

1 **Routes to achieving sustainable intensification in simulated dairy farms - the importance of**
2 **production efficiency and complimentary land uses**

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20 **ABSTRACT**

- 21 1. Sustainable intensification (SI) is a global challenge, aiming to increase food production
22 whilst conserving biodiversity and ecosystem services. This is contrary to the observed trend
23 of agricultural intensification degrading environmental quality. We developed a framework
24 integrating animal nutrition, crop yields, and biodiversity modelling to explore SI potential in
25 multiple model dairy farming systems through varying crop composition to provide cattle
26 feed rations. We then identified key drivers of biodiversity gain that may be applicable at a
27 wider scale.
- 28 2. We developed multiple feed rations to meet the nutritional demands of a high-yielding,
29 housed dairy herd. The land area required varied due to productivity and nutritional
30 differences between crops, generating spare land. We used published biodiversity models to
31 compare alpha- and beta-diversity of spiders and plants across 36 scenarios that used the
32 spare land in different ways, for either biodiversity maximisation or additional production.
- 33 3. Alpha and beta-diversity for both taxa was greatest in scenarios that maximised spare land
34 and utilised this for species-rich extensive grassland. However, commensurate biodiversity
35 gains for plant alpha-diversity, and spider and plant beta-diversity (respectively 100%, 76%
36 and 86% gain relative to that optimal scenario) were achievable when spare land was used
37 for additional crop production.
- 38 4. Maximising compositional heterogeneity and adding complementary productive land uses to
39 spared land were key to increasing production and beta-diversity, while adding species-rich
40 productive land uses drove increasing production and alpha-diversity.
- 41 5. *Synthesis and applications.* This study indicates the potential for SI of dairy farming through
42 manipulating feed rations to increase land-efficiency and spare land, which could then be
43 used to enhance production and biodiversity. The optimum land composition depends on
44 target goal(s) (e.g. maximising production and/or biodiversity). Greatest 'win-wins' were

45 achieved through increasing land cover heterogeneity and selecting crops that complement
46 each other in the species they support, highlighting the important role of heterogeneity in
47 the crop matrix. Our study provides a framework that integrates production efficiency and
48 biodiversity modelling to explore potential routes to achieve SI goals.

49

50 **KEYWORDS**

51 agriculture, alpha-diversity, beta-diversity, biodiversity, dairy, heterogeneity, agricultural production,
52 sustainable intensification

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54

55 **INTRODUCTION**

56 The challenge of protecting biodiversity and ecosystem services in the face of increasing food
57 production has led to the call for sustainable intensification (SI) of agricultural land; that is, the
58 simultaneous increase of food production and reduction of environmental pressure (Tilman *et al.*
59 2011; Garnett *et al.* 2013). This is now a key strategic objective of the UN's Food and Agriculture
60 Organisation (FAO 2015). A premise of SI is that increased production should be achieved on existing
61 farmland, because clearance of other habitats for agriculture creates greater environmental
62 degradation and biodiversity loss (Tilman *et al.* 2011; Garnett *et al.* 2013). Thus, a question central to
63 SI is whether we can increase production of existing land while maintaining or improving its
64 biodiversity.

65

66 **Livestock production and biodiversity**

67 Demand for meat and dairy products have increased substantially, with global cattle stock increasing
68 by 57% between 1961 and 2016 (FAOSTAT 2017). Grassland management has been intensified,
69 changing the functional composition of vegetation, with associated global biodiversity declines being
70 observed across taxa (Plantureux, Peeters & McCracken 2005). Functional and/or taxonomic
71 changes to vegetation composition have benefitted some ecosystem services (e.g. food provisioning
72 / nutrient cycling services), at the cost of others (e.g. regulating, cultural and biodiversity services)
73 (Allan *et al.* 2015).

74

75 To satisfy the nutritional demands (i.e. fat, carbohydrate, protein) of high-yielding dairy cows (≥ 40 L
76 milk d^{-1} animal $^{-1}$), feed rations comprise of multiple crops (Toma *et al.* 2013). Variation in the
77 composition of animal feeds and in-crop productivity produces large differences in the amount and
78 composition of land required to fulfil the dietary needs of a given herd at a target milk yield. In the
79 context of SI, this creates a dual opportunity: (1) if land-use composition can be modified to increase

80 production, modifications may be steered towards productive land compositions that maintain, or
81 even improve, biodiversity; (2) if efficiency improvements mean land-use composition can be
82 modified to produce spare land, whilst still maintaining or increasing production, this land might be
83 used for high biodiversity land-uses. Grassland simulations indicate heterogeneity of management
84 intensity can be varied to simultaneously increase arthropod populations and food production
85 (Simons & Weisser 2017). However, this has not been explored in mixed land-use systems where
86 there may be greater scope to manipulate crop composition to achieve multiple benefits.

87

88 Our study integrates animal nutrition, crop productivity, and biodiversity modelling to explore a
89 range of land-use scenarios that meet the feed requirements of a model dairy system to determine
90 the possibility of increasing food production whilst maintaining or enhancing biodiversity. We
91 developed a range of scenarios and manipulated the composition of land-covers to determine where
92 'win wins' could be achieved and to identify key drivers of production and/or biodiversity gains. All
93 scenarios provided feed for a herd of at least 100 permanently housed dairy cattle but differed in
94 terms of their land-use composition and thus land-efficiency (Fig. 1). More land-efficient scenarios
95 generated up to 18% 'spare land', which could then be used for additional production, or allocated
96 to a biodiversity-rich habitat (i.e. extensive grassland). Extending published land-use/biodiversity
97 models, we estimated indices for scenarios' alpha and beta-diversity for two functional groups
98 (plants and epigeal spiders) where extensive biodiversity data were available (Downie *et al.* 1999;
99 Wilson *et al.* 2003). We hypothesised that production of the system could be maintained or even
100 improved, whilst also improving or maintaining diversity of plants and spiders. We thus explore the
101 potential for SI within a dairy system and discuss implications for achieving SI goals more widely.

102

103 **MATERIALS AND METHODS**

104 **Land-use scenarios**

105 Our modelling process explored a 'home-grown feeds' dairy system, where nutritional requirements
106 of permanently-housed dairy cows are grown on the farm (Roberts & March 2014). We used an
107 industry-standard livestock nutrition feeding model, FeedByte (Scottish Agricultural College 2006), to
108 design alternative feed rations for a model herd of 100 Holstein-Friesian cows with a target milk
109 yield of 9,500 L yr⁻¹ (equivalent to 40 L of milk cow⁻¹ day⁻¹ including an unproductive period). This
110 commercially-used software uses least-cost diet formulation and linear-programming and is used by
111 industry and researchers to design real feed rations sufficient for livestock herds (Chagunda,
112 Flockhart & Roberts 2010). Rations needed to comprise of grass silage, barley, wheat, oilseed rape
113 and fodder beet as comprehensive biodiversity data existed for these crops and they varied with
114 respect to the availability of specific nutrients. Each crop alone would not provide the combination
115 of nutrients (e.g. proteins, carbohydrates or fats) required for high-yielding cattle. For each ration,
116 we used productivity estimates using both fresh-weight and dry-matter (DM) yields (kg ha⁻¹) as well
117 as nutritive value estimates (g kg⁻¹) for the constituting crops (Supporting Information Table S1) to
118 calculate the land area required. Due to differences in crop yields and nutritive values, the amount
119 of land required to meet the herds' nutritional requirements differed substantially between rations.
120 The feed ration requiring the most land for our target milk yield and herd size (i.e. the least land-
121 efficient ration) was designated the 'baseline scenario' (103.8 ha) (Fig. 1a). Our most land-efficient
122 feed ration provided the same milk yield and herd size on less land (88.0 ha). Consequently through
123 manipulating the quantities of different crops in the feed ration we could generate up to 15.8 ha
124 (18%) of spare land relative to the baseline. This generated our maximum spare land test-system
125 (Fig. 1b).

126

127 To compare a variety of scenarios where feed rations are met via different land areas and
128 compositions, we generated five intermediate test-systems varying in land-efficiency between the
129 baseline scenario and the max. spare land test-system (1%, 6%, 8%, 12% and 15% spare land c.f. the

130 baseline). The result was six test-systems (Fig. 1b) containing spare land; the choice of six allowed
131 generation of 36 'spare-land scenarios', considered a suitable sample size for exploring drivers of
132 biodiversity change across scenarios. We generated spare-land scenarios by replacing the spare land
133 component of each test-system (Fig. 1b) with one of six land uses (grass silage, barley, wheat,
134 oilseed rape, fodder beet or extensive grassland) (Fig. 1d). Spare land scenarios thus differed in both
135 the amount of spare land and the land use replacing the spare land component. Spare land scenarios
136 could be divided into:

137

138 (1) 'additional production' scenarios where spare land was used to grow more of one of the
139 productive crops (silage, wheat, barley, oilseed rape or fodder beet; Fig. 1d i).

140

141 (2) 'no additional production' scenarios where spare land was designated to extensive grassland (Fig.
142 1d ii). Of the land uses available in our empirical datasets, we selected extensive grassland to
143 represent a high-biodiversity, low/non-productive land use with no improvement or cutting regime.

144

145 Sparing land from production and designating to biodiversity-rich habitats, as in our 'no additional
146 production' scenarios, is a frequent focus of agri-environment prescriptions (e.g. fallow, floristically
147 diverse field margins). However, the original datasets we used (see below) did not contain data from
148 such habitats so we used data from extensively grazed, semi-natural grassland (e.g. calcifugous and
149 *Juncus*-dominated) to represent a low-production, high biodiversity land use as our alternative
150 strategy to increasing production. These are not directly equivalent to newly created agri-
151 environment habitats, since environmental (e.g. topography, altitude, soil, climate) and socio-
152 ecological (grazing regimes and underlying productivity of the land) constraints would have
153 historically prevented intensification on such areas with long-term extensive management resulting

154 in unique, species-rich, communities (Downie *et al.* 1999; Wilson *et al.* 2003; Cole *et al.* 2005). We
155 discuss the implications of this for our findings below.

156

157 We also explored an additional scenario where the desired outcome was to maximise milk
158 production ('max. herd size': Fig. 1c). This was achieved by scaling up the land composition of the
159 most land-efficient test-system, which had 18% spare land ('max. spare land'; Fig. 1b), to occupy the
160 area of the baseline scenario resulting in an increase from 100 to 118 cattle and thus increasing milk
161 production by 18%. Thus we generated 38 scenarios in total: the baseline scenario (Fig. 1a), the
162 max. herd size scenario (Fig. 1c), and the 36 spare land scenarios (Fig. 1d).

163

164 **Alpha diversity, beta-diversity, and additional production estimates**

165 For each of the 36 spare land scenarios (Fig. 1d) and the max. herd size scenario (Fig. 1c), we
166 calculated indices of alpha and beta-diversity for plants and spiders, and compared these with the
167 baseline scenario. This analysis framework is illustrated in Fig. 2. Diversity indices were generated
168 from published biodiversity models derived from field studies measuring plant and spider species
169 richness in the agricultural land-covers in our system (Downie *et al.* 1999; Wilson *et al.* 2003).

170

171 Data had been collected in nine geographical locations in Scotland ranging from intensive arable and
172 grassland landscapes, mixed farming and crofting. Vegetation surveys were conducted over three
173 years (1995-1997) at 87 sites with data being collected from permanent 10×10 m quadrats on three
174 occasions during peak growing season (June-September) (Wilson *et al.* 2003). Epigeal spiders were
175 surveyed over two years (1996-1997) at a total of 71 sites using a 16 m transect of nine pitfall traps
176 (75 mm diameter and 100 mm deep). Pitfall trapping was conducted May-September with contents
177 collected monthly (Downie *et al.* 1999).

178

179 Plants and spiders are key components of agricultural ecosystems, strongly driven by land
180 management (Wilson *et al.* 2003; Batáry *et al.* 2012). Plants are key drivers of invertebrate
181 biodiversity (Symstad, Siemann & Haarstad 2000) and provide shelter and breeding sites for many
182 species, while spiders are important polyphagous predators contributing to natural pest control
183 (Herzog *et al.* 2013). Alongside wild bees and earthworms, they provide appropriate and robust
184 metrics for measuring agricultural biodiversity (Herzog *et al.* 2013).

185

186 To generate alpha-diversity estimates for spiders and plants we used species richness (S) models
187 fitted by Downie *et al.* (1999) and Wilson *et al.* (2003). These models were developed to explore
188 drivers of field-scale S in a range of land uses. The process we used to generate an alpha-diversity
189 index (ADI) for each scenario is described in detail in Supporting Information SECTION B. Briefly, the
190 ADI for each scenario is defined as the mean predicted field-scale S across land-uses, weighted by
191 the proportional area of each land-use. Weighted mean S is a recognised metric to explore impacts
192 of agricultural land-use composition on biodiversity (e.g. Hiron *et al.* 2015).

193

194 To generate beta-diversity indices we used data describing the assemblage structure of our target
195 groups collected by Downie *et al.* (1999) and Wilson *et al.* (2003). Beta-diversity here describes the
196 extent of variation of species assemblages between different land-uses. Raw species data for the
197 models considered in the ADI analyses were not available. However, detrended correspondence
198 analysis (DCA) axes scores derived from the raw data were available (Murphy *et al.* 1998). The
199 distance between two sites in a DCA ordination provides a measure of similarity in species
200 composition, with smaller distances indicating greater similarity (Smol *et al.* 2005). The process we
201 used to generate beta-diversity indices (BDI) for each scenario is described in detail in Supporting
202 Information SECTION B. Briefly, the BDI for each scenario is defined as the median DCA distance

203 between random pairs of land-uses within each scenario, weighted by the proportional area of each
204 land-use. We provide R code for the estimation of ADI and BDI in Supporting Information SECTION C
205

206 While each spare-land scenario (Fig. 1d) maintained our target milk yield, a scenario's 'value' can be
207 modified relative to the baseline scenario in two main ways: (i) biodiversity value, indicated by ADI
208 and BDI; and (ii) production value, which can be increased when the spare-land component is used
209 for additional production. To determine how spider and plant ADI and BDI changed relative to the
210 baseline scenario we subtracted the baseline ADI and BDI values from those calculated for each
211 scenario, the results termed Δ_{ADI} and Δ_{BDI} (Fig. 2).

212

213 To allow us to simultaneously explore both the change in biodiversity and production for additional
214 production scenarios, we estimated the production capacity of the spare land component as
215 metabolisable energy ('ME', MJ kg⁻¹ DM) to standardise this benefit across different crops. ME
216 provided a more direct measure of production capacity than monetary value of crops, which is
217 dependent on a range of additional market factors. We derived ME of the spare land component for
218 each additional production scenario by multiplying industry estimates of ME by yield (kg DM ha⁻¹)
219 (SAC Consulting 2014) and area (ha). The baseline scenario did not produce any additional energy on
220 top of feeding the herd of 100 cattle, and consequently the calculated ME value reflects change
221 relative to the baseline (i.e. Δ_{ME}).

222

223 **Drivers of relative alpha and beta-diversity**

224 To investigate which factors drove the magnitude of Δ_{ADI} or Δ_{BDI} for each taxa, we generated four
225 candidate sets of general linear mixed models, with Δ_{ADI} or Δ_{BDI} for plants and spiders as the
226 response variables. Each spare land scenario provided a single estimate of Δ_{ADI} and Δ_{BDI} (Fig. 2) so the
227 sample size for the analysis was 36. We included test-system identity (Fig. 1b), and land-use

228 constituting the spare-land component (Fig. 1d) as random effects. We describe the fixed effects
229 included in our models in Table 1.

230

231 For each taxa (plant/spider) and response variable ($\Delta_{ADI}/\Delta_{BDI}$) we compared models using a small-
232 sample Akaike's Information Criterion (AICc) and Akaike's weights (w_i) (Johnson & Omland 2004).

233 We included several multivariate models and the appropriate null model. We restricted inference on
234 the key drivers of Δ_{ADI} or Δ_{BDI} to examining the smallest set of models containing a summed $w_i \geq 0.90$.

235

236 **RESULTS**

237 **Impact of land use on alpha and beta diversity**

238 Predicted estimates of S for spiders and plants from the alpha-diversity models for individual land-
239 uses are shown in Figs. 3a-b. Predictions of spider S were as low as 11.7 (lower 95% confidence limit
240 [CL₉₅] for silage) and as high as 41.9 (upper CL₉₅ for extensive grassland). For plants, values ranged
241 from 6.1 species (lower CL₉₅ for barley) to 29.6 (upper CL₉₅ for extensive grassland). These were
242 within the observed field-scale ranges from the original data-sets of 10-56 spider species (Downie *et*
243 *al.* 1999) and 5-57 plant species (Wilson *et al.* 2003).

244

245 Assemblage structure of spider and plant communities was most similar in oilseed rape and cereals
246 (i.e. barley and wheat) with communities in these crops showing the greatest disparity with those in
247 extensive grasslands and fodder beet (Figs. 3c-d).

248

249 **Comparison of alpha and beta diversity between scenarios**

250 The baseline scenario had a predicted ADI (the mean field-scale S across land-uses, weighted by the
251 proportional area of each land-use) of 19.8 (CL₉₅ 17.8-22.8) spider species and 13.4 (CL₉₅ 11.9-15.2)
252 plant species. Δ_{ADI} and Δ_{BDI} for each taxa and scenario are shown in Fig. 4. In all cases, 'no additional

253 production' scenarios with maximum spare land gave the highest biodiversity benefit (labelled 'NAP'
254 in Fig. 4). However, for both taxa Δ_{BDI} , and for plant Δ_{ADI} , additional production scenarios existed that
255 generated similar biodiversity gains to the latter (optimal scenarios labelled 'AP' in Fig. 4). For
256 spiders, additional production scenarios did not enhance ADI due to the baseline scenario having a
257 relatively high ADI (Fig. 4a).

258

259 **Drivers of change in alpha and beta-diversity**

260 For both spider and plant Δ_{ADI} , a single model was in the confidence set (Table 2). This contained the
261 estimated S of the added land-use, the area of spare land, and their interaction (Figs. 5a-b). Adding a
262 land-use with a comparatively high estimated S to the spare-land component increased Δ_{ADI} , and this
263 interacted positively with amount of spare land.

264

265 For spider Δ_{BDI} , two models were in the confidence set (Table 2), containing the mean DCA distance
266 for the land-use being added, the land-use evenness ($w_i = 0.87$) or heterogeneity ($w_i = 0.08$), and
267 their interaction. A higher mean DCA distance of the land-use being added increased Δ_{BDI} , but only
268 where land-use evenness was also increased (Fig. 5c). For plant Δ_{BDI} , four models were in the
269 confidence set (Table 2). The two best models contained either the land-use heterogeneity ($w_i =$
270 0.71) or evenness ($w_i = 0.13$), showing positive relationships (Fig. 5d).

271

272 **'Value' of spare-land scenarios**

273 For both Δ_{ADI} (Fig. 6a) and Δ_{BDI} (Fig. 6b) utilising spare land as extensive grassland delivered the
274 optimal biodiversity gain across taxa, but generated no Δ_{ME} gain. For Δ_{BDI} , not only was a max. spare
275 land + fodder beet scenario able to achieve gains almost commensurate with the best no additional
276 production scenario for both spiders and plants, but it did so while achieving the highest Δ_{ME} (Fig.
277 6b).

278

279 For Δ_{ADI} , the relatively high ADI value for spiders in the baseline scenario resulted in a complex
280 picture (Fig. 6a). All additional production scenarios showed a reduced ADI for spiders, but increased
281 ADI for plants. Some added fodder beet scenarios achieved relatively high plant Δ_{ADI} and moderate
282 Δ_{ME} gains but at a cost to spider Δ_{ADI} values (albeit with spider losses lower in magnitude than plant
283 gains). Some added silage scenarios achieved greater plant Δ_{ADI} gains than added fodder beet (equal
284 to plant Δ_{ADI} gain in the best no additional production scenario) but at a cost to spider Δ_{ADI} and a
285 lower Δ_{ME} , indicating trade-offs between potential gains.

286

287 **DISCUSSION**

288 **Sustainable intensification outcomes**

289 Simultaneous gains in production and biodiversity were simulated in our model dairy system
290 illustrating the potential for SI. We achieved the biggest simultaneous gains in beta-diversity and
291 production by increasing the system's efficiency to feed the dairy herd using a smaller area of land,
292 and allocating the spare land generated to a productive crop that complemented those already
293 present in the system with respect to the species supported. For plant alpha-diversity, we achieved
294 highest gains in production and species richness by allocating the spare land to a species-rich,
295 productive land use.

296

297 Our simulations challenge the well-observed negative relationship between productivity and
298 biodiversity in agriculture (Krebs *et al.* 1999). SI has been demonstrated in small farms in developing
299 countries using a combination of approaches including integrated plant nutrient systems, no-
300 till/conservation agriculture and integrated pest management (Chappell & LaValle 2011). Evidence of
301 SI in highly-productive agricultural systems is less well documented with gains in biodiversity
302 typically being accompanied by yield losses (Gabriel *et al.* 2010; Firbank *et al.* 2013). SI appears

303 particularly challenging in intensive dairy farms - a study exploring innovative management practices
304 found dairy farms notable in their failure to achieve simultaneous production and biodiversity gains
305 (Firbank *et al.* 2013). Our results highlight a potential route to SI in home-grown dairy systems.

306

307 With increasing pressure on our finite agricultural land, SI is important both for local and wider scale
308 biodiversity outcomes. Our 'no additional production' scenarios, increased farm-scale biodiversity,
309 but without increasing production. Increasing demand for food would therefore have to be met by
310 intensification of other farmland and/or generating new farmland (see Fischer *et al.* 2014), with
311 potentially negative biodiversity implications at a wider scale. Our 'additional production' scenarios
312 that achieved SI would not only benefit local biodiversity but also reduce production pressure on
313 land elsewhere. Ultimately, SI solutions will be important in allowing biodiversity to be increased
314 both on a farm scale through land-sharing, and by increasing production on existing farmland which
315 could protect biodiversity-rich areas at the landscape scale ('land-sparing'). The land sharing/sparing
316 debate, however, can overlook the wide range of ecosystem services agricultural land can provide
317 (Fischer *et al.* 2014) and measures that promote biodiversity often improve landscape multi-
318 functionality enhancing a wide-range of ecosystem services (Allan *et al.* 2015).

319

320 **Potential for implementation to real systems**

321 A key finding was the important role that crop heterogeneity played in increasing beta-diversity and
322 production. Loss of heterogeneity (of both semi-natural and agricultural habitats) is a key driver of
323 biodiversity declines, and its restoration represents a mitigation strategy (Benton, Vickery & Wilson
324 2003). Agricultural policies aimed at stemming biodiversity loss typically incentivise farmers to
325 increase heterogeneity via agri-environment schemes (AES), which may involve in-production (land-
326 sharing) or out-of-production (land-sparing) approaches (Batáry *et al.* 2015). Restoring semi-natural
327 habitats in intensive agricultural landscapes typically involves removing land from production, to

328 increase spatial and structural heterogeneity (Ovenden, Swash & Smallshire 1998). Our results
329 suggest that incentivising farmers to increase heterogeneity of their productive land could lead to
330 biodiversity gains whilst increasing production. At a regional level, that could involve a coordinated
331 approach to produce crops that have high complementarity and are not already dominant.

332

333 In introducing a crop diversification component within its compulsory greening measures (EU
334 Regulation 1307/2013), the EU's 2014 Common Agricultural Policy reform may represent a step in
335 the right direction. However, 'diversification' in this legislation narrowly focuses on compositional
336 heterogeneity, bringing its effectiveness under question. Josefsson et al. (2017) found that crop
337 composition *per se* did not influence bird species richness, but structural crop heterogeneity did
338 have a positive effect. For such measures to make a real impact, they may need to go further and be
339 backed-up by a political will to diversify farmland. Some AES are piloting a cluster farming approach
340 to provide landscape-scale benefits (e.g. Natural England 2017); SI strategies could also potentially
341 operate at a multi-farm scale.

342

343 With SI goals aiming to increase production and thus income, appropriate knowledge exchange may
344 enhance uptake of SI-focussed management without additional incentives, although in the UK some
345 innovative farms seen to achieve SI outcomes had relied on AES subsidies to enhance biodiversity
346 (Firbank *et al.* 2013). Improving links between researchers, advisors and farmers are identified as
347 important for uptake of SI practices in developing countries (Pretty, Toulmin & Williams 2011).
348 Promoting biodiversity can have direct economic benefits through enhancing ecosystem services
349 such as natural pest control and pollination, potentially contributing to SI via ecological
350 intensification (Tscharntke *et al.* 2012). Promoting the potential economic benefits of enhancing
351 biodiversity may also be important (Pywell *et al.* 2015). For example, insect pollination can increase

352 yield of oilseed rape (Bommarco, Marini & Vaissière 2012) while the presence of natural enemies of
353 aphids can increase yield of barley (Östman, Ekbom & Bengtsson 2003).

354

355 Incentivising heterogeneity requires careful consideration of costs and benefits. Crop heterogeneity
356 may promote economic sustainability, providing insurance against unpredictable growing conditions,
357 pest or disease outbreaks, or market variability (Garnett *et al.* 2013). In our home-grown system, the
358 production of additional crops not directly required for *in situ* cattle, requires additional market
359 engagement, but markets can be unpredictable. Growing new crops may also incur direct costs, such
360 as those for new machinery or alternative agrochemicals. Our simple measure of increased
361 production was solely based on the energetic yield of a crop, while demand depends on other socio-
362 economic drivers such as available income and consumer behaviour (Valin *et al.* 2014).

363

364 Simultaneously enhancing biodiversity and production clearly requires incorporating complex
365 information derived from disparate sources. For example, here we integrated biodiversity data from
366 both published literature, dietary modelling that combines nutritional equations to determine
367 protein and energy requirements, and finally crop production data. Farmers are familiar with a range
368 of decision-support tools, such as nutrition models, yield estimates, agronomist advice and
369 guidelines on incentives for AES. Comprehensive biodiversity datasets that evaluate biodiversity
370 across habitats are, however, often only available as summary information in scientific publications
371 (e.g. Cole *et al.* 2017). This could make it difficult for farmers to adequately consider biodiversity in
372 decision-making processes. There is great potential for existing monitoring schemes (e.g. UK's
373 Breeding Bird Survey: <https://www.bto.org/volunteer-surveys/bbs>; UK's Butterfly Monitoring
374 Scheme: <http://www.ukbms.org/>) to assist in the collection of comprehensive biodiversity data
375 across taxa and land covers, but more fundamental is providing the resultant data to land managers
376 in a usable format. Our framework highlights the potential for current databases (e.g. crop

377 productivity and land-cover/biodiversity) to be integrated to create a SI decision-support tool. In
378 addition to including production and biodiversity outcomes, such a tool could also include other
379 environmental (e.g. reducing greenhouse gas emissions, mitigating diffuse pollution) and agronomic
380 (e.g. reduced agrochemical applications) benefits.

381

382 Simulation studies are important first steps in assessing potential SI outcomes (e.g. Simons &
383 Weisser 2017). Ultimately, however, model predictions require trialling in real landscapes. While
384 simulated studies provide data-driven working hypotheses, they have inevitable limitations. For
385 example, we considered compositional but not configurational heterogeneity, which can drive
386 biodiversity patterns in birds (Hiron *et al.* 2015). In addition, data constraints meant that to
387 represent high-biodiversity, low-input habitats in our 'no additional production' scenarios we used
388 data from historical extensively grazed grasslands rather than potentially more appropriate AES
389 prescriptions (i.e. habitats formed from previously cultivated land that have not had a history of low-
390 input management). Extensive grasslands support unique species assemblages, and it is unlikely that
391 AES prescriptions (e.g. species-rich field margins) would reach the potential biodiversity value of
392 such grasslands (Downie *et al.* 1999; Wilson *et al.* 2003). Our 'no additional production scenarios'
393 may therefore over-estimate biodiversity gains. Agri-environment interventions can, however, not
394 only increase ecological connectivity and provide ecological contrast that enhances resource
395 diversity, stability and availability supporting a wider suite of species (Batáry *et al.* 2015; Cole *et al.*
396 2017), but can also enhance biodiversity-dependant ecosystem services thus benefitting production
397 (Pywell *et al.* 2015). Landscape trials of scenarios could elucidate effects of configurational,
398 structural and compositional heterogeneity, and test biodiversity benefits of AES prescriptions
399 against our assumptions using historical extensively grazed habitats.

400

401 A key reason for investigating potential for SI outcomes in a home-grown dairy system was the
402 closed nature of the system, whereby the land required to feed the herd is *in situ*. Feeding housed
403 cattle is a common dairy production system (e.g. 55% of UK dairy farms house cattle year-round, a
404 percentage which is growing - March *et al.* 2014) but housed cattle can be fed on home-grown or
405 bought-in feeds, or a combination. Home-grown systems represent one end of a spectrum of
406 possible feeding systems for housed dairy cattle (Roberts & March 2014), one which is fully self-
407 sufficient in terms of feeds. While data on the extent of feed self-sufficiency of farms are not widely
408 available, it can be regionally high (e.g. averaging 79-85% in W France: Brocard *et al.* 2016). Higher
409 self-sufficiency of feeds is seen to reduce consumption of non-renewable energy (i.e. reduced
410 transport of bought-in feeds) and raise nutrient efficiency (Gaudino *et al.* 2018). In Europe,
411 producing local sources of protein for dairy cattle is likely to reduce reliance on imported soybean
412 *Glycine max* imports, associated with high greenhouse gas emissions (Hörtenhuber, Lindenthal &
413 Zollitsch 2011), while programs have been established aiming to increase levels of dairy feed self-
414 sufficiency (Ineichen *et al.* 2014). Our simulations demonstrate a further potential environmental
415 benefit of home-grown systems - that composition of feed crops could be managed locally to
416 provide simultaneous productivity and biodiversity gains.

417

418 **Conclusions and application**

419 Achieving SI is an important but ambitious aim (Tilman *et al.* 2011; Garnett *et al.* 2013). Our study
420 combined biodiversity data, yield data and nutrition models to find routes to simultaneous increases
421 in production and biodiversity in a home-grown dairy system. This was optimised by maximising
422 land-efficiency and targeting additional production to a land cover that had relatively high species
423 richness (alpha-diversity), and complemented species in existing crops (beta-diversity). This
424 highlights the importance of integrating agronomic efficiency, land cover heterogeneity and species
425 richness/complementarity of both productive and non-productive land covers within an SI

426 framework. Where comprehensive biodiversity/production data exist, our framework could be
427 adaptable to other taxonomic groups, production systems and regions. Agri-environment policy
428 should focus not only on increasing the quality and heterogeneity of semi-natural habitats, but also
429 on enhancing agricultural efficiency and the complementarity and heterogeneity of productive land
430 covers. Through developing a framework that integrates crop productivity and biodiversity
431 modelling to seek optimal production-biodiversity scenarios, this study presents a route to identify
432 key drivers of production and biodiversity gain, a key goal of SI, that may be applicable at a wider
433 scale.

434

435 **AUTHORS' CONTRIBUTIONS**

436 All authors developed the initial concepts and MAL designed test scenarios. PJCW conducted
437 analyses and LJC sourced the datasets. PJCW and LJC wrote the initial draft and all authors
438 contributed to revisions.

439

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444

445 **DATA ACCESSIBILITY**

446 Data available from Edinburgh Napier University Repository. DOI: 10.17869/ENU.2018.1141073
447 (White *et al.*, 2018).

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450 **REFERENCES**

- 451 Allan, E., Manning, P., Alt, F., Binkenstein, J., Blaser, S., Bluthgen, N., Bohm, S., Grassein, F., Holzel,
452 N., Klaus, V.H., Kleinebecker, T., Morris, E.K., Oelmann, Y., Prati, D., Renner, S.C., Rillig, M.C.,
453 Schaefer, M., Schloter, M., Schmitt, B., Schoning, I., Schrupf, M., Solly, E., Sorkau, E., Steckel,
454 J., Steffen-Dewenter, I., Stempfhuber, B., Tschapka, M., Weiner, C.N., Weisser, W.W., Werner,
455 M., Westphal, C., Wilcke, W. & Fischer, M. (2015) Land use intensification alters ecosystem
456 multifunctionality via loss of biodiversity and changes to functional composition. *Ecology*
457 *Letters*, **18**, 834–843.
- 458 Batáry, P., Dicks, L. V., Kleijn, D. & Sutherland, W.J. (2015) The role of agri-environment schemes in
459 conservation and environmental management. *Conservation Biology*, **29**, 1006–1016.
- 460 Batáry, P., Holzschuh, A., Orci, K.M., Samu, F. & Tschardtke, T. (2012) Responses of plant, insect and
461 spider biodiversity to local and landscape scale management intensity in cereal crops and
462 grasslands. *Agriculture, Ecosystems & Environment*, **146**, 130–136.
- 463 Benton, T.G., Vickery, J.A. & Wilson, J.D. (2003) Farmland biodiversity: is habitat heterogeneity the
464 key? *Trends in Ecology & Evolution*, **18**, 182–188.
- 465 Bommarco, R., Marini, L. & Vaissière, B.E. (2012) Insect pollination enhances seed yield, quality, and
466 market value in oilseed rape. *Oecologia*, **169**, 1025–1032.
- 467 Brocard, V., Jost, J., Rouillé, B., Caillaud, D., Caillat, H. & Bossis, N. (2016) Feeding self-sufficiency
468 levels in dairy cow and goat farms in Western France: current situation and ways of
469 improvement. *Grassland Science in Europe*, **21**, 53–55.
- 470 Chagunda, M.G.G., Flockhart, J.F. & Roberts, D.J. (2010) The effect of forage quality on predicted
471 enteric methane production from dairy cows. *International Journal of Agricultural*
472 *Sustainability*, **8**, 250–256.
- 473 Chappell, M.J. & LaValle, L.A. (2011) Food security and biodiversity: can we have both? An
474 agroecological analysis. *Agriculture and Human Values*, **28**, 3–26.

475 Cole, L.J., Brocklehurst, S., Robertson, D., Harrison, W. & McCracken, D.I. (2017) Exploring the
476 interactions between resource availability and the utilisation of semi-natural habitats by insect
477 pollinators in an intensive agricultural landscape. *Agriculture, Ecosystems & Environment*, **246**,
478 157–167.

479 Cole, L.J., McCracken, D.I., Downie, I.S., Dennis, P., Foster, G.N., Waterhouse, T., Murphy, K.J., Griffin,
480 A.L. & Kennedy, M.P. (2005) Comparing the effects of farming practices on ground beetle
481 (Coleoptera: Carabidae) and spider (Araneae) assemblages of Scottish farmland. *Biodiversity
482 and Conservation*, **14**, 441–460.

483 Downie, I.S., Wilson, W.L., Abernethy, V.J., McCracken, D.I., Foster, G.N., Ribera, I., Murphy, K.J. &
484 Waterhouse, A. (1999) The impact of different agricultural land-uses on epigeal spider diversity
485 in Scotland. *Journal of Insect Conservation*, **3**, 273–286.

486 FAO. (2015) *FAO and the 17 Sustainable Development Goals*. Food and Agriculture Organisation of
487 the United Nations, Rome.

488 FAOSTAT. (2017) FAOSTAT: Food & Agriculture Organization of the United Nations Statistic Division,
489 <http://faostat3.fao.org/browse/Q/QA/E>

490 Firbank, L.G., Elliott, J., Drake, B., Cao, Y. & Gooday, R. (2013) Evidence of sustainable intensification
491 among British farms. *Agriculture, Ecosystems & Environment*, **173**, 58–65.

492 Fischer, J., Abson, D.J., Butsic, V., Chappell, M.J., Ekroos, J., Hanspach, J., Kuemmerle, T., Smith, H.G.
493 & von Wehrden, H. (2014) Land Sparing Versus Land Sharing: Moving Forward. *Conservation
494 Letters*, **7**, 149–157.

495 Gabriel, D., Sait, S.M., Hodgson, J.A., Schmutz, U., Kunin, W.E. & Benton, T.G. (2010) Scale matters:
496 the impact of organic farming on biodiversity at different spatial scales. *Ecology Letters*, **13**,
497 858–869.

498 Garnett, T., Appleby, M.C., Balmford, A., Bateman, I.J., Benton, T.G., Bloomer, P., Burlingame, B.,
499 Dawkins, M., Dolan, L., Fraser, D., Herrero, M., Hoffmann, I., Smith, P., Thornton, P.K., Toulmin,

500 C., Vermeulen, S.J. & Godfray, H.C.J. (2013) Sustainable intensification in agriculture: premises
501 and policies. *Science*, **341**, 33–4.

502 Gaudino, S., Reidsma, P., Kanellopoulos, A., Sacco, D., van Ittersum, M., Gaudino, S., Reidsma, P.,
503 Kanellopoulos, A., Sacco, D. & van Ittersum, M.K. (2018) Integrated Assessment of the EU's
504 Greening Reform and Feed Self-Sufficiency Scenarios on Dairy Farms in Piemonte, Italy.
505 *Agriculture*, **8**, 137.

506 Herzog, F., Jeanneret, P., Ammari, Y., Angelova, S., Arndorfer, M., Bailey, D., Balazs, K., Báldi, A.,
507 Bunce, R.G.H., Choisis, J.-P., Dennis, P., Dyman, T., Eiter, S., Fjellstad, W., Fraser, M.D., Frank, T.,
508 Friedel, J.K., Garchi, S., Geijzendorffer, I., Gomiero, T., Jerkovich, G., Jongman, R.G.H., Kainz, M.,
509 Kakudidi, E., Kelemen, E., Kolliker, R., Kwikiriza, N., Kovács-Hostyánszki, A., Last, L., Luscher, G.,
510 Moreno, G., Nkwiine, C., Opio, J., Oschatz, M.-L., Paoletti, M.G., Pointereau, P., Sarthou, J.-P.,
511 Schneider, M.K., Siebrecht, N., Sommaggio, D., Stoyanova, S., Targetti, S., Viaggi, D., Wolfrum,
512 S. & Yashchenko, S. (2013) Measuring farmland biodiversity. *Solutions*, **4**, 52–58.

513 Hiron, M., Berg, Å., Eggers, S., Berggren, Å., Josefsson, J. & Pärt, T. (2015) The relationship of bird
514 diversity to crop and non-crop heterogeneity in agricultural landscapes. *Landscape Ecology*, **30**,
515 2001–2013.

516 Hörtenhuber, S.J., Lindenthal, T. & Zollitsch, W. (2011) Reduction of greenhouse gas emissions from
517 feed supply chains by utilizing regionally produced protein sources: the case of Austrian dairy
518 production. *Journal of the Science of Food and Agriculture*, **91**, 1118–1127.

519 Ineichen, S., Piccand, V., Chevalley, S., Reidy, B. & Cutullic, E. (2014) Feeding strategies and feed self-
520 sufficiency of dairy farms in the lowland and mountain area of Western Switzerland. *Grassland
521 Science in Europe*, **19**, 680–682.

522 Johnson, J.B. & Omland, K.S. (2004) Model selection in ecology and evolution. *Trends in Ecology and
523 Evolution*, **19**, 101–108.

524 Krebs, J.R., Wilson, J.D., Bradbury, R.B. & Siriwardena, G.M. (1999) The second Silent Spring? *Nature*,

525 **400**, 611–612.

526 March, M.D., Haskell, M.J., Chagunda, M.G.G., Langford, F.M. & Roberts, D.J. (2014) Current trends
527 in British dairy management regimens. *Journal of Dairy Science*, **97**, 7985–7994.

528 Murphy, K.J., McCracken, D.I., Foster, G.N., Waterhouse, A., Furness, R., Abernethy, V.J., Downie,
529 I.S., Wilson, W.L., Adam, A. & Ribera, I. (1998) *Functional Analysis of Plant-Invertebrate-Bird*
530 *Biodiversity on Scottish Agricultural Land. Final Report to SOAEFD No: UGW/814/94*, 51.
531 University of Glasgow, Glasgow.

532 Natural England. (2017) Farmer Clusters - working together to achieve more,
533 [https://naturalengland.blog.gov.uk/2017/03/21/farmer-clusters-working-together-to-achieve-](https://naturalengland.blog.gov.uk/2017/03/21/farmer-clusters-working-together-to-achieve-more/)
534 more/

535 Östman, Ö., Ekblom, B. & Bengtsson, J. (2003) Yield increase attributable to aphid predation by
536 ground-living polyphagous natural enemies in spring barley in Sweden. *Ecological Economics*,
537 **45**, 149–158.

538 Ovenden, G.Y., Swash, A.R. & Smallshire, D. (1998) Agri-environment schemes and their
539 contribution to the conservation of biodiversity in England. *Journal of Applied Ecology*, **35**, 955–
540 960.

541 Plantureux, S., Peeters, A. & McCracken, D. (2005) Biodiversity in intensive grasslands: Effect of
542 management, improvement and challenges. *Agronomy Research*, **3**, 153–164.

543 Pretty, J., Toulmin, C. & Williams, S. (2011) Sustainable intensification in African agriculture.
544 *International Journal of Agricultural Sustainability*, **9**, 5–24.

545 Pywell, R.F., Heard, M.S., Woodcock, B.A., Hinsley, S., Ridding, L., Nowakowski, M. & Bullock, J.M.
546 (2015) Wildlife-friendly farming increases crop yield: evidence for ecological intensification.
547 *Proceedings of the Royal Society of London B: Biological Sciences*, **282**, 20151740.

548 Roberts, D.J. & March, M.D. (2014) Feeding systems for dairy cows: homegrown versus by-product
549 feeds. *Recent Advances in Animal Nutrition 2013* (eds P.C. Garnsworthy & J. Wiseman), pp. 61–

550 69. Context Publications, Packington.

551 Scottish Agricultural College. (2006) *FeedByte*. Scottish Agricultural College, Edinburgh.

552 Simons, N.K. & Weisser, W.W. (2017) Agricultural intensification without biodiversity loss is possible
553 in grassland landscapes. *Nature Ecology & Evolution*, **1**, 1136–1145.

554 Smol, J.P., Wolfe, A.P., Birks, H.J.B., Douglas, M.S. V, Jones, V.J., Korhola, A., Pienitz, R., Rühland, K.,
555 Sorvari, S., Antoniades, D., Brooks, S.J., Fallu, M.-A., Hughes, M., Keatley, B.E., Laing, T.E.,
556 Michelutti, N., Nazarova, L., Nyman, M., Paterson, A.M., Perren, B., Quinlan, R., Rautio, M.,
557 Saulnier-Talbot, E., Siitonen, S., Solovieva, N. & Weckström, J. (2005) Climate-driven regime
558 shifts in the biological communities of arctic lakes. *Proceedings of the National Academy of*
559 *Sciences of the United States of America*, **102**, 4397–402.

560 Symstad, A.J., Siemann, E. & Haarstad, J. (2000) An experimental test of the effect of plant functional
561 group diversity on arthropod diversity. *Oikos*, **89**, 243–253.

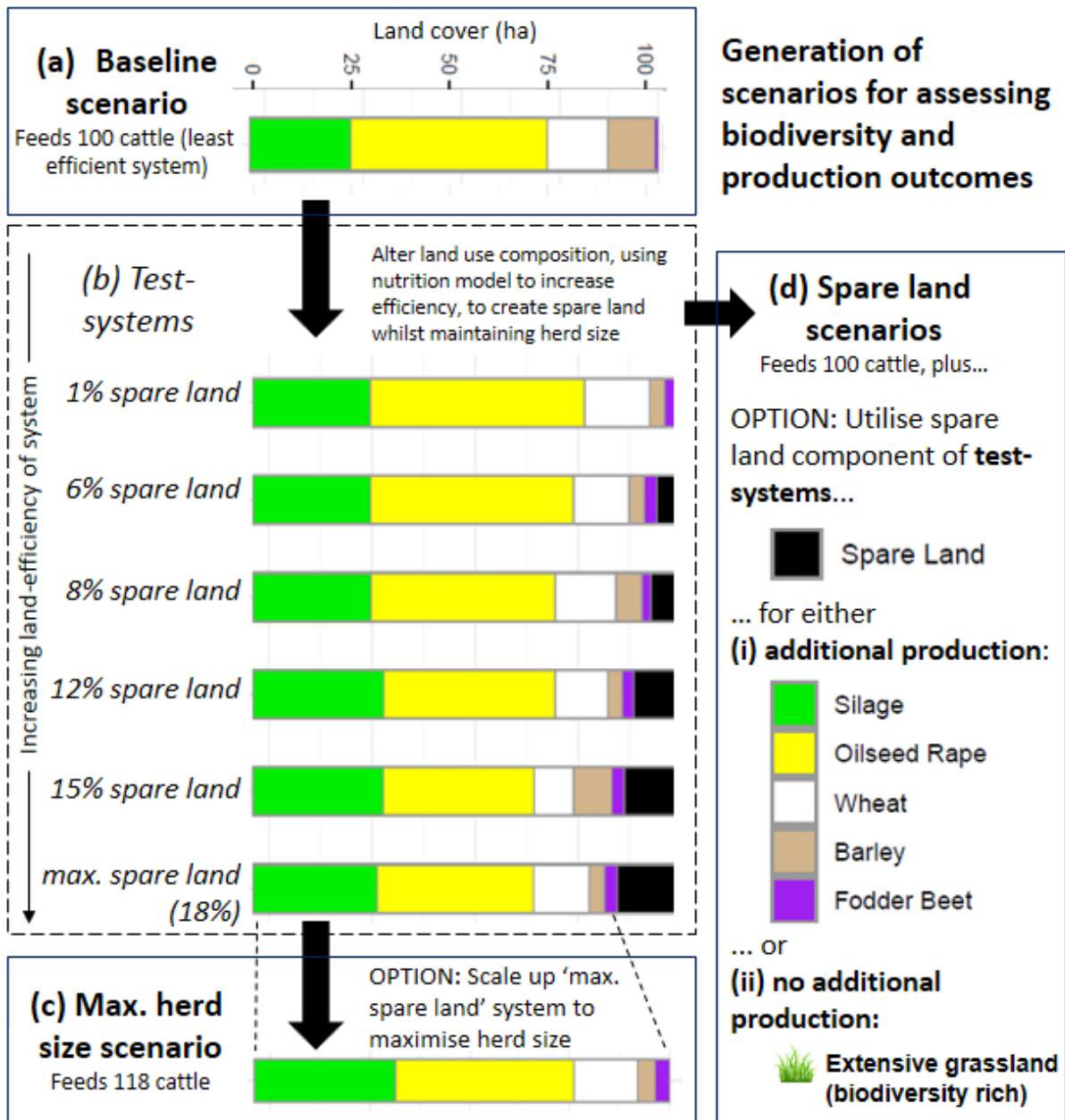
562 Tilman, D., Balzer, C., Hill, J. & Befort, B.L. (2011) Global food demand and the sustainable
563 intensification of agriculture. *Proceedings of the National Academy of Sciences of the United*
564 *States of America*, **108**, 20260–4.

565 Toma, L., March, M., Stott, A.W. & Roberts, D.J. (2013) Environmental efficiency of alternative dairy
566 systems: A productive efficiency approach. *Journal of Dairy Science*, **96**, 7014–7031.

567 Tschardtke, T., Clough, Y., Wanger, T.C., Jackson, L., Motzke, I., Perfecto, I., Vandermeer, J. &
568 Whitbread, A. (2012) Global food security, biodiversity conservation and the future of
569 agricultural intensification. *Biological Conservation*, **151**, 53–59.

570 Valin, H., Sands, R.D., Van Der Mensbrugge, D., Nelson, G.C., Ahammad, H., Blanc, E., Bodirsky, B.,
571 Fujimori, S., Hasegawa, T., Havlik, P., Heyhoe, E., Kyle, P., Mason-D’croz, D., Paltsev, S., Rolinski,
572 S., Tabeau, A., Van Meijl, H., Von Lampe, M. & Willenbockel, D. (2014) The future of food
573 demand: understanding differences in global economic models. *Agricultural Economics*, **45**, 1–
574 17.

575 Wilson, W., Abernethy, V., Murphy, K., Adam, A., McCracken, D., Downie, I., Foster, G., Furness, R.,
576 Waterhouse, A. & Ribera, I. (2003) Prediction of plant diversity response to land-use change on
577 Scottish agricultural land. *Agriculture, Ecosystems & Environment*, **94**, 249–263.
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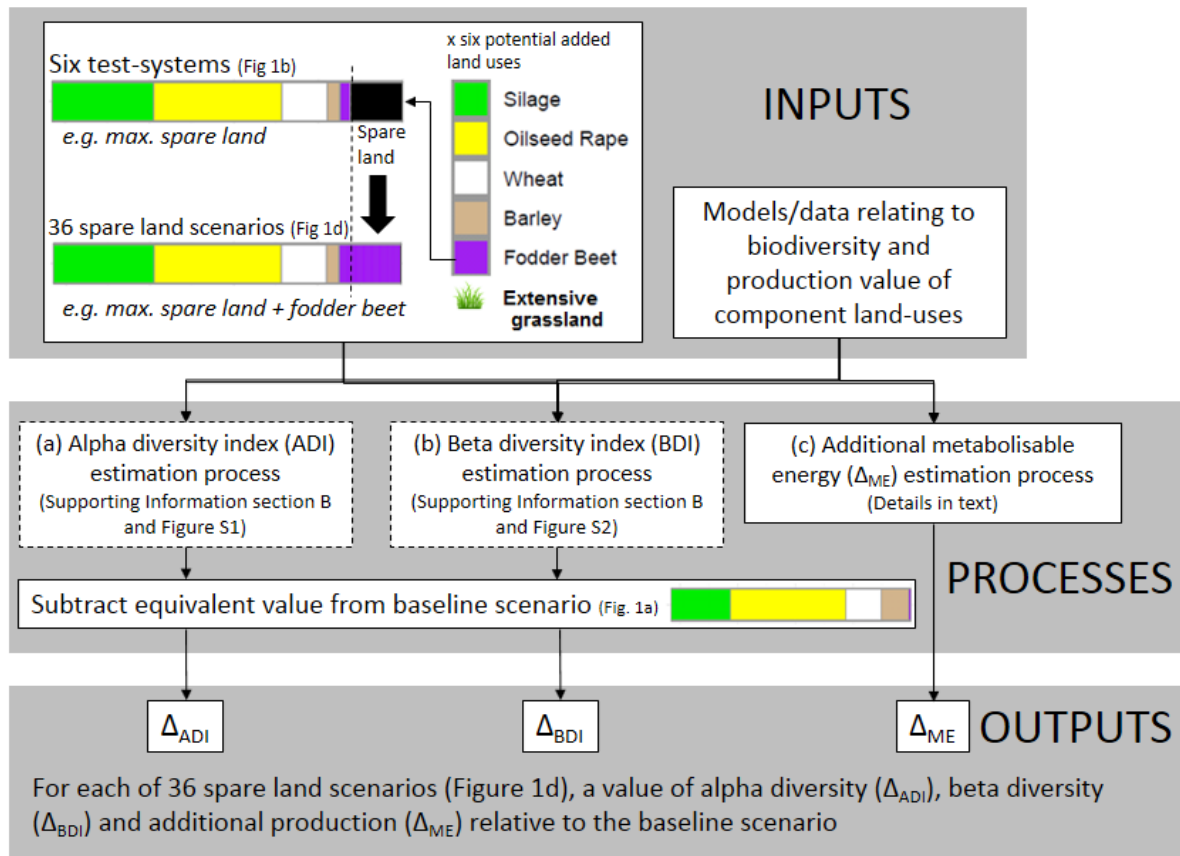
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FIGURE 1. The generation of 38 dairy system scenarios. The feed ration requiring the most land (103.8 ha) was designated the baseline scenario. Altering the farm's crop composition generated spare land (b), without reducing herd size or milk yield (see text). This spare land could be used to (c) scale up the system to maximise herd size, (d i) for additional production or (d ii) for maximising biodiversity through addition of extensive grassland (no additional production).



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FIGURE 2. Workflow for producing estimates of alpha-diversity, beta-diversity and additional production for the 36 spare land scenarios (Fig. 1d), relative to the baseline scenario (Fig. 1a).

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Further information is provided in the text. More detailed information on the estimation of (a)

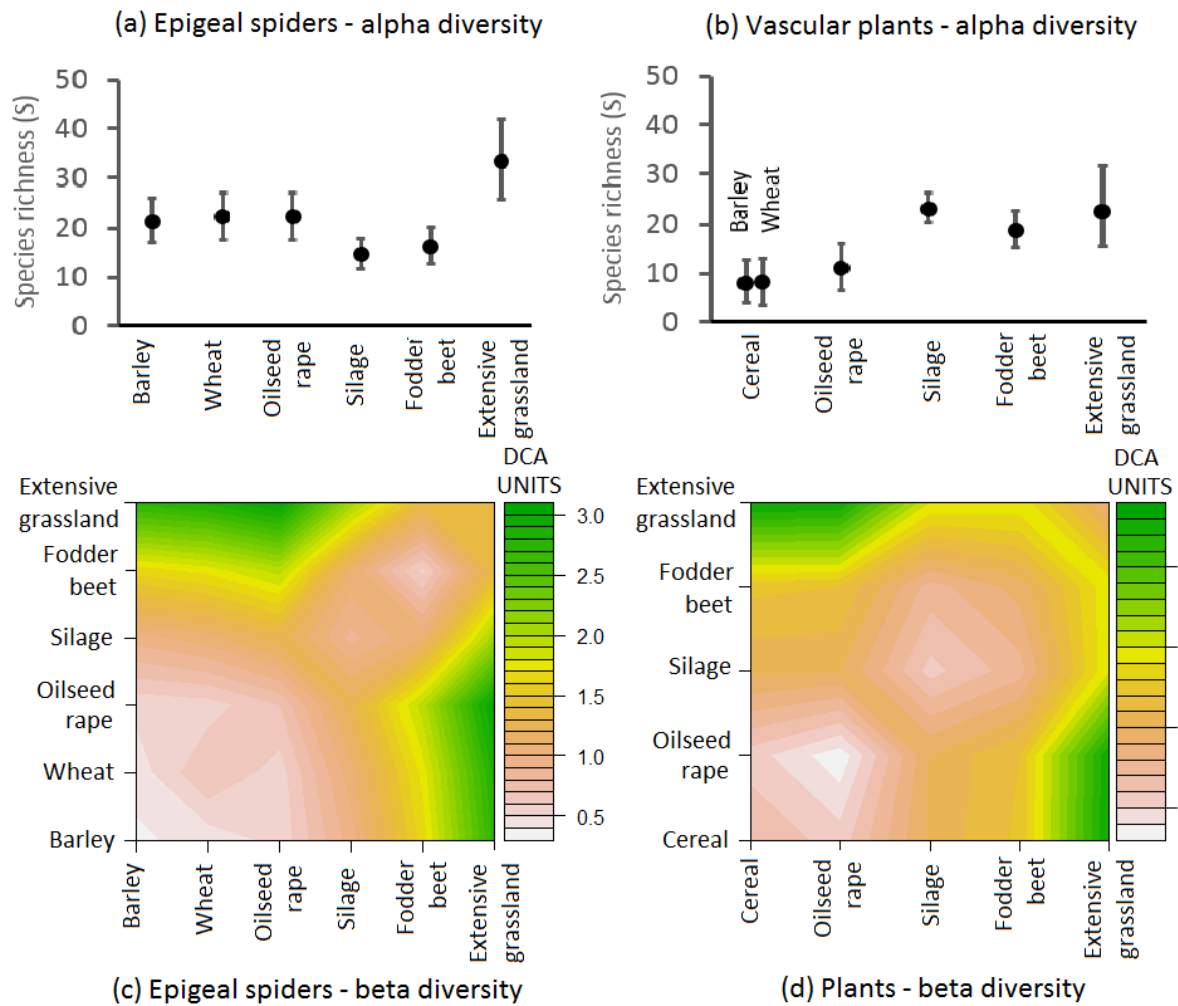
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alpha-diversity and (b) beta-diversity indices (shown in dashed boxes), with sub-workflows and

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model code, are provided in the Supporting Information.

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593

594 **FIGURE 3. Alpha and beta-diversity estimates for plants and epigeal spiders for each land-use from**

595 **datasets in Downie *et al.* (1999) and Wilson *et al.* (2003): (a)-(b) estimated field-scale species**

596 **richness (bars representing upper and lower 95% confidence limits); (c)-(d) contour plots**

597 **representing mean detrended correspondence analysis (DCA) distances between and within land-**

598 **uses (a measure of beta-diversity). Land-uses are ordered to minimise DCA distances across the**

599 **primary and secondary diagonals in (c)-(d).**

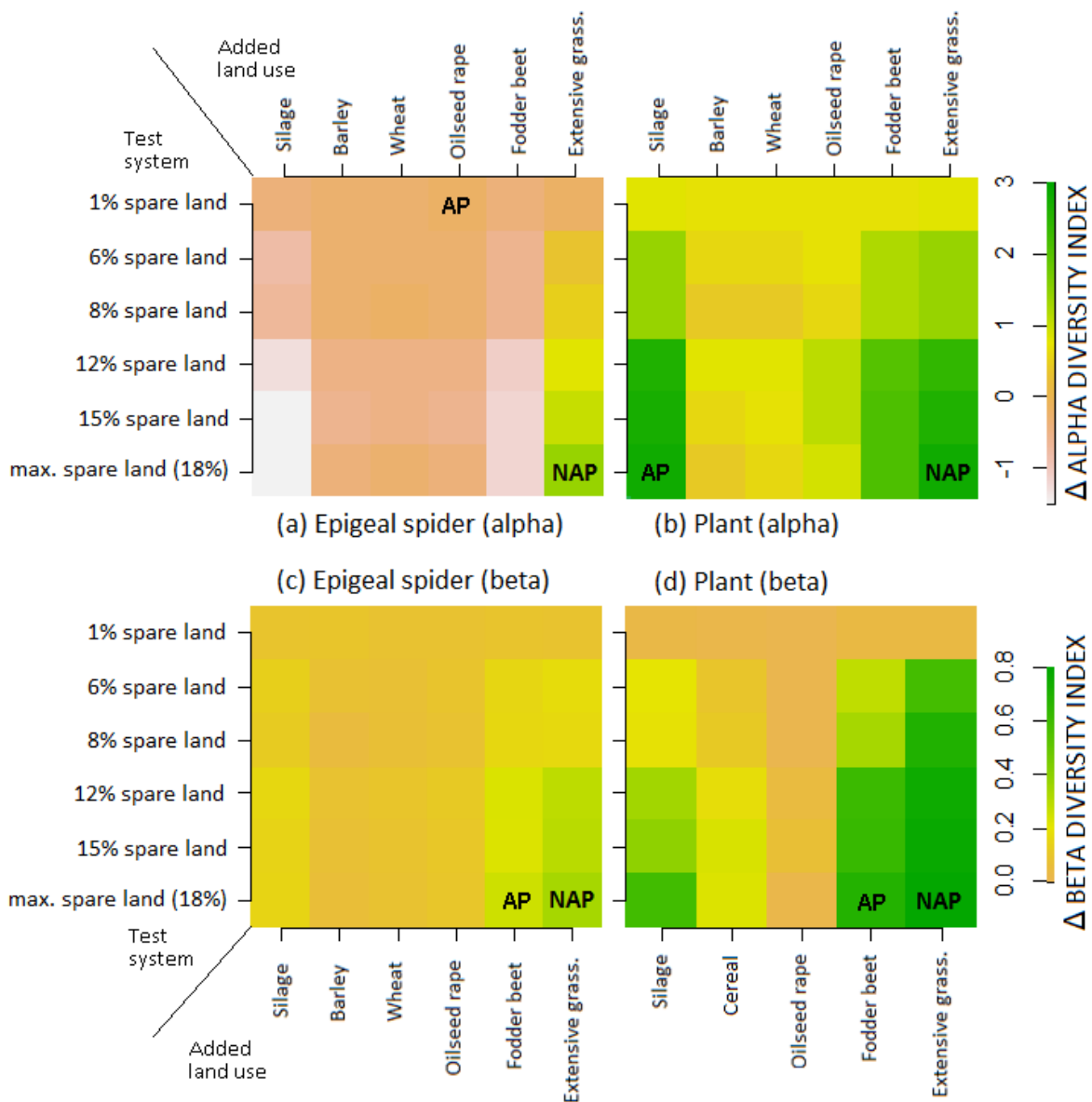
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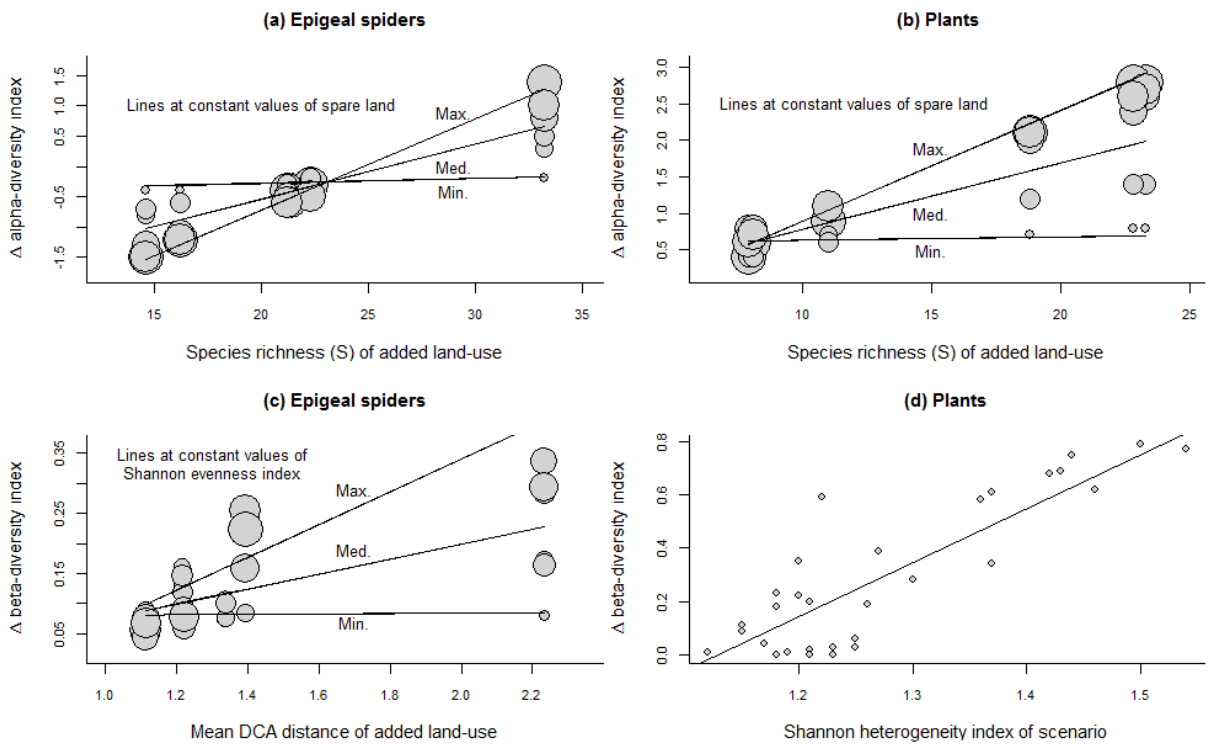
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607 **FIGURE 4. The (a)-(b) change in alpha-diversity index (Δ_{ADI}) and (c)-(d) change in beta-diversity**
 608 **index (Δ_{BDI}) for 36 spare-land scenarios relative to the baseline scenario, for spiders and plants.**
 609 **Each spare-land scenario is defined by a test-system (y-axis) and a land-use that is added (x-axis)**
 610 **to the spare land component of that test-system (Fig. 1). For each plot, the scenario marked ‘AP’**
 611 **represents the highest value for an ‘additional production’ scenario, and ‘NAP’ represents the**
 612 **highest value for a ‘no additional production’ scenario (Fig. 1d). Derivation of alpha- and beta-**
 613 **diversity indices from field-scale biodiversity data are described in the text.**



615

616 **FIGURE 5. Plots of the best AIC_c models presented in Table 2. For presentation purposes, on (a)-(c)**
 617 **circle size is indicative of the relative value on a z-axis (in [a] and [b] this represents the quantity of**
 618 **spare land available, and in [c] this represents the natural logarithm of the Shannon land-use**
 619 **evenness index of the scenario). Interactions on (a)-(c) have been indicated by selecting three**
 620 **constant values on the z-axis (the minimum, median and maximum), and showing the cross-**
 621 **section of the modelled plane at that value. Derivation of alpha- and beta-diversity indices from**
 622 **field-scale biodiversity data are described in the text.**

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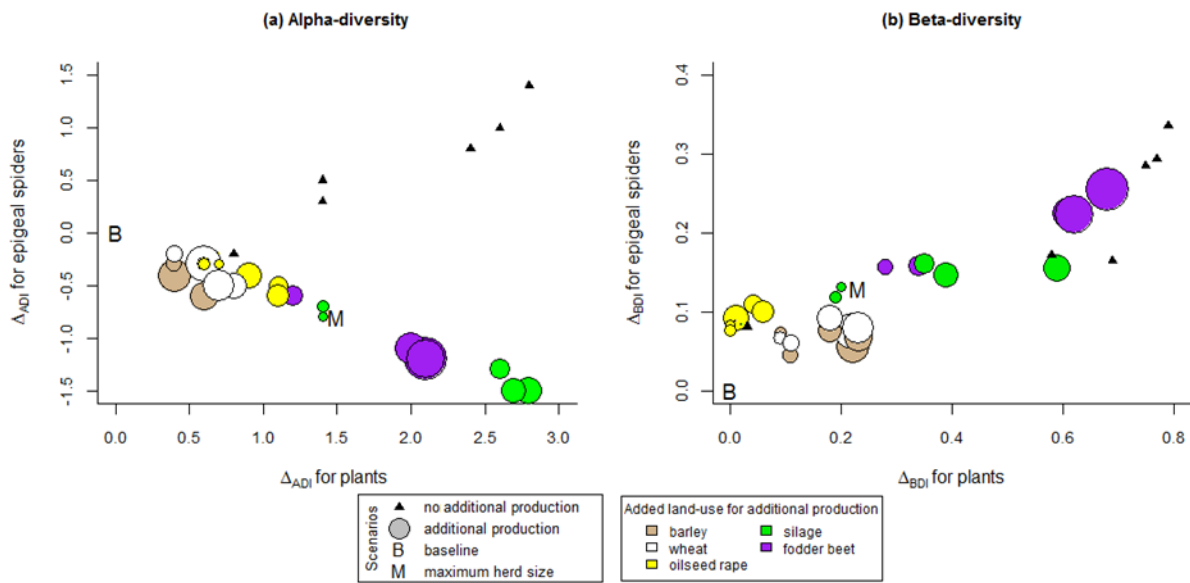
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632 **FIGURE 6. Plots of diversity indices, (a) Δ_{ADI} and (b) Δ_{BDI} , for spiders and plants for spare-land**
633 **scenarios (Fig. 1d). For ‘additional production’ scenarios, the estimated additional metabolisable**
634 **energy (ME) is indicated by the relative radius of the circle (max for both plots is 1,783 GJ dry**
635 **matter). The ‘no additional production’ scenarios (addition of extensive grassland to spare land)**
636 **do not have additional ME so are shown by \blacktriangle . For comparison, the baseline scenario (Fig. 1a) and**
637 **max. herd size scenario (Fig. 1c) are shown by ‘B’ and ‘M’ respectively. Derivation of alpha- and**
638 **beta-diversity indices from field-scale biodiversity data are described in the text.**

639 **Table 1. Fixed effects included in model sets for investigating drivers of alpha (Δ_{ADI}) and beta (Δ_{BDI})**
 640 **diversity indices of scenarios relative to the baseline scenario (Fig. 1a).**

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		In model set	
Code	Description	Δ_{ADI}	Δ_{BDI}
SPARE	Area (ha) of spare land available in the test-system	X	X
HETER	Shannon heterogeneity index of the land-use composition of the scenario	X	X
EVEN	Shannon evenness index of the land-use composition of the scenario	X	X
LANDUSES	Number of land-uses within the scenario (5 or 6)	X	X
COVER	Initial area (ha) in the test-system for the land cover replacing the spare land component	X	X
RICHNESS	Mean estimated S of the given taxa of the land-use replacing the spare land component (see Fig. 2)	X	
DCA	Mean Euclidean detrended correspondence analysis distance for the given taxa of the land-use replacing the spare-land component against each other land-use (including itself)		X

671 **Table 2. Ranking table for models of changes in alpha- and beta-diversity from the baseline**
672 **scenario, with the number of model parameters (k), small-sample AIC (AICc), difference in AICc**
673 **from the lowest AICc value ($\Delta AICc$) and the Akaike's weight (w_i) of each. Model terms are defined**
674 **in Table 1. [NULL] = null model. The form $x*z$ indicates an interaction between x and z . The**
675 **confidence set (summed $w_i \geq 0.90$) is in bold. For brevity, only the confidence set, the model**
676 **immediately outside it, and the null model are displayed. The sample size for each model was 36,**
677 **representing the 36 spare land scenarios. Parameter estimates and SEs for all confidence set**
678 **models are in Supporting Information Table S2.**

	Epigeal spiders					Plants				
DIVERSITY	MODEL	k	AICc	$\Delta AICc$	w_i	MODEL	k	AICc	$\Delta AICc$	w_i
Alpha (Δ_{ADI})	RICH*SPARE	4	-50.4	0.0	>0.99	RICH*SPARE	4	-46.3	0.0	>0.99
	RICH*EVEN	4	20.0	70.4	<0.01	RICH*EVEN	4	50.3	96.6	<0.01
10 models...					...11 models...				
	[NULL]	1	50.5	100.9	<0.01	[NULL]	1	69.4	115.7	<0.01
	... 4 models...					...3 models...				
Beta (Δ_{BDI})	DCA*EVEN	4	-117.3	0.0	0.87	HETER	2	-25.8	0.0	0.71
	DCA*HETER	4	-112.4	4.8	0.08	EVEN	2	-22.33	3.5	0.13
	DCA*SPARE	4	-111.6	5.6	0.05	DCA+HETER	3	-20.57	5.2	0.05
	...4 models...					DCA+EVEN	3	-20.53	5.3	0.05
	[NULL]	1	-93.22	24.0	<0.01	DCA*EVEN	4	-19.9	5.9	0.04
	... 9 models...					...3 models...				
					[NULL]	1	-3.5	22.3	<0.01	
					...8 models...					

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