APPENDIX 3C

INVERTEBRATE MODELLING

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INTRODUCTION

The aim of the invertebrate model was to predict the long-term changes in invertebrate species composition and relative abundance under a range of different grazing scenarios. Results from the Systems Studies (Appendix 4) indicated that whilst there was some evidence of grazing regimes having direct effects on the invertebrate fauna, the effects of management were also mediated through alteration of the vegetation structure and composition. A decision was therefore made early on to use the outputs of the vegetation model (Appendix 3a) as the inputs into the invertebrate model. Whilst this has some limitations, in particular the absence of metrics to describe plant structure in the current version of the vegetation model, the approach has the advantage of linking the predicted invertebrate community directly to predictions of one of its primary drivers, the vegetation community.

Model structure

The outputs of the vegetation model are in the form of predicted plant species cover in each of six major plant community types: *Molinia*-dominated grassland, *Nardus*-dominated grassland, *Juncus* (rush) communities, *Calluna* moor, mixed heath and *Carex* (sedge) communities. Whilst the vegetation model also produces output at the whole-moor scale, amalgamated across all plant communities, this does not provide the level of detail necessary in order to make predictions of the invertebrate communities. Within each of the six major plant communities, the vegetation model also quantifies the abundance of 16 species or 'species groups' (see Appendix 3a for full details). The most detailed and comprehensive sets of invertebrate field samples, and associated vegetation quadrat data, were from the systems studies at Redesdale, and these were therefore used to provide the raw data needed to calibrate the model. The main steps in construction of the invertebrate model were as follows:

1. *Ordinate species in year zero of vegetation model*. This ordination (PCA) summarised the variation across the 16 species by 6 communities matrix

at the start of a series of runs of the vegetation model. The species composition of a given community was assumed to be identical at the starting point irrespective of the subsequent grazing regime. Linear methods of ordination were used as species turnover was relatively low (Leps & Smilauer, 2005).

2. *Calculate predicted ordination scores for field vegetation quadrats*. The 16 species or species groups used in the vegetation model were created and/or abstracted from the full list of species in the field data. The predicted ordination scores for each vegetation quadrat were then created by treating these quadrats as passive samples (supplementary samples) in the ordination created in step one, to create a predicted ordination score for each quadrat.
3. *Determine expected community membership of each field quadrat*. An inverse distance metric was used to calculate the probability, *P*, of each field quadrat *i*, belonging to the vegetation community *j* :

$$P_{ij} = \frac{1/d_{ij}}{\sum_{t=1}^{k} 1/d_{ij}} \qquad \text{Eqn. 1}$$

   where k = 6 (number of plant communities) and d_{ij} = distance in ordination space of quadrat *i* to plant community *j*.
4. *Calculate invertebrate species by plant community matrix*. Matrix multiplication was used to post-multiply a matrix of invertebrate species abundance by quadrats with the matrix of quadrats by plant community memberships calculated in step 3 above. The result is a matrix describing the abundance of each invertebrate species in the six vegetation model communities.
5. *Run the vegetation model*. The vegetation model was run for fifty years under four different grazing scenarios: low sheep grazing (0.66 ewes/ha), high sheep only (1.5 ewes/ha), low mixed grazing (0.66 ewes/ha plus 0.75 cows/ha) and high mixed grazing (1.5 ewes/ha plus 0.75 cows/ha). In each scenario the predicted abundances of the 16 key species were

output annually, and the positions of the predicted vegetation scenario placed as a passive sample into the baseline ordination created in step 1 above.

6. *Predict annual plant community membership.* Equation 1 was used to predict the membership of quadrats in the six broad community types under each grazing scenario annually. The resulting matrix quantifies changes in community membership for each of the initial quadrats (in year zero all belong exactly to their starting community, but these memberships change over time).
7. *Predict invertebrate species composition*. The plant community membership matrix (across all years) was matrix multiplied by the invertebrate by plant community matrix created in step 4 above, to create a matrix showing predicted abundance of each invertebrate species within the six broad vegetation types every year for a given management scenario.

All calculations for the invertebrate model were undertaken within the R statistical package. (The vegetation model operates within Mathematica – Appendix 3a).

RESULTS

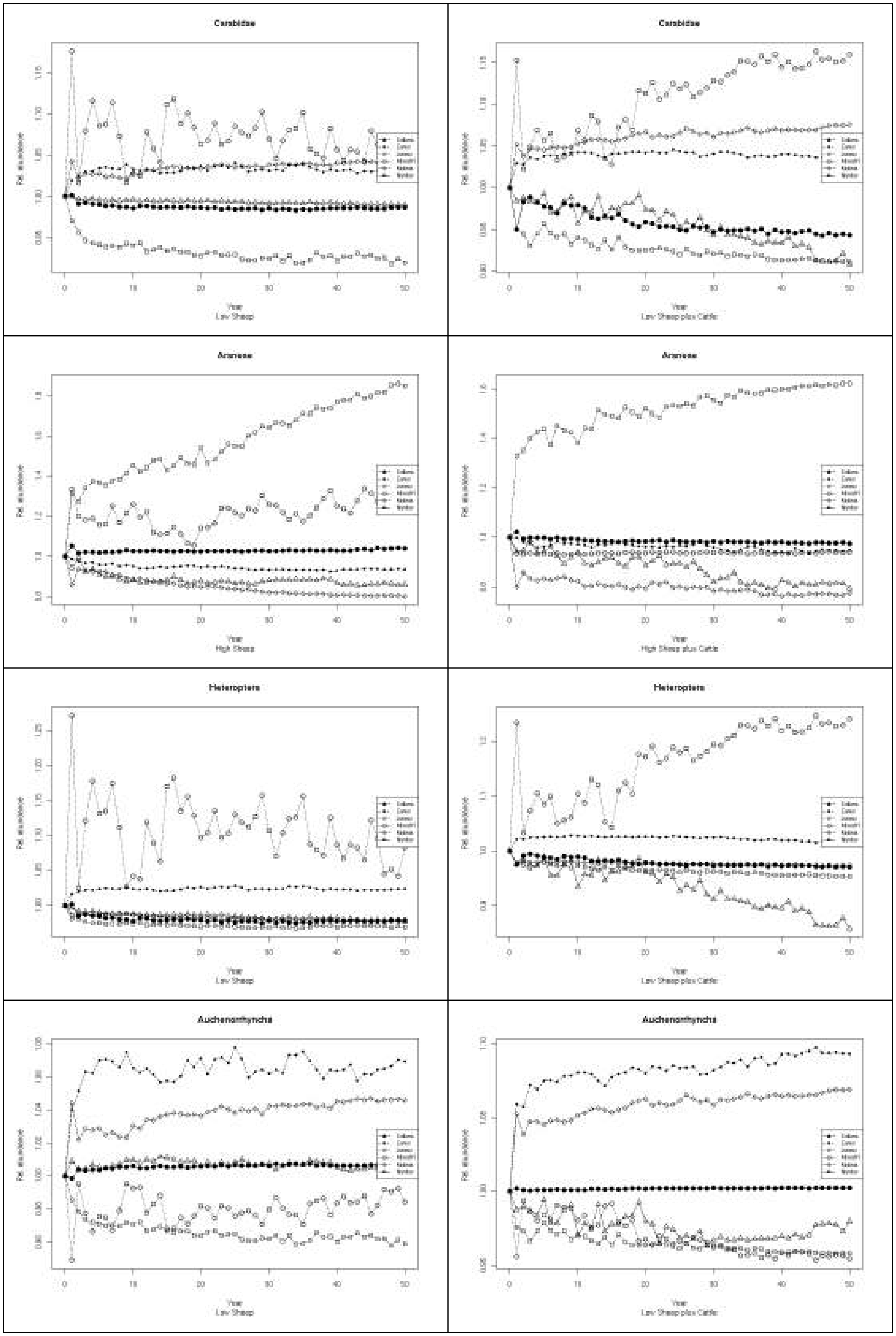
Although the invertebrate model produces predictions every year at the level of individual species, for simplicity only summary data, showing changes in the relative abundance of broad taxa, are shown here. Changes in most of the invertebrate communities were relatively gradual, as can be seen in Fig. 1 below. In the majority of taxa and grazing regimes, most changes in invertebrate abundance were predicted to occur within the first 10 years of the particular grazing regime being imposed. There was some evidence of model instability, with year one predictions showing a sudden variation in relative abundance on some plant communities (especially *Juncus* – see for examples outputs). The main changes for the individual invertebrate groups are summarised below.

Overall, predicted changes tended to be most dramatic after the introduction of cattle. As the vegetation drives the model, this is probably a reflection of the response of the key model input to different management.

Table 1 Summary of changes in relative abundance of invertebrate taxa over 50 simulated years in the six vegetation communities

Taxon	**MODEL PREDICTIONS**
Araneae	Decline in relative abundance with high mixed grazing on all plant communities except mixed heath
Auchenorrhyncha	Slight increase in relative abundance predicted for *Molinia* community under high mixed grazing and high sheep-only
Carabidae	High mixed grazing predict a decline in Carabidae in the *Juncus* community, but increase in *Molinia*
Coleoptera (all)	Similar to Carabidae, although an increase in beetle relative abundance also predicted in mixed heath
Diptera (all)	Predictions for most treatments fairly similar
Heteroptera	High mixed grazing predicted to result in decline in Heteroptera in *Nardus* vegetation
Tipulidae	High sheep-only predicted to result in increase in *Calluna* and mixed heath; declines in most vegetation in high sheep and cattle

Fig. 1 Predicted change in relative abundance of selected taxa under different grazing management regimes on each of the six plant communities



DISCUSSION

There have been very few attempts to produce a modelling framework that integrates the effects of different grazing management regimes with a vegetation community model, and then uses the outputs of the latter as inputs into an invertebrate model. Integration of different models, each with its own strengths, weaknesses and inherent assumptions is inevitably difficult, and prediction errors from one model can be propagated into subsequent ones. The approach used here should therefore be considered as a 'proof of concept', as there has been no attempt to validate assumptions within the model, or to compare predictions with independent sets of field data collected over long time periods.

There are several key areas where the model needs to be strengthened. First, there is no direct inclusion of any measure of vegetation structure. Whilst vegetation species composition and vegetation structure are known to be closely correlated, there is also evidence (including from the current project) that vegetation structure has separate effects on the invertebrates, distinct from the species composition. This is particularly apparent for taxa such as Araneae (spiders), which of course do not feed on the vegetation, but use it to provide supports for building webs. Second, changes in the predicted vegetation community over time were very gradual under all management scenarios. Indeed, it was relatively rare for predicted vegetation communities to move into a different community type, even over 50 years. As the invertebrate model relies on the vegetation model for inputs, this very slow change then cascades into the invertebrate model. Third, the formulation of the model, such that an invertebrate quadrat had to belong to one of the six plant communities, has the side-effect that movement in ordination space of a passive sample towards one plant community, leads to a decline in membership for the others. This means that in the graphs showing predicted relative abundance (compared to year zero) of a taxon over time, the invertebrate abundance in each plant community type cannot be considered independent. Finally, no attempt has been made to incorporate invertebrate dispersal activity, or the impacts of invertebrate communities at neighbouring sites into the model (Sanderson *et al*., 1995; Sanderson *et al*., 2005). Both of these phenomena are known to be important in many taxa, and indeed the model formulation in terms of the invertebrates (although not vegetation) is currently aspatial.

Nevertheless, despite these limitations the invertebrate model provides a useful first step towards building more sophisticated and biologically realistic models of moorland management, plant communities and invertebrates. Ideally such models need to be extended, to incorporate the key role that invertebrates play in bird diets birds (Buchanan *et al*. 2006), so that more complete predictions of the whole moorland ecosystem can be created.

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