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Modelling and optimising associated biodiversity in alley cropping systems

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1 Introduction

Agricultural landscapes have replaced natural ecosystems in 40% of the world's land area and are associated with 70% of global freshwater withdrawals (Bonsch et al., 2015). Modern, intensive, large-scale agriculture is also perceived as a critical threat to our common future, due to the disruption of socio-ecological systems, biodiversity loss and degradation of ecosystem services (Vanbergen et al., 2020). The global increase in the area occupied by industrial/large-scale agriculture has been jeopardising the integrity of ecosystems and the way they function. Due to its huge dependence on fossil fuels, agrochemicals and machinery, modern agriculture is a significant contributor to climate change, soil erosion, environmental pollution and other problems (DeLonge et al., 2016).

Modern intensive agriculture can be contrasted with alternative, more sustainable farming systems. Although definitions vary, the common foundation for what are commonly seen as 'sustainable' alternatives to modern, intensive systems is the concept of 'agroecology'. This has been defined as an integrated approach applying ecological (as well as social) principles to the design and management of food and agricultural systems (https://www.fao.org/agroecology/home/en/). Agriculture, in this context, is viewed as an adapted form of ecosystem in which an understanding of fundamental biogeochemical flows/cycles and functional interactions between organisms within this type of ecosystem can be used to optimise its ability to deliver a range of ecosystem services, including food production. Examples of 'sustainable' practices promoting agroecosystem function include optimising the physical, chemical and biological health of soils to promote crop growth and health (reducing the need for external inputs such as fertilisers and pesticides), promoting biodiversity (e.g. to encourage beneficial species such as pollinators or predators of crop pests), and ensuring diversity in agricultural landscapes (to optimise functional interactions between species) (Nicholls et al., 2016; Wezel et al., 2020).

Because they seek to work with and enhance natural processes, these alternative, more 'sustainable' practices are usually recognised as more beneficial to the environment not only from the point of view of crop production but also from the point of view of optimising delivery of ecosystem services (Schröder et al., 2019). Sustainable agriculture is considered pivotal for ensuring food for an increasing world population and for enhancing

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other ecosystem services such as the maintenance of soil health, carbon sequestration, management of water flow and quality as well as biodiversity conservation, among others (Santos et al., 2023). These services ultimately result in additional resilience and adaptation of agroecosystems and local communities to climate and environmental extremes, contributing to human well-being and health (Horrigan et al., 2002). Sustainable practices based on agroecological principles are seen as being able to outperform industrial agriculture by enhancing ecosystem services (including food production) while avoiding damage to the environment (Struik & Kuyper, 2017). Agroecology is seen as transformative as it can potentially integrate aspects of economics, ecology, health and social cohesion, thus meeting a range of the United Nations Sustainable Development Goals (SDGs) (Santos et al., 2022a).

Agroforestry is an agroecological approach that associates trees with livestock or crops in the same space. It is considered a particularly promising technique to promote sustainability by reconciling different needs such as agricultural production and ecological and societal sustainability. There are a number of different types of agroforestry system, including silvoarable systems, silvopastoral systems, forest farming, riparian buffer strips and windbreaks/hedgerows (Mosquera-Losada et al., 2023).

For many years, agroforestry was considered a traditional and outdated system by many decision-makers and underrated and undersupported by agricultural policies. Instead, governments and others actively encouraged removal of trees to create open fields to better enable large-scale intensive agriculture reliant, in part, on large machines such as combine harvestors. Agroforestry practices were widely abandoned and areas converted to open fields, pastures or forests (Den Herder et al., 2017). However, agroforestry is now increasingly seen as a key sustainable practice with the potential to reconcile agriculture production with maximising ecosystem services and reducing environmental impacts, including climate change (Santos et al., 2022b; Menezes et al., 2024). The regulating and supporting services provided by agroforestry may be particularly significant when facing potentially more extreme and unpredictable future climatic conditions. Trees, e.g. have the capacity to improve carbon sequestration, improve functional biodiversity, promote water regulation and soil fertility, optimise microclimate control and the adsorption of agrochemicals which then do not pollute neighbouring landscape features such as watercourses (Moreno et al., 2018).

Alley cropping agroforestry systems consist of alternating crop alleys, which constitute the arable part of the system, with rows of trees, typically accompanied by an understory vegetation strip. These systems are compatible with modern agriculture practices such as mechanisation and robotics (Garrett et al., 2021). The conservation and management of biodiversity in agroecosystems, and particularly in alley cropping, is currently an important

topic (Nair et al., 2021). Even if alley cropping has the potential to contribute to biodiversity conservation in agricultural landscapes through structural complexity, habitat and landscape heterogeneity, a limited understanding of the interrelated effects of micro-habitats on diversity patterns reduces our ability to project its impacts on biodiversity (Santos et al., 2022a).

2 Using ecological models to predict biodiversity outcomes from alley croping

Ecological models are frequently employed to analyse space and/or time dynamics as well as the overall behaviour of complex systems (Bakiş et al., 2021). Spatial, dynamic and spatio-temporal ecological models might incorporate variables that are otherwise difficult to integrate. They can be used to simulate trade-offs between provisioning, regulating and supporting services as well as informing policies to promote biodiversity in alley cropping systems (Arosa et al., 2017). Nevertheless, models are dependent on a range of assumptions, supporting data quality and knowledge of how parameters change with environmental stochasticity (Rumohr et al., 2023).

To predict biodiversity outcomes and benefits from different agroforestry programmes involves linking different input variables (e.g. the species chosen by the farmer, such as different cultivated/bred species and plant/animal varieties) with associated biodiversity outputs (e.g. the species colonising an agroecosystem, including agriculturally beneficial, neutral and harmful organisms), in what can be termed 'planned biodiversity'. Planned biodiversity (to achieve specific outcomes) is one of the main levers to promote the success of agroforestry programmes because choosing the right species combination for each location will optimise provision of target ecosystem services, including crop production and yiels (Barrios et al., 2018). In this context, the term 'associated biodiversity' refers to species associated with ecosystem services (as well as ecosystem disservices). The term 'reactive biodiversity' relates to the diversity of species' responses to environmental stimuli. Both are interconnected and contribute to the resilience of ecosystems in the face of disturbances (Ulanowicz, 2018).

To better understand the interaction between planned biodiversity and associated biodiversity within alley cropping systems, a cell-based spatial modelling approach has been developed (Wilensky, 1999). This approach makes it possible to simulate a range of agroecosystems to explore the way different combinations deliver planned biodiversity targets to optimise associated biodiversity (and, therefore, the delivery of ecosystem services). Specific simulation objectives include:

1 establishing the main cause-effect relationships between crop/tree combinations and the associated biodiversity;

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2 predicting biodiversity enhancement under different management paradigms and environmental conditions; and
3 discussing the added-value of alley cropping systems for biodiversity conservation and ecosystem services.

The following sections describe setting up and running a simulation.

3 Simulation in practice: materials and methods

3.1 Virtual field description

A virtual field was parameterised to represent different types of agroecosystems, including monocropping, intercropping, agroforestry and forestry systems, defined as follows:

1 monocropping (Fig. 1A) represents an agricultural field associated with a single use;
2 intercropping (Fig. 1B) mimics an agricultural field with two alternating in-line crops;
3 simple intensive alley cropping (Fig. 1C) depicts a field with rows of trees and/or shrubs, creating alleys within which agricultural or horticultural crops are produced;
4 simple biodiverse intensive alley cropping (Fig. 1D) depicts a field with rows of native trees and/or shrubs to create conservation/ecosystem services and alleys within which agricultural or horticultural crops are produced;

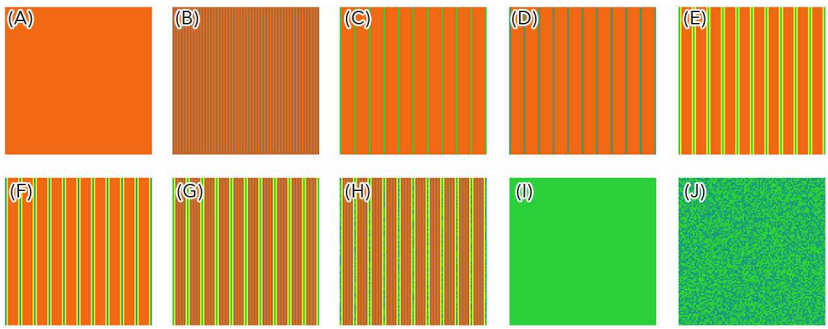

Figure 1 Interface of the model used to simulate the gradient of agroecosystems' planned biodiversity (Planned Biodiversity): (A) monocropping; (B) intercropping; (C) simple intensive alley cropping; (D) simple biodiverse intensive alley cropping; (E) simple extensive alley cropping; (F) biodiverse extensive alley cropping; (G) extensive alley cropping with intercropping; (H) biodiverse extensive alley cropping with intercropping; (I) simple forest; (J) conservation forest. Further explanations in Virtual Landscape Description.

5 simple extensive alley cropping (Fig. 1E) depicts a field with rows of trees and/or shrubs with understory vegetation strips, to create conservation/ ecosystem services and alleys within which agricultural or horticultural crops are produced;
6 biodiverse extensive alley cropping (Fig. 1F) depicts a field with rows of native trees and/or shrubs with understory vegetation strips, to create enhanced conservation/ ecosystem services and alleys within which agricultural or horticultural crops are produced;
7 extensive alley cropping with intercropping (Fig. 1G) depicts a field with rows of trees and/or shrubs with understory vegetation strips, to create enhanced conservation/ ecosystem services and alleys within which intercrops are produced;
8 biodiverse extensive alley cropping with intercropping (Fig. 1H) depicts a field with rows of two species of trees and/or shrubs (one of which is native) with understory vegetation strips, to create enhanced conservation/ ecosystem services and alleys within which intercrops are produced;
9 simple forest (Fig. 1I) simulates a single species tree production forest;
10 conservation forest (Fig. 1J) simulates a forest co-dominated by two tree species.

The conceptual description of the model follows a simplified version of the specifications of the standard Overview, Design Concepts and Details (ODD) protocol (Grimm et al., 2020). The software NetLogo 6.3 (Wilensky, 1999) was chosen to create virtual landscapes and to compute the biodiversity outcomes.

3.2 Purpose

The model investigates how associated biodiversity emerges from the interplay between planned biodiversity and management, separated within tree, crop or understory vegetation-dominated patches and integrating the influences of different production systems (ecological vs conventional). By partitioning patch biodiversity according to phytophagous richness, structural richness, shadow richness and edge/border richness, we intend to understand associated biodiversity patterns linked with different agricultural options and compare the outcomes with types of alley cropping systems (Garret et al., 2021).

3.3 Entities, state variables and scales

The model includes 10 000 patches (unit cells) that make up the 4 ha field (please see Fig. 1 and Table 1 for details). Each patch was characterised by its land use (tree, crop or understory vegetation) and the associated biodiversity

Table 1 Description of the variables of each conceptual entity used in the model

Entity	Variable	Brief description
Patches	*Number*	• 10 000 patches arranged in a square grid (100 × 100 patches), which corresponds to a total of 4 ha.
	Size	• Individual patch of 4 square metres (2 × 2 metres).
	Land-use Richness	• Each patch corresponds to a single dominant land use, crop, tree or understory vegetation, identified by different colours. • Associated biodiversity (SuR) was partitioned between phytophagous species richness (PhR), structural species richness (StR), shadow species richness (ShR) and edge/border richness (BoR). PhR, StR and ShR were defined considering the maximum values set related with each patch use (see please Methods – Diversity predictions). In the case of BoR, the calculations are made considering 8 as the maximum number of edges by patch (eight possible neighbours with different land uses).
	N_Rx	• Richness was normalised using equation 1.
	Field	• *Field* sets the agroecosystem, namely (A) monocropping; (B) intercropping; (C) simple intensive alley cropping; (D) simple biodiverse intensive alley cropping; (E) simple extensive alley cropping; (F) biodiverse extensive alley cropping; (G) extensive alley cropping with intercropping; (H) biodiverse extensive alley cropping with intercropping; (I) simple forest; and (J) conservation forest.
	Management	• *Management* defines the intensity of the production system applied to the field, specifically (X) ecological farming, (XX) conventional pest control of crops, and (XXX) conventional pest control of the overall field (including the tree/understory vegetation patches).

was gauged accordingly to the sum of the components considered (phytophagous richness, structural richness, shadow richness, and edge/border richness).

3.4 Simulating different agroecosystems

Each patch in the virtual agroecosystem represents a single use, either crop patches, tree patches or understory vegetation. Two types of crops, two types of trees, and an understory vegetation strip were considered, within multiple combinations, to illustrate different agroecosystems (planned biodiversity) (Fig. 1). To simulate pest control methods, three management/level conditions were defined, namely (Main et al., 2020; Gunstone et al., 2021; Stein-Bachinger et al., 2021; Serrão et al., 2022; Beaumelle et al., 2023):

1 ecological farming, with no implication for the associated biodiversity;
2 conventional pest control of crops, which implies a reduction in the associated biodiversity of crop patches; and
3 conventional pest control of the overall field, that leads to a reduction in the associated biodiversity of crop patches, tree patches, and understory vegetation patches.

3.5 Predictions of associated biodiversity

Associated biodiversity predictions per patch were partitioned according to (see e.g. Loreau et al., 2021; Wright et al., 2021):

- phytophagous species richness (PhR);
- structural species richness (StR);
- shadow species richness (ShR);
- edge/border species richness (BoR); and
- overall richness (SuR, sums the contributions of the previous estimates).

Species richness was parametrised from databases and previous publications in this scope (explained below).

PhR was defined for each type of crop (for each crop patch, from a random distribution considering a maximum value for each type: a more biodiverse crop and less biodiverse crop), tree (for each tree patch, from a random distribution considering a maximum value for each type: a more biodiverse tree and less biodiverse tree), and understory vegetation patches (for each understory vegetation patch, from a random distribution considering a maximum value) respectively, assuming phytophagous diversity increasing, in general, from crop to tree or understory vegetation, using relative values up to a limit supported on the Database of Insects and their Food Plants (https://dbif.brc.ac.uk/homepage.aspx).

In the case of StR, a similar approach was considered, supported by publications relating vegetation structure and richness of non-phytophagous species (Vasconcellos-Neto et al., 2017; Ebeling et al., 2018; Koricheva et al., 2018; Prather et al., 2020; Corcos et al., 2021; Kuchenbecker et al., 2022; Eo et al., 2023; Silva et al., 2023).

ShR was linked with the age/size of the tree patches, and their projection to the bordering patches, assuming an increasing relation between shadow and soil organism's richness (Coyle et al., 2017; Ashraf et al., 2018; Robinson et al., 2018; Pardon et al., 2019; Sáenz-Romo et al., 2019; Ampoorter et al., 2020; Le Provost et al., 2021).

On the other hand, BoR, associated with species using more than one habitat/species, was gauged only when the number of dissimilar bordering

patches was equal to or greater than 1 (Pardon et al., 2019; Kranz et al., 2019; Gallé et al., 2020; Van Schalkwyk et al., 2020; Gayer et al., 2021; Cuperus et al., 2023). In this case, border richness is limited by the number of neighbouring patches different from the evaluated one.

All metrics of diversity (PhR, StR, ShR, BoR and SuR) were normalised (Rnorm,*i*, Eq. 1) using Rmax, the maximum value of Richness possible. The normalised values (NPhR, NStR, NShR, NBoR and NSuR), ranging from 0 to 1, allow direct comparisons between the different metrics and the different combinations (Gotelli & Colwell, 2001). The model was run 3000 times (combining 100 independent replicates of each Diversity and Management option) and the mean value was set aside by simulation (details in Supplementary Appendix A):

$$\text{Rnorm},i = \text{R}i/\text{Rmax} \quad (1)$$

3.6 Comparing predicions of associated biodiversity

A generalised linear model (GLzM) was used to discriminate the magnitude of the normalised differences in the average richness between the agroecosystems and management options simulated (and their interaction), complemented by Partial Eta Square of the terms of the analysis of variance (ANOVA) of the GLzM, a standardised estimate of the effect size of factors (Nakagawa & Cuthill, 2007). Pairwise differences were determined using Tukey multiple comparisons of means with a 95% family-wise confidence level (Rafter et al., 2002). Statistical analyses were implemented using R 4.0.3 (R Core Team, 2020), through the effect size (v 0.4.0; Ben-Shachar et al., 2020), ggplot2 (Wickham, 2016), nmle (Pinheiro and Bates, 2023), and the ezr packages (Kanda, 2013).

4 Results: trends in associated biodiversity along a gradient of agroecosystem practices

Partial biodiversity metrics' predictions responded differently to the simulated agroecosystems planned biodiversity (Figs 2, 3, 4 and 5) (Casagrande et al., 2017). NPhR (Fig. 2) was associated with an increasing trend along the gradient considered from monocropping (A) until conservation forest (J). It is worth highlighting the value of NPhR for intercropping (B), whose median exceeds (or is equivalent to, depending on the management system) the following simple intensive alley cropping (C) and simple biodiverse intensive alley cropping (D), and the higher dispersion observed in forest systems ((I) simple forest and (J) conservation forest).

On the other hand, the normalised structural richness (NStR) (Fig. 3) is predicted to increase stepwise (with reductions associated with the intensity of the management system) in the following order:

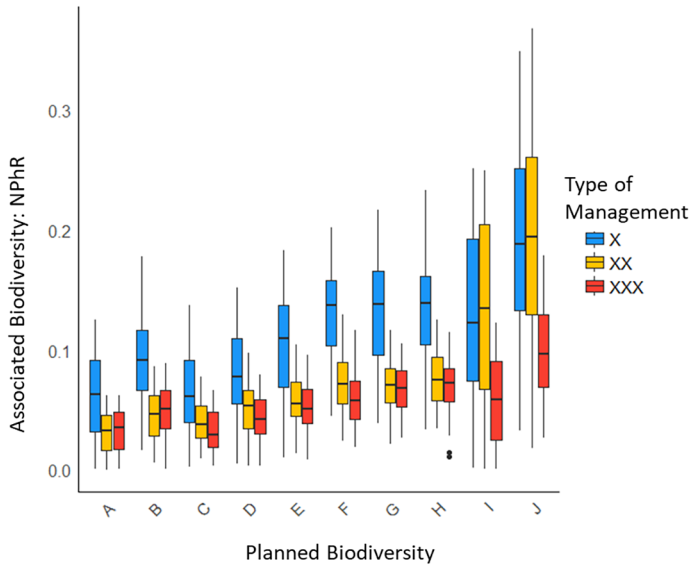

Figure 2 Box and Whisker plots expressing the differences in the normalised phytophagous richness (Associated Biodiversity: NPhR) associated with the different simulated agroecosystems/planned biodiversity (Planned Biodiversity) and management intensity/levels (Type of Management): (A) monocropping; (B) intercropping; (C) simple intensive alley cropping; (D) simple biodiverse intensive alley cropping; (E) simple extensive alley cropping; (F) biodiverse extensive alley cropping; (G) extensive alley cropping with intercropping; (H) biodiverse extensive alley cropping with intercropping; (I) simple forest; (J) conservation forest; (X) ecological farming; (XX) conventional pest control of crops; (XXX) conventional pest control of the overall field (including the tree/understory vegetation patches). Box-plot details: lower and upper box boundaries 25th and 75th percentiles, respectively, line inside box median, lower and upper lines limit 10th and 90th percentiles, respectively, filled circles data falling outside 10th and 90th percentiles.

- starting with crop-only systems ((A) monocropping and (B) intercropping);
- followed by the alley cropping systems ((C) simple intensive alley cropping);
- then, (D) simple biodiverse intensive alley cropping;
- (E) simple extensive alley cropping;
- (F) biodiverse extensive alley cropping;
- (G) extensive alley cropping with intercropping;
- (H) biodiverse extensive alley cropping with intercropping); and
- (highly dispersed again) forest systems ((I) simple forest and (J) conservation forest).

A similar response is predicted for the normalised shadow richness (NShR), even if with nil results for the crop-only systems (Fig. 4) (with a stepwise decrease associated with the management intensity).

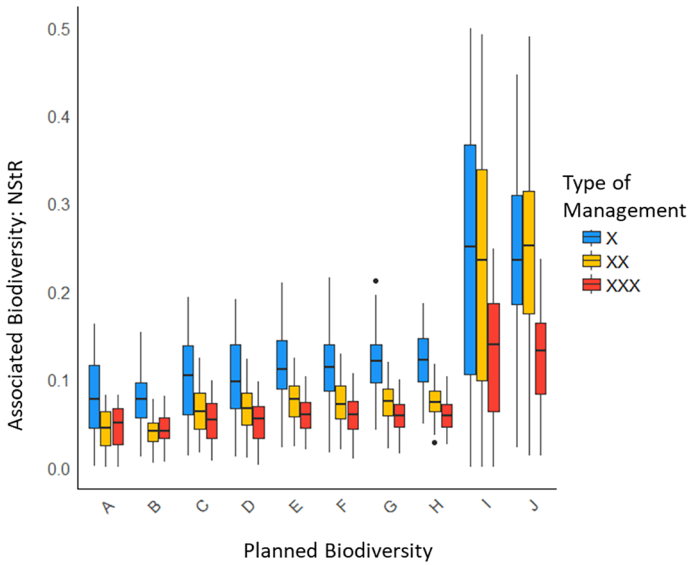

Figure 3 Box and Whisker plots expressing the differences in the normalised structural richness (Associated Biodiversity: NStR) associated with the different simulated agroecosystems/planned biodiversity (Planned Biodiversity) and management intensity/levels (Type of Management): (A) monocropping; (B) intercropping; (C) simple intensive alley cropping; (D) simple biodiverse intensive alley cropping; (E) simple extensive alley cropping; (F) biodiverse extensive alley cropping; (G) extensive alley cropping with intercropping; (H) biodiverse extensive alley cropping with intercropping; (I) simple forest; (J) conservation forest; (X) ecological farming; (XX) conventional pest control of crops; (XXX) conventional pest control of the overall field (including the tree/understory vegetation patches). Box-plot details: lower and upper box boundaries 25th and 75th percentiles, respectively, line inside box median, lower and upper lines limit 10th and 90th percentiles, respectively, filled circles data falling outside 10th and 90th percentiles.

Finally, the normalised edge/border richness (NBoR) (Fig. 5) is nil for the simple systems ((A) monocropping and (I) simple forest) intermediate for the other and higher for (B) intercropping, (G) extensive alley cropping with intercropping and (H) biodiverse extensive alley cropping with intercropping (with stepwise reductions associated with the management intensity/levels).

The overall associated biodiversity (NSuR) results are depicted in Fig. 6. Even if the management intensity/levels tend to reduce the NSuR obtained per agroecosystem, higher values were simulated for (B) intercropping, (G) extensive alley cropping with intercropping, (H) biodiverse extensive alley cropping with intercropping and (J) conservation forest.

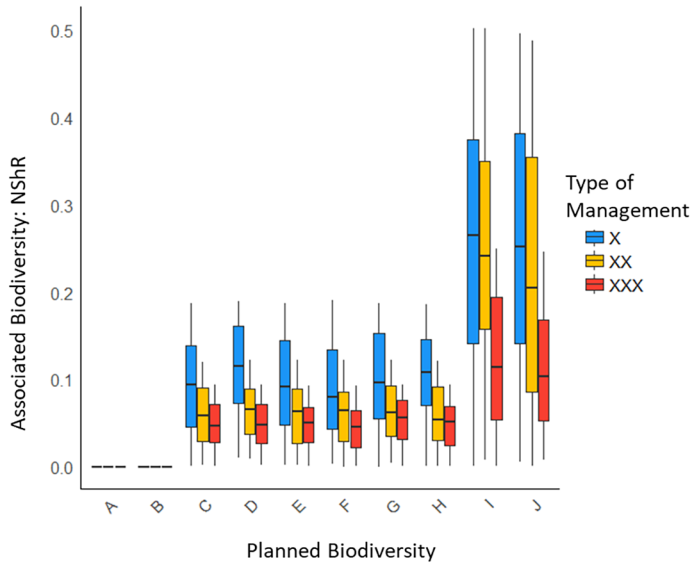

Figure 4 Box and Whisker plots expressing the differences in the normalised shadow richness (Associated Biodiversity: NShR) associated with the different simulated agroecosystems/planned biodiversity (Planned Biodiversity) and management intensity/levels (Type of Management): (A) monocropping; (B) intercropping; (C) simple intensive alley cropping; (D) simple biodiverse intensive alley cropping; (E) simple extensive alley cropping; (F) biodiverse extensive alley cropping; (G) extensive alley cropping with intercropping; (H) biodiverse extensive alley cropping with intercropping; (I) simple forest; (J) conservation forest; (X) ecological farming; (XX) conventional pest control of crops; (XXX) conventional pest control of the overall field (including the tree/understory vegetation patches). Box-plot details: lower and upper box boundaries 25th and 75th percentiles, respectively, line inside box median, lower and upper lines limit 10th and 90th percentiles, respectively, filled circles data falling outside 10th and 90th percentiles.

5 Results: comparing predictions of associated biodiversity

The global influence of the factors agroecosystems/planned biodiversity (Planned Biodiversity) and type of management (Type of Management) on the associated biodiversity (Associated biodiversity: NSuR) and their interaction are depicted in Table 2. Both factors and their interaction were associated with statistically significant effects in the NSuR.

The effect size for the factors of the ANOVA estimated by Eta square, a standardised estimate, is presented in Table 3.

As the simulated decrease in NSuR is proportional to the Management level defined (Type of Management X, XX or XXX), pairwise differences for NSuR (Associated Biodiversity: NSuR) considering only the Planned Biodiversity factor (including all Management levels) were assessed in Fig. 7 and Table 4.

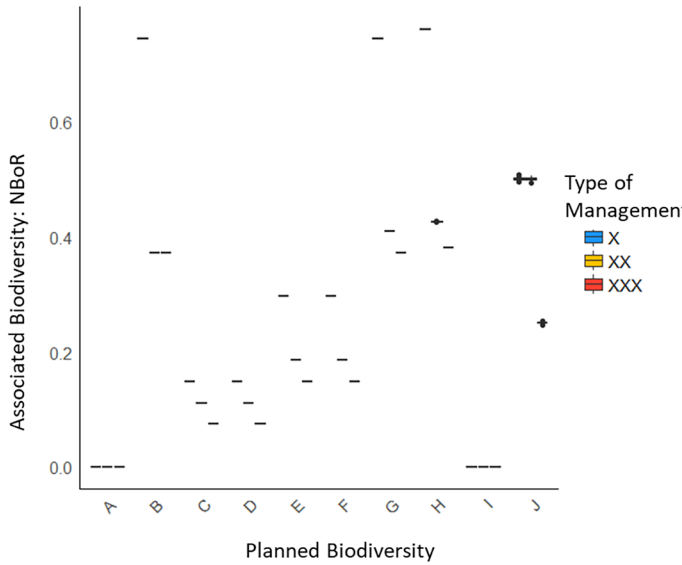

Figure 5 Box and Whisker plots expressing the differences in the normalised edge/border richness (Associated Biodiversity: NBoR) associated with the different simulated agroecosystems/planned biodiversity (Planned Biodiversity) and management intensity/levels (Type of Management): (A) monocropping; (B) intercropping; (C) simple intensive alley cropping; (D) simple biodiverse intensive alley cropping; (E) simple extensive alley cropping; (F) biodiverse extensive alley cropping; (G) extensive alley cropping with intercropping; (H) biodiverse extensive alley cropping with intercropping; (I) simple forest; (J) conservation forest; (X) ecological farming; (XX) conventional pest control of crops; (XXX) conventional pest control of the overall field (including the tree/understory vegetation patches). Box-plot details: lower and upper box boundaries 25th and 75th percentiles, respectively, line inside box median, lower and upper lines limit 10th and 90th percentiles, respectively, filled circles data falling outside 10th and 90th percentiles.

The pairwise differences for NSuR (Associated Biodiversity: NSuR), considering only the Management (Type of Management) factor (including all Planned Biodiversity agroecosystems) were assessed in Table 5.

6 Assessing implications for different management strategies to optimise associated biodiversity

The associated biodiversity (NSuR) results suggest that intercropping, extensive alley cropping with intercropping, biodiverse extensive alley cropping with intercropping and conservation forest are optimal choices for biodiversity conservation in the case of applying ecological management methods, as discussed by Santos et al. (2022b). In the case of the other management options, such as conventional pest control of crops or conventional pest control

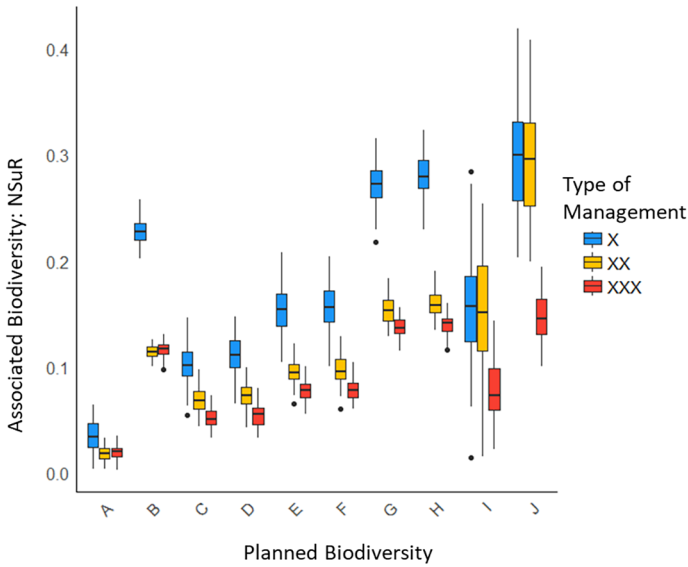

Figure 6 Box and Whisker plots expressing the differences in the normalised richness (Associated Biodiversity: NSuR) associated with the different simulated agroecosystems/planned biodiversity (Planned Biodiversity) and management intensity/levels (Type of Management): (A) monocropping; (B) intercropping; (C) simple intensive alley cropping; (D) simple biodiverse intensive alley cropping; (E) simple extensive alley cropping; (F) biodiverse extensive alley cropping; (G) extensive alley cropping with intercropping; (H) biodiverse extensive alley cropping with intercropping; (I) simple forest; (J) conservation forest; (X) ecological farming; (XX) conventional pest control of crops; (XXX) conventional pest control of the overall field (including the tree/understory vegetation patches). Box-plot details: lower and upper box boundaries 25th and 75th percentiles, respectively, line inside box median, lower and upper lines limit 10th and 90th percentiles, respectively, filled circles data falling outside 10th and 90th percentiles.

Table 2 Analysis of Variance of the Generalised Linear Model relating the factors associated with the agroecosystem/planned biodiversity (Planned Biodiversity) and type of management (Type of Management) with the normalised richness (Associated Biodiversity: NSuR)

Factors	*Df*	Sum Sq	Mean Sq	*F* value	Pr(>*F*|)
Planned Biodiversity	9	11.543	1.2825	2486.9	<2e−16
Type of Management	2	4.113	2.0563	3987.4	<2e−16
Planned Biodiversity × Type of Management	18	1.805	0.1003	194.4	<2e−16
Residuals	2970	1.532	0.0005		

Degrees of freedom (Df), Sum of squares (Sum sq), Mean squares (Mean Sq), *F* value (*F* value) and probability of *F* (Pr(>|*F*)). Variables explanation in Table 1.

Table 3 The effect size of factors of the Analysis of Variance (ANOVA) of the Generalised Linear Model relating the agroecosystem/planned biodiversity (Planned Biodiversity) and type of management (Type of Management) with the normalised richness (Associated Biodiversity: NSuR) (Table 2)

Factors	Eta2 (partial)	95% CI
Planned Biodiversity	0.88	[0.83, 1.00]
Type of Management	0.73	[0.72, 1.00]
Planned Biodiversity × Type of Management	0.54	[0.52, 1.00]

Partial Eta squared (Eta2 (partial)) and 95% confidence interval of the standardised estimate (95% CI). Variables explanation in Table 1.

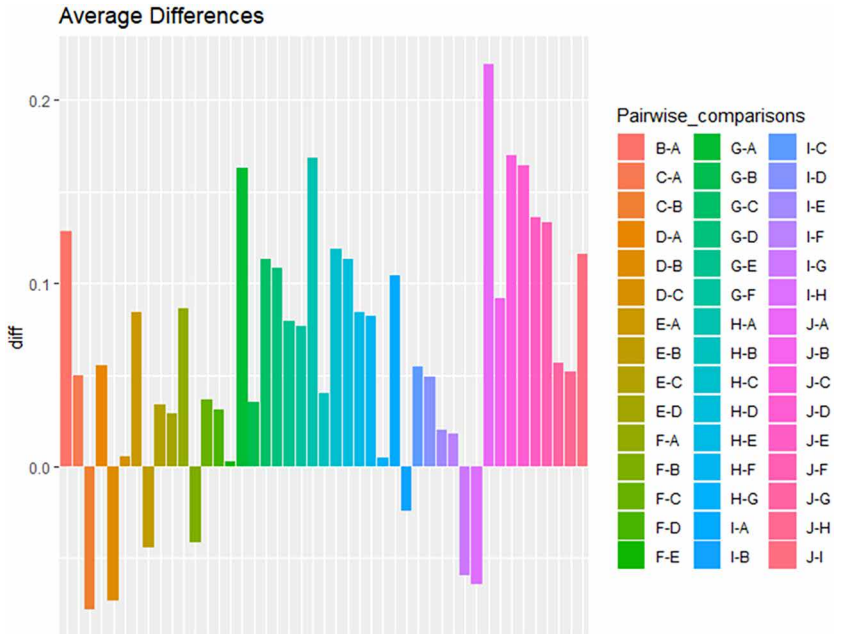

Figure 7 Bars expressing the average pairwise differences (diff) in the normalised richness (Associated Biodiversity: NSuR) associated with the different simulated agroecosystems/planned biodiversity (Planned Biodiversity) (considering all management intensity/levels): (A) monocropping; (B) intercropping; (C) simple intensive alley cropping; (D) simple biodiverse intensive alley cropping; (E) simple extensive alley cropping; (F) biodiverse extensive alley cropping; (G) extensive alley cropping with intercropping; (H) biodiverse extensive alley cropping with intercropping; (I) simple forest; (J) conservation forest. Details are provided in Table 4.

of overall field, only extensive alley cropping with intercropping, biodiverse extensive alley cropping with intercropping and conservation forest maintain a high level of associated biodiversity (even if reduced when compared with

Table 4 Pairwise average differences for the normalised biodiversity predictions (Associated Biodiversity: NSuR) between the different combinations simulated of planned biodiversity/agroecosystems (Planned Biodiversity) and associated significance accordingly with the Tukey multiple comparisons of means with a 95% family-wise confidence level (***$P < 0.001$).

AD (R–C)	A	B	C	D	E	F	G	H	I
A	–	–	–	–	–	–	–	–	–
B	0.128 (***)	–	–	–	–	–	–	–	–
C	0.049 (***)	−0.078 (***)	–	–					
D	0.055 (***)	−0.073 (***)	0.005 (n.s.)	–					
E	0.083 (***)	−0.044 (***)	0.034 (***)	0.028 (***)					
F	0.086 (***)	−0.041 (***)	0.036 (***)	0.031 (***)	0.002 (n.s.)				
G	0.163 (***)	0.035 (***)	0.113 (***)	0.108 (***)	0.079 (***)	0.076 (***)			
H	0.168 (***)	0.040 (***)	0.118 (***)	0.113 (***)	0.084 (***)	0.082 (***)	0.005 (n.s.)		
I	0.104 (***)	−0.024 (***)	0.054 (***)	0.048 (***)	0.020 (***)	0.017 (***)	−0.059 (***)	−0.064 (***)	
J	0.219 (***)	0.091 (***)	0.169 (***)	0.164 (***)	0.135 (***)	0.133(***)	0.056 (***)	0.051 (***)	0.115 (***)

AD, MSuR average differences; R, rows; C, columns. (A) monocropping; (B) intercropping; (C) simple intensive alley cropping; (D) simple biodiverse intensive alley cropping; (E) simple extensive alley cropping; (F) biodiverse extensive alley cropping; (G) extensive alley cropping with intercropping; (H) biodiverse extensive alley cropping with intercropping; (I) simple forest; (J) conservation forest.

Table 5 Pairwise average differences for the normalised biodiversity predictions (Associated Biodiversity: NSuR) between the management levels considered (Type of Management) and associated significance accordingly with the Tukey multiple comparisons of means with a 95% family-wise confidence level (***$P < 0.001$)

AD (R-C)	X	XX
XX	−0.057 (***)	–
XXX	−0.089 (***)	−0.032 (***)

AD, NSuR average differences; R, rows; C, columns. (X) ecological (organic) farming; (XX) chemical pest control of crops; (XXX) chemical pest control of the overall field (including the tree/understory vegetation patches).

ecological management) (for additional information, please see Beaumelle et al., 2023).

The statistical tests corroborate the visual results, namely by depicting the importance of both factors (planned biodiversity and management) and their interaction for the associated biodiversity outcome. Additionally, the pairwise differences integrating all management levels are also particularly informative, namely considering the diversity in farmer's options and variations in management within an agricultural landscape (Delonge et al., 2016). The pairwise comparisons also call attention to the relevance of alley cropping with intercropping systems and the maintainnce of natural forests to enhance biodiversity in agricultural landscapes, as pointed out by several publications (Delonge et al., 2016; Casagrande et al., 2017; Gallé et al., 2020; Chen et al., 2022).

Even considering the pre-parameterisation of the patches' partial biodiversities, the results obtained for each planned biodiversity/agroecosystem combination, of the associated diversity components, were not fully anticipated.

Considering normalised phytophagous richness (NPhR), the performance of intercropping-associated biodiversity, higher than the simple intensive alley cropping and simple biodiverse intensive alley cropping, independent of management level, was unexpected (e.g. Kaiser et al., 2017; Jactel et al., 2021). Similarly, the higher values of NPhR for biodiverse extensive alley cropping, extensive alley cropping with intercropping and biodiverse extensive alley cropping with intercropping, when compared with simple forest (at least considering the ecological management) was also an interesting outcome, in agreement with the Database of Insects and their Food Plants (https://dbif.brc.ac.uk/homepage.aspx).

On the other hand, the NStR and the NShR results were anticipated (e.g. Le Provost et al., 2021; Eo et al., 2023; Silva et al., 2023), namely the crops' lower values (monocropping, intercropping), the intermediate results in the case of alley cropping (simple intensive alley cropping, simple biodiverse intensive

alley cropping, simple extensive alley cropping, biodiverse extensive alley cropping, extensive alley cropping with intercropping, biodiverse extensive alley cropping with intercropping), and the higher structural and shadow richness related with the forests (simple forest, conservation forest).

Concerning the edge/border richness (NBoR), the most interesting result was the very high and almost equivalent values obtained (at least for the ecological management) for the intercropping, extensive alley cropping with intercropping, and biodiverse extensive alley cropping with intercropping, congruent with Gayer et al. (2021) outcomes.

7 The nexus between alley cropping, biodiversity and sustainable agriculture

The world faces the important challenge of feeding an increasing population but from an agriculture that is sustainable (Struik & Kuyper, 2017). In fact, sustainable agriculture could be a win–win solution: producing more food while reducing negative impacts of convential agriculture on the environment, including biodiversity loss and climate change (Mosquera-Losada et al., 2023). Alley cropping systems (and in general agroforestry) are a key approach integrating the three dimensions of sustainable development (economic, social and environmental) and jointly addressing food security and climate challenges.

Agroforestry has been recognised as a sustainable land use practice and system, mixing modern and traditional practices, the promotion of genetic resources of ancient crops or livestock breeds vulnerable to extinction and wildlife conservation (Nair et al., 2021). Moreover, agroforestry systems include high-value fruit and timber trees, soil protection and contribute to healthy diets and the well-being of consumers (Mosquera-Losada et al., 2023).

Our results support the hypothesis that alley cropping (and intercropping) has positive impacts on biodiversity, within several crop/tree species' (and understory vegetation) combinations (Gayer et al., 2021). Still, the simple model did not consider mechanisms operating at larger scales, and management issues were approached in a very basic way (Gotelli et al., 2001; Gunstone et al., 2021; Le Provost et al., 2021). The results obtained agree with the literature showing that management plays an essential role in shaping agroecosystem biodiversity. The shift to ecological (or at least organic) farming combined with alley cropping systems is linked with enhancement of planned biodiversity, but associated biodiversity also increases as a result of more complex microenvironments (e.g. Kovács-Hostyánszki et al., 2017).

Positive effects of alley cropping (and in general agroforestry) were noted for diverse taxonomic groups and systems (Pardon et al., 2019), improving valuable ecosystem services such as habitat for pollinators and natural

enemies of crop pests (Hostyánszki et al., 2020). The crop(s) and tree(s) species chosen have a significant effect on associated biodiversity, namely when combinations include traditional crops and native tree species (and understory vegetation) (Santos et al., 2022b). Associated biodiversity is also coupled with species thresholds to environmental conditions impacting physiology, demography, dispersal, interspecific interactions and adaptation (Moreno et al., 2018).

The model presented here was relatively simple when compared with most agroforestry modelling studies, since we relied on parameterising dimensions of species richness from databases and previous publications. We also took into consideration that environmental measures are implemented at the farm level but recognise that many of the associated biodiversity species depend on upscaling to the agricultural landscape scale (Gallé et al., 2020).

The current study might be regarded as preliminary and with several limitations. Most notably, the model's assumptions and outputs need to be tested to demonstrate its usefulness and applicability (Santos et al., 2013). Performance comparisons might be achieved by parameterising the model to realistic species combinations and comparing the results with field studies (Santos et al., 2018). Several authors state that the fundamental step for framework acceptance is pre-defining the context of application and objectives (e.g. Grimm et al., 2020).

8 Conclusion

Agricultural intensification, as well as the abandonment of traditional agriculture practices, can result in reduced biodiversity and ecosystem services that are difficult to reverse because of the long-time lags characterising the dynamics of socio-ecological systems (Santos et al., 2022b). Societal and ecological mechanisms interact, generating changes in biological communities and degradation of ecosystem functions that are misunderstood and, at a human generation time-scale, mostly irreversible.

Our modelling approach complements previous work relating to agroforestry, management and biodiversity conservation. The simple demonstration, supported by partial contributions for overall diversity, reinforces the idea that agroforestry (in our case study, alley cropping) seems critical to halt biodiversity loss in agricultural landscapes. Despite the limitations inherent to a preliminary modelling exercise, the methodology developed provides a starting point to anticipate the changes in associated biodiversity induced by farmer choices and management options, guiding pertinent future strategies to integrate crop production with nature.

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10 Where to look for further information

For additional information, please refer to the Research Topic titled "Can the Trees Save the Crops? Predicting the Services Provided by Traditional and Novel Agroforests in Changing Mediterranean Landscapes". It can be accessed at: https://www.frontiersin.org/research-topics/12712/can-the-trees-save-the-crops-predicting-the-services-provided-by-traditional-and-novel-agroforests-in-changing-mediterranean-landscapes

11 Appendix: Modelling parameters

Part 1. Netlogo code of the model used to predict the associated biodiversity of agroecosystems

Global Variables:

```
Globals [Mean_diversity Median_diversity Modes_diversity dph25 dph65
    dph45 dph35 dph75 dst25 dst65 dst45 dst35 dst75 dsh ]
```

Patch variables:

```
Patches-own [phyto_richness phytotoabundance species_list structure_
    richness shadow_richness border_richness sum_richness man_richness
    distance_shadow]
```

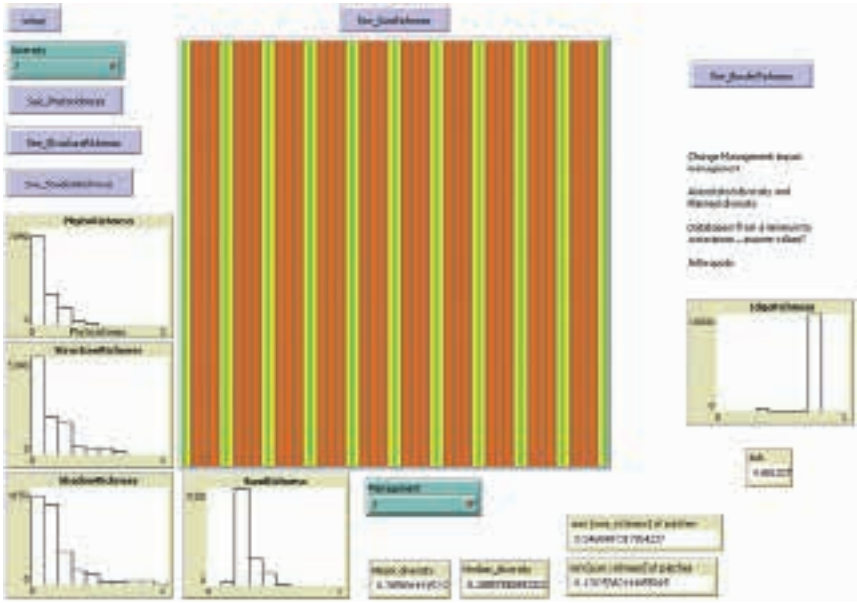
```
Defining the model initial conditions:
to setup
clear-all
set dph25 random-float 1
set dph65 random-float 2
set dph45 random-float 4
set dph35 random-float 2
set dph75 random-float 4
set dst25 random-float 1
set dst65 random-float 3
set dst45 random-float 2
set dst35 random-float 1
set dst75 random-float 3
set dsh random-float 5
Agroforest
Management_Richness_estimation
PhytoRichness_estimation
StructureRichness_estimation
ShadowRichness_estimation
EdgeRichness_estimation
SumRichness_estimation
Diversity_estimations
reset-ticks
end
Defining the type of planned biodiversity:
to Agroforest
If Diversity = 1 [ask patches [set pcolor 25 ]]
If Diversity = 2 [ask patches [set pcolor 25 if pxcor mod 2 = 0 [set pcolor 35
    ]]]
If Diversity = 3 [ask patches [set pcolor 25 if pxcor mod 10 = 0 [set pcolor 65]]]
If Diversity = 4 [ask patches [set pcolor 25 if pxcor mod 10 = 0 [set pcolor 75]]]
If Diversity = 5 [ask patches [set pcolor 25 if pxcor mod 10 = 0 [set pcolor 65]
    if pxcor mod 10 = 9 or pxcor mod 10 = 1 [set pcolor 45]]]
If Diversity = 6 [ask patches [set pcolor 25 if pxcor mod 10 = 0 [set pcolor 75]
    if pxcor mod 10 = 9 or pxcor mod 10 = 1 [set pcolor 45]]]
If Diversity = 7 [ask patches [set pcolor 25 if pxcor mod 2 = 0 [set pcolor 35]
    if pxcor mod 10 = 0 [set pcolor 65] if pxcor mod 10 = 9 or pxcor mod 10
    = 1 [set pcolor 45]]]
If Diversity = 8 [ask patches [set pcolor 25 if pxcor mod 2 = 0 [set pcolor 35] if
    pxcor mod 10 = 0 [set pcolor 65 + 10 * random 2 ] if pxcor mod 10 = 9 or
    pxcor mod 10 = 1 [set pcolor 45]]]
If Diversity = 9 [ask patches [set pcolor 65 ]]
```

```
If Diversity = 10 [ask patches [set pcolor 65 + 10 * random 2 ]]
end
Calculating the management effects on biodiversity:
to Management_Richness_estimation
ask patches [if Management = 1 [set man_richness 1] ifelse Management = 2
    and pcolor != 65 and pcolor != 75 [set man_richness 2][set man_richness
    1] if Management = 3 [set man_richness 2]]
end
Calculating the phytophagous associated biodiversity:
to PhytoRichness_estimation
ask patches [if pcolor = 25 [set phyto_richness (random-float dph25 )/ 4 /
    man_richness set species_list (list "a" "b" "c")]
if pcolor = 65 [ set phyto_richness (random-float dph65) / 4 / man_richness]
if pcolor = 45 [set phyto_richness (random-float dph45) / 4 / man_richness]
if pcolor = 35 [set phyto_richness (random-float dph35) / 4 / man_richness
    set species_list (list "d" "e" "f" "g" "h" "i")]
if pcolor = 75 [set phyto_richness (random-float dph75) / 4 / man_richness] ]
end
Calculating the species associated with the structural complexity of plants
    (associated biodiversity):
to StructureRichness_estimation
ask patches [if pcolor = 25 [set structure_richness (random-float dst25) / 3 /
    man_richness]
if pcolor = 65 [ set structure_richness (random-float dst65) / 3 / man_richness
    ]
if pcolor = 45 [set structure_richness (random-float dst45) / 3 / man_richness]
if pcolor = 35 [set structure_richness (random-float dst35)/ 3 / man_richness ]
if pcolor = 75 [set structure_richness (random-float dst75) / 3 / man_richness]]
end
Calculating the soil species associated with the shadow (associated
    biodiversity):
to ShadowRichness_estimation
ask patches [ (ifelse remainder abs (pxcor) 10 >= 5 [set distance_shadow (10
    - remainder abs (pxcor) 10)]
[set distance_shadow remainder abs (pxcor) 10] ) Ifelse (Diversity > 2 and
    diversity < 9)
[ ifelse pxcor mod 10 = 0 [set shadow_richness random-float dsh / 5 / man_
    richness][set shadow_richness random-float (dsh / (distance_shadow + 1
    )) / 5 / man_richness] ][set shadow_richness 0] if diversity = 9 or diversity =
    10 [set shadow_richness (random-float dsh) / 5 / man_richness ]]
end
```

```
Calculating the generalist species taking advantage of edge systems
   (associated biodiversity):
to EdgeRichness_estimation
ask patches [set border_richness (count neighbors with [pcolor != [pcolor]
   of myself]) / 8 / man_richness] ;repeat world-width [ask patches [ask
   neighbors with [pcolor = [pcolor] of myself] [if number > [number] of
   myself [set number [number] of myself]]]]
end
Calculating the associated biodiversity:
to SumRichness_estimation
ask patches [ set sum_richness (phyto_richness + structure_richness +
   shadow_richness + border_richness) / 4 ]
end
Calculating world statistics:
to Diversity_estimations
set Mean_diversity mean [sum_richness] of patches
set Median_diversity median [sum_richness] of patches
set Modes_diversity modes [sum_richness] of patches
end
Visualising Phytophagous richness associated biodiversity:
to See_Phytorichness
ask patches [ set pcolor phyto_richness * 10 ]
end
Visualising Structural richness associated biodiversity:
to See_StructureRichness
ask patches [ set pcolor structure_richness * 10]
end
Visualising Shadow richness associated biodiversity:
to See_ShadowRichness
ask patches [ set pcolor shadow_richness * 10]
end
Visualising Edge/border richness associated biodiversity:
to See_BorderRichness
ask patches [ set pcolor border_richness * 10]
end
Visualising the associated biodiversity:
to See_SumRichness
ask patches [set pcolor sum_richness * 10]
end
```

Part 2 Example of a simulation

a) Interface of the Netlogo model used to predict the associated biodiversity of agroecosystems



b) Phytophagous richness graphical results

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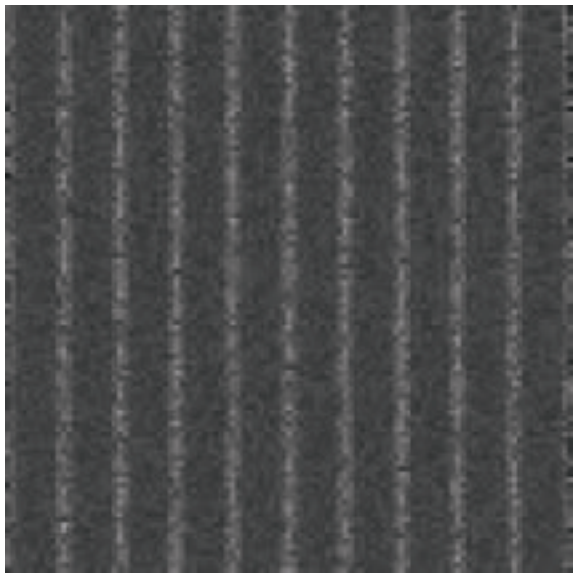
c) Structural richness graphical results

d) Shadow richness graphical results

e) Border/edge richness graphical results

f) Associated Richness graphical results



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