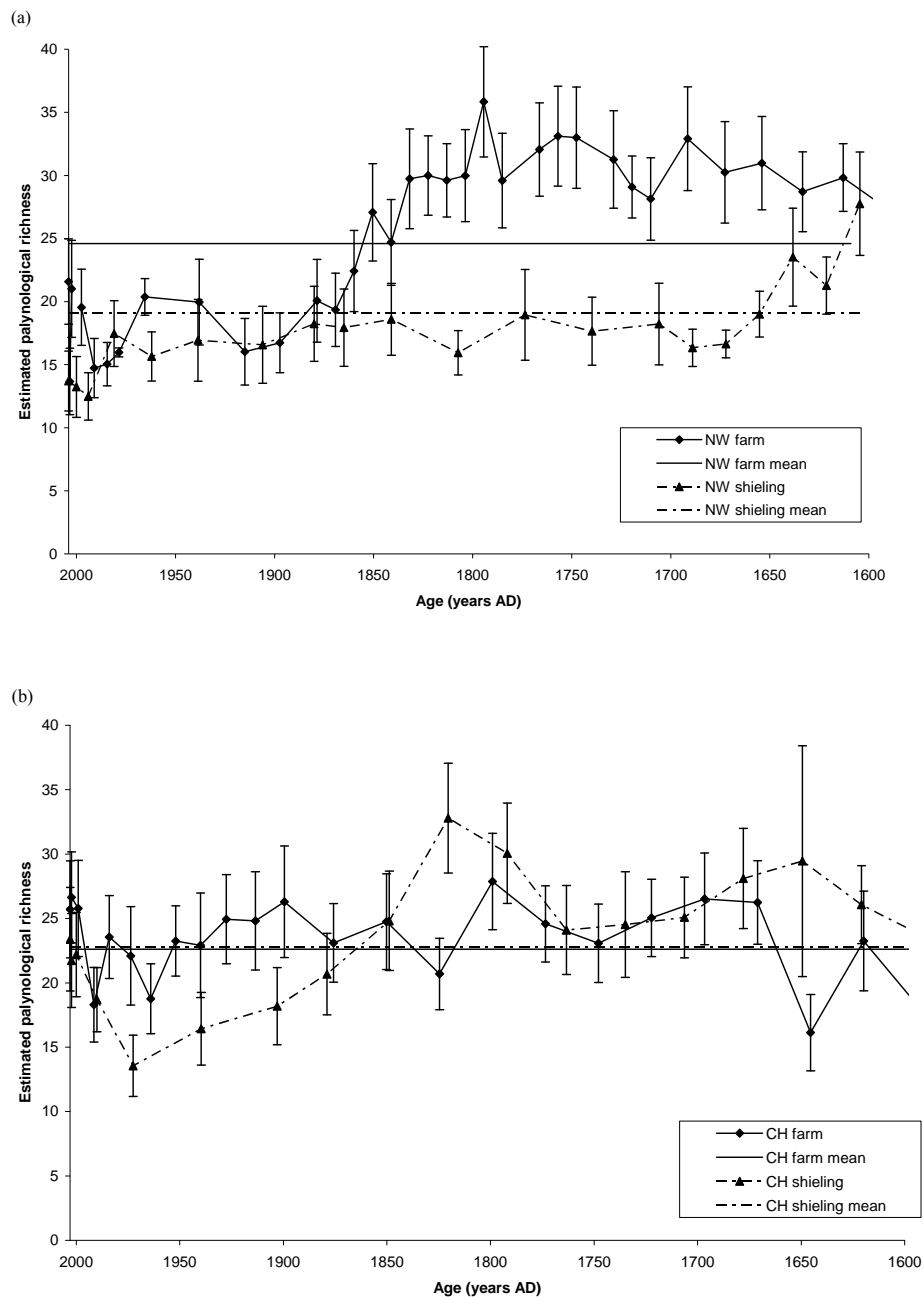Figure 2. Estimated pollen diversity over time for two pairs of sites between c.1600 and present with 95% confidence intervals, in (a) far NW Scotland (NW) and (b) Central Highlands (CH). The differing diversity impacts are attributed to the greater intensity of use at CH shieling compared with NW shieling, and continuity of occupation and closer stewardship at the CH farm compared with abandonment of the NW farm.

Table 1. Variables used in the regression analysis

Variable Name	Meaning	Main sources	Type of data
Dependent Variable:			
Plant diversity B_{it}	Pollen-derived proxy for estimated plant diversity at site i in year t	Pollen analysis	Continuous
Explanatory Variables:			
Lagged plant diversity, B_{it-1}	Estimated plant diversity value in previous 20 year period	Pollen analysis	Continuous
Management intensity, *mgtinten*	Intensity of use through year (5=year round, occupied; 1= abandoned)	Estate records	Categorical
Size change, *sizechange*	Property amalgamation or split	Estate records	Count over 20 yr period
Management change, *mgtchange*	Changes in site management such as enclosures and draining	Estate records	Count over 20 yr period
Animal disease, *anndisease*	Outbreaks of disease in cattle or sheep	Estate records	Yes/no
New breeds of animal, *annewbreed*	New breeds of cattle or sheep introduced	Estate records	Yes/no
Sheep prices, *psheep*	Regional market price	Estate records; Royal Highland Agricultural Society,	In £/240
Cattle prices, *pcattle*	Regional market price	Estate records; Royal Highland Agricultural Society	In £/240
Temperature, *temp*	Mean monthly	English data	Degrees C
Rainfall, *rain*	Total annual	English data	mm
Extreme weather events, *extrweather*	Storms, floods unusual enough to be recorded.	Estate records	Count over 20 year period
Extreme civil events, *extrcivil*	Civil wars, human disease, famine outbreaks	Estate records and secondary historical sources	Count over 20 year period

Table 2. The effect of grazing pressure on estimated plant diversity, 1600-2000, using livestock prices as a proxy for grazing pressure. There are 119 observations in columns (1) and (2) and 85 in columns (3) and (4). All regressions include dummies for each site. t-ratios are shown in parentheses below the estimated coefficients. An asterisk denotes significance at the 10% level and two asterisks significance at the 5% level.

Dep. variable: Biodiversity index (B_{it})	(1): full model, cattle prices.	(2): full model, sheep prices	(3)full model, cattle price, with climate variables added.	(4)full model, sheep prices, with climate variables added.
B_{t-1}	0.571**	0.576**	0.513**	0.507**
	(3.88)	(3.86)	(2.91)	(2.79)
Pcattle	-0.006**	-	-0.009**	-
	(-2.16)		(-2.28)	
Psheep	-	-0.078**	-	-0.116**
		(-2.06)		(-2.13)
Sizechange	0.599	0.581	0.679	0.615
	(0.53)	(0.51)	(0.56)	(0.50)
Mgtchange	-0.091	-0.076	-0.187	-0.166
	(-0.40)	(-0.34)	(-0.85)	(-0.75)
Andisease	-0.619	-0.583	-0.716	-0.663
	(-0.56)	(-0.53)	(-0.85)	(-0.52)
Annewbread	1.626	1.637	0.479	0.505
	(1.15)	(1.15)	(0.31)	(0.31)
Mgtinten	0.516**	0.505**	0.059	0.060
	(2.31)	(2.24)	(0.21)	(0.21)
Extrweather	-0.228	-0.219	0.801**	0.835**
	(-0.62)	(-0.60)	(2.01)	(2.06)
Extrcivil	-0.093	-0.109	0.639	0.640
	(-0.13)	(-0.17)	(0.59)	(0.58)
Temperature	-	-	1.205	1.543
			(0.43)	(0.51)
Rain	-	-	0.004	0.004
			(0.25)	(0.20)
Constant	7.784**	7.741**	-6.438	-8.451
	(2.46)	(2.39)	(-0.35)	(-0.44)
First-stage F (B_{t-1})	$F(6,95)=8.99$	$F(6,95)=8.99$	$F(5,61)=5.28$	$F(5,61)=5.28$
	(0.000)	(0.000)	(0.000)	(0.000)
First-stage F (prices)	$F(6,95)=115.45$	$F(6,95)=114.07$	$F(5,61)=81.93$	$F(5,61)=70.51$
	(0.000)	(0.000)	(0.000)	(0.000)

Table 3. The effect of parish livestock numbers on estimated plant diversity change, 1860-2000. There are 56 observations. All regressions include dummies for each site. The estimation method is 2SLS. The instrument used for B_{t-1}, is B_{t-2},. t-ratios are shown in parentheses below the estimated coefficients. An asterisk denotes significance at the 10% level and two asterisks significance at the 5% level.

Dep. variable: *Biodiversity index (B_{it})*	*(1)full model, cattle numbers*	*(2)full model, sheep numbers*	*(3)full model, cattle numbers, with climate variables*	*(4)full model, sheep numbers, with climate variables*	*(5) full model, including both sheep and cattle numbers*	*(6) full model, cattle numbers plus cattle/sheep ratio.*
B_{t-1}	0.222	0.428	-0.123	0.049	0.197	0.193
	(0.72)	(1.62)	(0.22)	(0.09)	(0.63)	(0.69)
Cattle	-0.002**	-	-0.003**	-	-0.002**	-0.004**
	(-2.45)		(-2.22)		(-2.43)	(-3.45)
Sheep	-	-0.0001	-	-0.0001	-0.000	-
		(-1.16)		(-1.10)	(-0.45)	
Cattle/sheep	-	-	-	-	-	90.044**
						(3.24)
sizechange	-14.821**	-16.955**	-11.221*	-12.734*	-15.672**	-13.511**
	(-2.62)	(-2.57)	(-1.93)	(-1.93)	(-2.63)	(-2.69)
mgtchange	1.498*	2.198* *	0.577	1.037	1.670*	1.493**
	(1.77)	(2.17)	(0.48)	(0.80)	(1.80)	(1.98)
andisease	-0.783	-0.512	-1.640	-2.081	-1.783	-1.328
	(-0.68)	(-0.37)	(-1.14)	(-1.19)	(-0.81)	(-1.28)
annewbread	4.644**	5.208**	2.349	2.993	4.859**	4.647**
	(2.09)	(2.09)	(0.82)	(0.97)	(2.14)	(2.34)
Mgtinten	2.930**	2.338**	3.233**	1.938*	2.900**	2.181**
	(2.41)	(2.01)	(2.39)	(1.67)	(2.37)	(2.11)
Extrweather	1.770**	0.963	2.682*	1.364	1.739**	0.908
	(2.03)	(1.19)	(1.90)	(1.26)	(1.99)	(1.24)
Temperature	-	-	-4.301	-7.418	-	-
			(-0.99)	(-1.27)		
Rain	-	-	-0.012	0.040	-	-
			(-0.47)	(1.32)		
Constant	13.558**	7.906	72.619	47.343	14.374**	4.763
	(2.19)	(1.64)	(1.34)	(0.98)	(2.24)	(1.00)