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Inter-species feedbacks drive emergent productivity in agroforestry systems - an agent-based analysis

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Introduction: Conventional agricultural intensification has increased global food production but has also accelerated deforestation, soil degradation, and biodiversity loss. Agroforestry offers a sustainable alternative by integrating trees into farming systems to enhance ecosystem functions. However, predicting how reciprocal interactions between a focal crop species and multiple associated tree species shape long-term productivity under adaptive management remains a major scientific challenge.

Methods: We developed an empirically calibrated Agent-Based Model (ABM) based on a decade of measurements from a 25-year old multispecies agroforestry experiment integrating *Ilex paraguariensis* (yerba mate) with nine tree species. The model simulates species-specific growth, canopy shading, harvest, pruning, soil organic matter (SOM) feedbacks, and management interventions. It represents 778 interacting perennial individuals and enables quantitative exploration of reciprocal inter-species feedbacks under fixed and adaptive management strategies. Because the model is deterministic, statistical replication of simulation runs is not applicable.

Results: Simulations reproduce key field-observed patterns with quantitative agreement. Starting from degraded soil conditions, both management strategies show an initial fertility decline followed by recovery driven by endogenous SOM accumulation. Adaptive management yields a ~56% higher net productivity than fixed management, shortens the recovery time of soil fertility from ~260 weeks to ~88 weeks, and produces nearly threefold higher total biomass. Across species, the model reproduces observed relative *Ilex paraguariensis* yield differences, correctly predicting that *Toona*, *Cañafístola*, *Petiribi*, *Anchico*, and *Kiri* support higher harvest yields than the control (no trees), consistent with experimental field observations over a 10-year period. This quantitative agreement strengthens the model's validity in capturing beneficial inter-species synergies.

Conclusion: The simulations reveal that the focal crop responds to tree-mediated shade and nutrient inputs while actively reorganizing soil fertility gradients through biomass extraction and residue return, thereby reshaping tree regrowth and competitive structure. Together, these dynamics define a mechanistically transparent and predictive framework linking empirical field data with long-term system forecasting.

KEYWORDS
agent-based model, agroforestry, Araucaria, biodiversity, lapacho, multi-species systems, soil restoration, sustainability

Introduction

Agent-based modelling (ABM) has emerged as a widely accepted methodology across biological research, from cellular to population and community levels. ABMs are bottom-up computational frameworks where complex, population-level behaviors emerge from the programmed interactions of autonomous agents with each other and their environment (Zhang and DeAngelis, 2020; Wilensky, 1999; Railsback and Grimm, 2012).

Against the backdrop of urgent environmental threats posed by conventional agriculture—including deforestation, soil degradation, and biodiversity loss—agroforestry offers a promising pathway toward sustainability. This approach integrates trees into farming systems to mimic natural ecosystems, emphasizing complexity, diversity, and recycling to enhance vital ecosystem services. The inherent complexity of multi-species, multi-temporal agroforestry systems pose major challenges for design, management, and optimization. Traditional agricultural research methods often struggle to capture the emergent properties and intricate feedbacks that define these systems (Grimm et al., 2005, 2010; Dupraz et al., 2019; Berger and Schreinemachers, 2011; Shahpari and Eversole, 2024; Burgess et al., 2019). ABMs are well-suited to address these challenges by simulating complex, localized dynamics that are difficult to observe empirically, enabling exploration of emergent patterns arising from individual interactions (Railsback and Grimm, 2012; Grimm et al., 2010; Millington and Wainwright, 2016; Spies, 2017). This bottom-up approach is crucial for understanding how species-level relationships collectively influence system-wide outcomes.

Models that treat agriculture and agroforestry as complex adaptive systems—where interactions among heterogeneous agents shape collective outcomes—have been applied to a wide range of topics including improved plant breeding and sustainability, land-use change, structural transitions, innovation diffusion, market dynamics, environmental change, and agricultural policy evaluation (Soualihou et al., 2021; Burgess et al., 2019; Rivest et al., 2025; Johnson and Salemi, 2022; Millington and Wainwright, 2016; Spies, 2017). These frameworks move beyond homogeneous-agent assumptions, allowing a more realistic representation of coupled human–environment systems.

Despite growing interest in agroforestry, few existing models can predict emergent properties arising from the coexistence of multiple perennial species and long-term management interventions. Current approaches rarely capture both the mechanistic processes through which inter-species interactions drive system-level outcomes and the spatial heterogeneity and network topology characteristic of perennial, multi-species systems (Grimm et al., 2005, 2010). Addressing this gap is essential for advancing from descriptive to predictive frameworks capable of guiding real-world design and management. The overarching goal of developing ABMs for agroforestry is to build science-based tools that can forecast long-term patterns, enabling the design of multi-species systems whose ecological feedbacks simultaneously optimize ecosystem services and economic performance (Brady et al., 2012; Page et al., 2013; Liu et al., 2021; Torralba et al., 2018; Levin, 1998; Holling, 2001; Rahman et al, 2023; Pimbert, 2018; Jose, 2009; Liu et al., 2018; Edmonds and Meyer, 2013).

In plant science, ABMs have predominantly been applied at two distinct scales (Zhang and DeAngelis, 2020): the population and community level—modelling collections of interacting individual plants (Grimm et al., 2005; Burgess et al., 2019; Rahman et al., 2023; Page et al., 2013)— and the individual plant scale, including functional–structural plant models (FSPMs) that describe architectural growth and physiological processes used in crop science (Zhang and DeAngelis, 2020; Soualihou et al., 2021; Dupraz et al., 2019; Grimm et al., 2010). The agents in this case are modules (metamers) within the plant and simulations model branching patterns by which the plants grow, resulting in different morphologies for different species (Zhang and DeAngelis, 2020; Soualihou et al., 2021). Effective ABMs prioritize the minimal number of individual-level attributes needed to provide meaningful insights, enabling flexibility compared to analytical approaches (Zhang and DeAngelis, 2020; Wilensky, 1999; Railsback and Grimm, 2012).

This study develops an ABM to simulate inter-species interactions within an established, long-term agroforestry system integrating *Ilex paraguariensis* (yerba mate) with nine associated tree species. The model represents 400 *I. paraguariensis* plants and 378 trees belonging to nine species within a 200 × 200 m area (Comolli et al., 2024, 2025a) (Full implementation details are provided in Materials and Methods). The field, experimental agroforestry system modelled here is an integrated, multispecies perennial system developed and monitored over more than 25 years in northeastern Argentina, centered on *I. paraguariensis* consociated with these nine native and exotic tree species. Trees are planted directly within the crop matrix rather than in alley configurations, enabling strong local interactions mediated by shade, biomass management, and soil organic matter (SOM) dynamics. Detailed descriptions of species selection, spatial layout, management practices, and long-term experimental outcomes are provided in Comolli et al (Comolli et al., 2024, 2025a). The present study builds directly on this empirical foundation to develop an agent-based modelling framework aimed at understanding and forecasting emergent system-level dynamics.

We chose an ABM approach because the phenomena of interest —species-specific shade and soil interactions, grid-level neighborhood effects, and discrete harvest events—depend critically on local heterogeneity and network topology. These characteristics violate the well-mixed and homogeneity assumptions underlying traditional differential-equation models, which impose top-down population wide parameters. The ABM captures emergent spatial patterns—such as community modularity, clustering of yields, and competition structures—that cannot be represented through mean-field approximations. Moreover, this framework allows gradual model refinement by incorporating new features only when they improve predictive capacity.

Our model explicitly represents the physical location of all plants, species-specific growth rates, and inter-species competition effects manifested through shading and modulation of photosynthetically

active radiation (PAR). Management interventions—including *I. paraguariensis* harvesting, crown trimming, and tree density thinning—are simulated along with their contributions to soil organic matter (SOM). Indirect effects, such as species-specific contributions to key soil nutrients (N, Ca, P) and the buffering capacity of SOM, are also included, indirectly, through enhancement factors influencing fertilizer effectiveness.

At this stage, the model's parameters are grounded in empirically observed data from a decade-long field experiment rather than functional–structural plant models. Calibrated parameters include growth rates (measured by diameter at breast height (DBH) and height (H)) (Sterck and Bongers, 1998; Sumida et al., 2013), shade generation, PAR dynamics, differential species growth, and observed changes in soil chemistry (Comolli et al., 2024, 2025a). This calibration ensures that simulated dynamics reflect real-world agroforestry behavior. Numerical values and calibration procedures are described in Materials and Methods.

The overarching objective of this study is to develop an ABM algorithm that captures the long-term evolution of a multispecies agroforestry system under diverse scenarios, revealing emergent behaviors that arise from nonlinear inter-species dynamics and management. We show that production in multispecies agroforestry is an emergent, network-level property driven by the feedback between the focal crop and its associated tree species. By integrating long-term empirical data with simulation, we demonstrate how embedding trees within perennial cropping systems—here exemplified by *I. paraguariensis* (Roca, 2017; Heck and De Mejia, 2007; Gawron-Gzella et al., 2021; Bracesco et al., 2011; Sarreal, 2023; UNESCO World Heritage Centre, 2023) as case study—can harness ecological synergies, sustain soil fertility, restore biodiversity, and enhance climate resilience. Following the challenge formulated by Grimm (Grimm et al., 2005), this work contributes an ABM framework for designing, testing, and analyzing bottom-up models in agroforestry. The simulation results closely parallel field observations of cumulative harvest per species over a ten-year period (Comolli et al., 2015b), providing an empirically validated baseline for future extensions that incorporate e.g. differential humidity regulation, below ground, and microclimatic processes to the attributes of the agents.

Despite the growing body of empirical research on multispecies agroforestry systems, there remains a lack of mechanistic, empirically grounded models capable of linking species-level interactions, management interventions, and soil feedbacks to long-term, system-level outcomes. In particular, existing studies rarely integrate long-term field data into spatially explicit modelling frameworks that can capture emergent dynamics, critical thresholds, and feedback-driven transitions between degradation and self-sustaining productivity. This gap limits the ability to generalize experimental findings, explore alternative management strategies, and forecast system behavior beyond observed time horizons. Addressing this limitation requires modelling approaches that are both grounded in real agroforestry systems and capable of generating predictive, testable hypotheses. The framework presented can be adapted to other perennial systems provided local climatic, edaphic, and biogeographic conditions are considered.

Materials and methods

Our ABM was developed using NetLogo (version 6.4.0; Northwestern University, Evanston, IL) — a widely used, open-source simulation platform for modelling complex systems in biology and ecology (Wilensky, 1999). NetLogo can be freely downloaded at https://ccl.northwestern.edu/netlogo/6.4.0/, and an introductory guide is available at https://ccl.northwestern.edu/netlogo/bind/article/getting-started-with-netlogo.html. The complete model code (EnsayoF_2.0.nlogo) is provided in Appendix I of the Supplementary Materials and is also publicly available at https://github.com/lrcomolli/ABM-of-Inter-Species-Interactions-in-Agroforestry. Once NetLogo is installed, opening this file and pressing *Run* reproduces the full set of simulations and figures presented in this manuscript. This computational framework enables simulations through a parameterized, agent-based approach. The model employs structured breed definitions and modular agent creation to represent multiple species and management strategies, supporting flexibility, readability, and scalability. Because the model is deterministic, all runs using identical parameters produce identical results, ensuring complete reproducibility. The figures presented in the manuscript correspond directly to the NetLogo graphical interface outputs, allowing users to visualize the same system dynamics when running the model themselves. This design prioritizes transparency and direct verifiability over aesthetic stylization, preserving the reproducibility and interpretability of results.

Agent set

The simulated environment consists of a 210 × 210-pixel field representing a 210 × 210 m section of the larger experimental plot. The spatial arrangement mirrors the real-life design of the integrated agroforestry system, consisting of *I. paraguariensis* ("yerba mate") plants as the base crop and nine consociated tree species. *I. paraguariensis* plants are positioned on a 20 × 20 grid, with coordinates at {10, 20, 30, …, 200} in both x and y dimensions. Tree agents are placed on a parallel grid offset by 5 pixels, with x-coordinates {5, 15, 25, …, 205} and y-coordinates {5, 15, 25, …, 205}. Each of the nine tree species occupies two adjacent columns, ensuring that every *I. paraguariensis* plant is consociated with four equidistant tree neighbors. Conversely, each tree interacts with four surrounding *I. paraguariensis* plants. A control area, devoid of trees but containing *I. paraguariensis*, occupies the final two columns (x = 195 and x = 205).

In summary, the model initially contains 400 *I. paraguariensis* plants arranged in a 20 × 20 grid. Of these, 360 plants are consociated with trees, while 40 plants, located in the control area (two rightmost columns), grow without tree association. The simulation includes 42 trees per species, for a total of 378 tree agents representing nine different species. Collectively, these agents occupy a 200 × 200 m section of the larger 10-hectare experimental field, which contains approximately 7,460 trees and 37,000 *I. paraguariensis* plants in total (Comolli et al., 2024, 2025a). The tree species included in the model are listed in Table 1, and representative visualizations of the simulated field under different

TABLE 1 Tree species in the multispecies agroforestry system.

Popular name	Scientific name	Code abbreviation
Lapacho negro	*Handroanthus heptaphyllus*	La
Petiribi (loro negro)	*Cordia trichotoma*	Pet
Araucaria	*Araucaria angustifolia*	Ar
Cañafístola	*Peltophorum dubium*	Cana
Anchico Colorado	*Parapiptadenia rigida*	An
Guatambú	*Balfourodendron riedelianum*	Gu
Toona (Australian cedar)	*Toona ciliata*	Toona
Grevillea	*Grevillea robusta*	Ge
Kiri	*Paulownia* sp	Ki

initial soil conditions are shown in Supplementary Figure 1. The spatial configuration mirrors that of the real-world experimental design, ensuring that model-derived dynamics correspond directly to measurable field processes.

The design of the real-life experimental plot, the selection of tree species, and the allometric parameters used for calibration are detailed in (Comolli et al., 2024, 2025a). For clarity within the model's code, specific abbreviations are used for each species: *I. paraguariensis* (ilex); *Peltophorum dubium* (Cana); *Handroanthus heptaphyllus* (La); *Cordia trichotoma* (Pet); *Parapiptadenia rigida* (An); *Araucaria angustifolia* (Ar); *Balfourodendron riedelianum* (Gu); *Grevillea robusta* (Gr); *Paulownia* sp. (Ki); *Toona ciliata* (Toona); Control (Con). The details of the original randomized trial plot, which spans 10 hectares and is divided into four equivalent blocks with varying species distributions, are available in Supplementary Table 1 and in (Comolli et al., 2024, 2025a).

Parameters

The attributes of the agents in our model are parameterized based on measured field data, as presented in Comolli et al (Comolli et al., 2024, 2025a). Diameters at breast height (DBH —at 1.30 meters from the ground) and heights (Hts) were measured in the field across all tree species and provide estimates for their growth rates presented in Table 2. These data, which are the most commonly used measures of tree growth (Sterck and Bongers, 1998; Sumida et al., 2013), were measured at the ages of 4, 5, and 8 years, and are presented in Supplementary Table 2, taken (with permission) from (Comolli et al., 2024) Species-specific growth rates were derived directly from measured increments in DBH and height, as the average of the two (see "Overview of the NetLogo Code" in Supplementary Materials). This simplification captures the development of the trees during the first few years but cannot be used to model the long-term development of trees. In this model, we focus on a five-to-ten-year period, primarily examining the interplay of competition and synergies between the trees and the harvest-producing plant, *I. paraguariensis*, as the plants develop from their juvenile growth stages to productive maturity. The measured photosynthetically available radiation (PAR) for each species underpins the modelling of competition caused by shade and physical occlusion incorporated into the model (see "Overview of the NetLogo Code" in Supplementary Materials). Additionally, the model includes human interventions, such as harvesting *I. paraguariensis* and managing the trees through crown trimming and thinning (reducing the number of trees). The parametrization therefore is based on data acquired over a period of ten years, as published in Comolli et al (Comolli et al., 2024, 2025a).

Agent's attributes

The simulation commences with the choice of one of five distinct soil quality levels, ranging from degraded to restored, which are represented by a dimensionless 'energy' proxy that plants consume for growth. This framework reflects our system's objective of sustainable soil improvement over time. Each species' initial energy value is contingent on the designated soil quality level, with the variable 'et' (energy trees) assigning dimensionless energy values to all plants based on a soil-factor multiplier. This proxy is a simplified yet realistic representation of soil fertility, calibrated to qualitatively mimic observed field conditions.

As *I. paraguariensis* plants and trees grow, they draw energy from the soil, thus depleting its quality. Their energy is periodically reduced through harvesting, trimming, and thinning interventions. This dimensionless cyclical process of growth and intervention facilitates the reintroduction of carbon-rich matter to the soil, which the model tracks as dimensionless 'soil-multipliers.' These multipliers subsequently update the 'soil-energy' and 'soil' values (dimensionless). SOM, a critical component acting as both a buffer and a carbon source, also gradually enhances the efficacy of external inputs, particularly synthetic fertilizers. As soil quality changes, plant energy allocations are recalibrated, simplifying the cycle representation while maintaining realism (Bashir et al., 2021; Hoffland et al., 2020; Tian et al., 2023; Abdu et al., 2023; Gao et al., 2011).

The growth rate for all plant and tree agents is species-specific and dependent on soil quality. These growth rates are modelled from allometric field data collected in 2014 and 2015, as presented in Supplementary Table 2 (Comolli et al., 2024). Photosynthetically active radiation (PAR), measured in 2018 (Comolli et al., 2024),

TABLE 2 Rate of growth for each species.

Species	Annual increment	Rate of increment
I. paraguariensis	1.22	0.22
Cañafístola	1.33	0.33
Anchico	1.32	0.32
Lapacho	1.49	0.49
Loro negro	1.44	0.44
Araucaria	1.25	0.25
Guatambú	1.56	0.56
Toona	1.64	0.64
Grevillea	1.35	0.35
Kiri	1.54	0.54

Average experimental parameters computed from data for 4, 5, and 8 years of growth.

serves as a control to verify that simulated competition attributable to consociations scales appropriately with field experimental observations. Roots are not included in this model.

Agent interactions are categorized as either direct or indirect. Direct interactions, such as physical competition and PAR occlusion, directly impact *I. paraguariensis* plants through shading, reducing their growth rate when light occlusion exceeds 30%. Concurrently, shade promotes soil humidity conservation, which is beneficial. Indirect interactions primarily involve soil enrichment from decomposing trimmed branches, harvest remnants, and thinned logs. These represent endogenous sources of organic matter, which exhibit minor species-specific differences. SOM, in turn, enhances the plant availability of exogenous fertilizers, constituting a second-order, indirect interaction within the model. Additionally, each tree species uniquely affects soil micronutrient composition, such as phosphorus content, further contributing to indirect agent interactions. While challenging to parameterize directly, these complex factors could be incorporated through a maximum entropy formulation.

Human interventions, including *I. paraguariensis* harvesting and tree trimming and thinning, are integrated as periodic reductions in plant biomass that directly contribute organic matter back to the soil, thus closing the growth-reincorporation cycle. The management of the agroforestry system including the schedule of *I. paraguariensis* harvest, trimming and thinning of the different tree species as determined by their growth, external fertilizer additions, as well as shade competition, incorporation of SOM from the biomass harvested from the trees and left on the ground are described in the section "Overview of the NetLogo Code" of the Supplementary Materials. The algorithm is included in Appendix I of the Supplementary Materials.

State-of-soil

Soil energy is represented as a dimensionless index integrating fertility, organic matter availability, and nutrient-use efficiency. Absolute field measurements were rescaled to preserve relative differences and empirically observed thresholds rather than physical units. This approach maintains internal commensurability while enabling comparison across management scenarios and initial soil states.

The 'State-of-soil' plot depicts the temporal evolution of soil fertility, represented as 'energy' within the model. The initial soil state is configured using the 'Fertility' slider, which categorizes the soil into five distinct types ranging from zero to ten thousand dimensionless units. The five selected soil quality levels, along with the represented energy flow between soil and plants, are dimensionless and qualitative. The critical determinants are that their relative scaling and evolution accurately reflect observed reality, and that this simplified representation facilitates the discernment of system behavior beyond readily apparent observations.

As the simulated system evolves, the soil classification may dynamically change. Tree agents deplete soil energy through nutrient absorption; however, pruning and thinning interventions replenish the soil with organic matter. This process incorporates atmospheric carbon and nitrogen from rainfall (released during electrical storms). These endogenous factors not only enrich the soil but also enhance the efficacy of exogenously added fertilizers. SOM, a critical component serving as both a buffer and a carbon source, gradually increases the solubility and, consequently, the availability of exogenous industrial fertilizers (Comolli et al., 2024, 2025a).

Soil quality is discretized into five empirically grounded ranges based on long-term field observations and published measurements of soil organic matter dynamics in the experimental agroforestry system:

Soil scaling (soil quality index)

- 'Soil 1' (restored high quality): soil >= 8,000.
- 'Soil 2': 6,000 <= soil < 8,000.
- 'Soil 3': 4,000 <= soil < 6,000.
- 'Soil 4': 2,000 <= soil < 4,000.
- 'Soil 5' (degraded quality): soil < 2,000.

Supplementary Figure 1 illustrates the simulation's starting configurations for the three highest soil qualities: 'Soil 3' (low), 'Soil 2' (intermediate), and 'Soil 1' (high), distinguished by different color coding. While this scaling, along with the 'energy of trees' and 'soil energy' values, is arbitrary, serving primarily to qualitatively represent the experimental reality, we expect to develop a calibration. Future research could establish a more realistic scaling derived from a reduction of multiple regional soil parameters, potentially following methodologies similar to Abdu et al (Abdu et al., 2023) and others.

Crucially, it is imperative to accurately scale soil dynamics to account for irreversible fertility loss (Abdu et al., 2023; Gao et al., 2011). In our soil index, if the soil is severely degraded (soil < 2,000 units), initiating agricultural activity is not possible. Conversely, if the soil has been restored through fallowing (soil > 6,000 units), an integrated agroforestry system that combines endogenous SOM generation with external inputs (compensating for a portion of extraction) can establish a self-reinforcing trajectory. This trajectory simultaneously increases soil quality while producing economic output (harvest) with diminishing reliance on external inputs.

Energy metrics

The 'Energy-trees' monitor displays the energy available to plants for growth. The soil state, or energy level, is simplified into a 'soil-factor' value, derived from the five defined soil types within the dynamic range set by the Fertility slider. This soil-factor modulates both the energy available to plants and their growth rates. All these states and factors are expressed in dimensionless units.

Nutrient flow and balance within the system are complex processes, involving multiple interconnected variables. Nutrients represent the soil resources available for plant uptake, providing the energy essential for growth. The reincorporation of tree branches and trunks into the soil creates a crucial feedback loop, contributing nutrients both directly and indirectly. This continuous process significantly enhances soil fertility and supports sustained plant growth within the agroforestry system.

Model realism and scaling

Growth rates and photosynthetically active radiation (PAR) values for all species were derived directly from field measurements, ensuring that relative sizes among species and competition levels scale realistically within the model. All other quantities were expressed in dimensionless units rather than absolute measures such as kilograms or hectares, maintaining internal consistency while emphasizing causal relationships between allometric parameters, management choices, and emergent system patterns. Model outputs—such as the cumulative harvest—therefore represent relative magnitudes per plant, allowing direct comparison among consociated tree species rather than absolute production per area. When excessive canopy shading reduces PAR availability to *Ilex paraguariensis*, external interventions such as trimming or thinning are triggered, converting a proportion of plant biomass into soil organic matter (SOM). Thinning entire rows of trees contributes additional SOM through decomposition, accelerated by increased light and runoff after canopy removal. These processes are parameterized according to their relative scaling rather than absolute values, preserving realism while keeping the model generalizable across systems.

As simulations progress, the model allows for the investigation of differences in soil evolution, plant and tree growth and sizes, harvest amounts, and the effects of competition and endogenously generated SOM. Soil quality directly impacts the growth rates of trees and *I. paraguariensis*, which in turn influences the feedback to the soil from trimming and thinning, as well as the competition due to occlusion. The varying growth rates among tree species necessitate a localized representation of their impact on soil, leading to differential growth rates in adjacent *I. paraguariensis* plants. Consequently, *I. paraguariensis* plant growth and harvest yields exhibit variation across the simulated system due to differential competition and SOM increases. A control land plot, devoid of trees, provides a basis for comparison with tree-less monocultures. Trimmed tree branches are assumed to be evenly distributed, consistent with field observations, while larger trunks and crown parts remain localized. This endogenous, tree-derived SOM also enhances the availability of external fertilizers, adding a layer of complexity to the system's dynamics. External inputs, being a choice variable, are modelled as a range of values scaled as a percentage of matter replacement extracted during harvest.

Aims and validation of the model

The parameterization of agent growth and competition, utilizing metrics of growth and allometric relationships (Table 1 and Supplementary Table 2), is precisely defined. This foundation, combined with the explicit definition of human interventions, enables the ABM simulations to yield a unique and accurate set of predicted system-wide behaviors. However, representing the intricate dynamics of soil processes, including restoration and species-specific growth responses, presents a challenge beyond the current scope of this work (Bashir et al., 2021; Hoffland et al., 2020; Tian et al., 2023; Abdu et al., 2023; Gao et al., 2011). Consequently, our model currently employs a simplified "soil quality index." This index, while not attempting precise numerical scaling or replication, accurately captures the qualitative behaviors observed in our experimental project (Comolli et al., 2024, 2025a). This approach successfully reproduces key system dynamics: tree growth patterns, biomass accumulation, and the effects of external inputs commensurate with the chosen scaling relative to resource extraction.

The validation of our model is underpinned by over 20 years of experimental data (Comolli et al., 2024, 2025a), with a particular focus on the evolution of SOM and harvest yields. Additional data streams, encompassing biodiversity metrics and pest control observations, are available and should be used for future modelling efforts. Our simulations reveal clear long-term patterns of cause and effect for various combinations of human interventions and agent metrics that would be difficult to envision otherwise. The overarching goal of this model is to demonstrate how this multispecies agroforestry system can sustain and restore soil fertility while simultaneously creating a viable long-term cultivation strategy. Future models will address broader objectives, such as biodiversity restoration and enhanced climate resilience.

Data analysis

The agent-based model presented here is deterministic under fixed parameters and management rules. While individual simulations are deterministic, systematic exploration of the parameter space (varying initial soil conditions, fertilizer regimes, harvest intensity, etc.) allows us to map system behavior across ecologically relevant gradients and identify critical thresholds, optimal management strategies, and emergent patterns. Accordingly, figures and time series represent exact model trajectories rather than statistical averages. Several variables are expressed in dimensionless, scaled units to preserve internal proportionality and causal structure across species and management scenarios. These scaled values should be interpreted comparatively rather than as absolute physical quantities. Error bars are therefore not applicable, as no stochastic sampling or parameter resampling is performed in the simulations reported here.

Results

The temporal structure of the simulation was aligned with the experimental monitoring phases to enable direct comparison with field measurements across equivalent time steps. Each simulation tick corresponds to one week of field time, encompassing annual growth cycles, harvest events, and management interventions such as thinning and pruning. This alignment ensures that emergent patterns—such as changes in SOM, canopy structure, and yield—can be quantitatively compared with observed trends from the empirical system.

The simulated agroforestry network reproduces the main features of the real system's evolution (Comolli et al., 2024, 2025a), capturing both its nonlinear dynamics and characteristic transitions between facilitation- and competition-dominated

phases. Through this calibration, the ABM algorithm provides a dynamic representation of how inter-species interactions, management actions, and feedback loops to the soil jointly drive system-level resilience and productivity.

To maintain focus and conciseness in the main text, detailed descriptions of simulation runs corresponding to low and baseline soil quality conditions are discussed in the Supplementary Results section. These include scenarios initialized with soil indices below 2,000 (*Soil 5*), 3,000 (*Soil 4*), 4,400 (*Soil 3*), and 6,400 (*Soil 2*). The Supplementary Materials presents the full temporal evolution of these systems, highlighting threshold effects, adaptive management responses, and the emergence of positive feedback loops that lead to soil restoration and sustained productivity. Together, these simulations provide the broader context for the higher-quality soil scenarios discussed here in the main *Results*, ensuring continuity between degraded and restored system dynamics.

Simulations with fertility 8100 (Soil 1) as initial conditions

These simulations represent a system established on fully restored soil ('Soil 1'), typically achieved through intensive restoration efforts such as establishing artificial forests with fast-growing species like eucalyptus or conifers. These conditions match those of the implementation and experimental measurements of the multispecies agroforestry trial, spanning ten hectares, described in Comolli et al (Comolli et al., 2024, 2025a). While this higher initial soil quality enables examination of system trajectories attending optimization from favorable initial conditions rather than restoration, our simulations reveal that even these favorable conditions require careful management. Without any reposition, the system cannot maintain itself, as extraction and plant growth exceed the endogenous fertility maintenance capacity. We examine two management scenarios: fixed minimum repositions and adaptive reposition.

Fixed reposition strategy (30%)

Scenario. We simulate the system starting from a fully restored starting condition (soil quality index = 8,100; "Soil 1") with a fixed external reposition set to 30% of the extracted biomass and a 40% harvest rate. Despite high initial fertility supporting robust early growth, soil quality first declines for several years until endogenous SOM accrues enough to flip the system into a positive feedback loop. Figure 1 shows representative spatial snapshots across the 10-year run; Figure 2 tracks soil quality and cumulative harvest over time.

Initial phase (0–3 years). Soil quality drops from "Soil 1" to the "Soil 3" range (≈5,000 units) by 137 weeks (~2.6 years) and remains near that level through year 4 (Figure 2a). Plant growth is still robust during this window (Figure 1a), buoyed by the high starting fertility. Fast-growing trees undergo 50% thinning, but incorporation of biomass into soil lags; early soil gains are driven mainly by external inputs. As trimming and thinning begin to contribute measurable

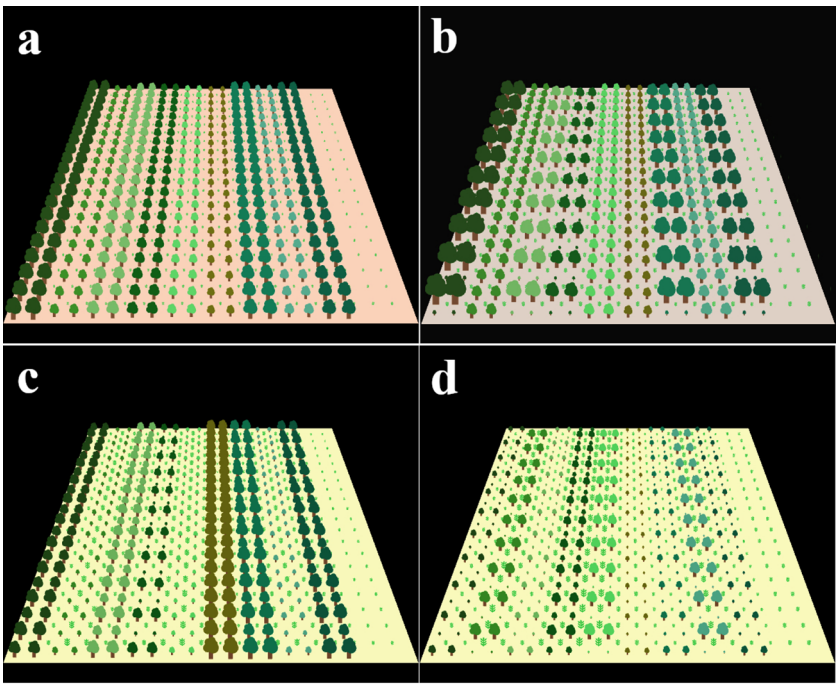


FIGURE 1
Evolution of the simulated agroforestry system over 10 years, starting from a fully restored soil quality index (8,100; "Soil 1"), with 40% harvest intensity and a 30% fixed reposition strategy. **(a)** Early phase (137 weeks; 2 years 4 months): initial growth patterns before thinning. Fast-growing trees are marked for 50% thinning. **(b)** Transition phase (228 weeks; 4 years 5 months): 50% thinning along the lines of fastest growing trees increases SOM locally; biomass production initiates a virtuous cycle as thinning increases local soil organic matter (SOM). **(c)** Mature phase (430 weeks; 8 years 3 months): growing structural heterogeneity as additional thinning, regrowth, and trimming cycles are completed. Ilex paraguariensis plants in the control area (without trees) are smaller than consociated plants along tree rows. **(d)** Final phase (520 weeks; 10 years): configuration at the end of simulation, showing the dynamic mosaic of growth stages and regrowing trees.

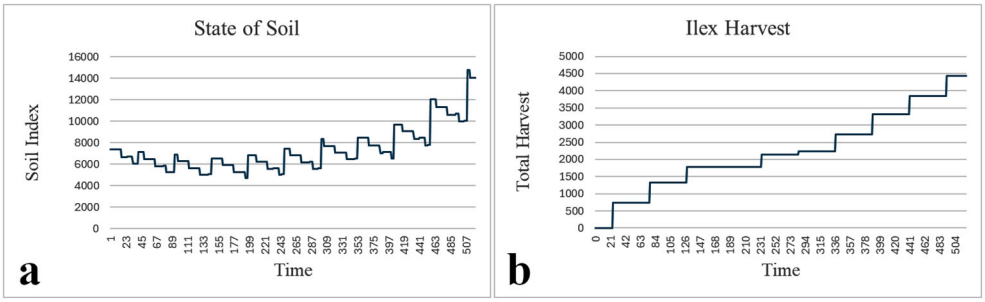


FIGURE 2
Evolution of soil quality and cumulative Ilex paraguariensis harvest under a fixed reposition strategy (dimensionless units). Plots show system dynamics over a 10-year simulation starting with an initial soil quality index of 8,100 and a fixed 30% repositioning strategy. **(a)** Soil quality index (fertility) over time, showing an initial decline followed by recovery and subsequent increase beyond initial conditions. **(b)** Total cumulative *I. paraguariensis* harvest, illustrating reduced increments during the early soil deterioration phase and clear recovery as soil fertility improves. Step size corresponds to variations per harvest cycle.

SOM, the fertilizer-to-harvest ratio declines, and net soil gains stabilize (Figures 3, 4).

Transition phase (3–5 years). By 4 years 5 months (228 weeks), the fastest-growing trees have already undergone 50% thinning and are regenerating (Figure 1b). The slower species will undergo 50% thinning during this period, along the cutting of the remaining 50% of the fastest growing trees. The largest *I. paraguariensis* plants occur between recently thinned tree lines—zones of minimal shading and high SOM input from felled biomass. Conversely, the smallest plants appear in the control rows without trees, where soil improvement is limited. A critical transition occurs as accumulated endogenous SOM and stable external inputs jointly trigger a self-reinforcing positive feedback loop, driving soil fertility above initial values (Figures 1b, 2a, 3, 4). The *I. paraguariensis* harvest, which previously declined during soil depletion, begins a sustained recovery (Figure 2b).

Mature phase (5–10 years). After year five, the system develops increasing structural heterogeneity. Multiple thinning cycles across species generate alternating patches of mature and regenerating trees (Figures 1a–d). The largest *I. paraguariensis* individuals consistently occur near fast-growing species, benefiting from localized SOM enrichment following thinning. The fertilizer-to-harvest ratio declines steadily as soil quality improves (Figure 4), indicating that fertilizer costs represent a diminishing share of harvest value. By the end of the 10-year simulation (520 ticks), soil quality has increased by ~6,000 units—from ~8,000 to ~14,000—and cumulative *I. paraguariensis* harvest reaches ~4,500 units. Across all individuals, sizes exceed those observed in simulations starting from lower soil indices, reflecting a self-sustaining cycle of SOM-driven soil improvement, enhanced growth, and reduced external input dependence.

The combined patterns observed in Figures 3 and 4 reveal how the system transitions from dependence on external fertilizers to a self-reinforcing equilibrium driven by endogenous SOM accumulation. Initially, external inputs dominate the nutrient balance, sustaining productivity while soil reserves are rebuilding. As thinning, trimming, and harvest residues progressively enrich the soil, endogenous SOM becomes the primary driver of fertility gains, leading to a steep rise in soil quality (Figures 3b, 4a). This shift coincides with a marked increase in total biomass production and a sharp decline in the fertilizer-to-harvest ratio (Figure 4b). By year ten, the system operates in a low-input, high-yield regime where most nutrient cycling is internally maintained. The efficiency gain—expressed as declining fertilizer costs relative to total harvest—

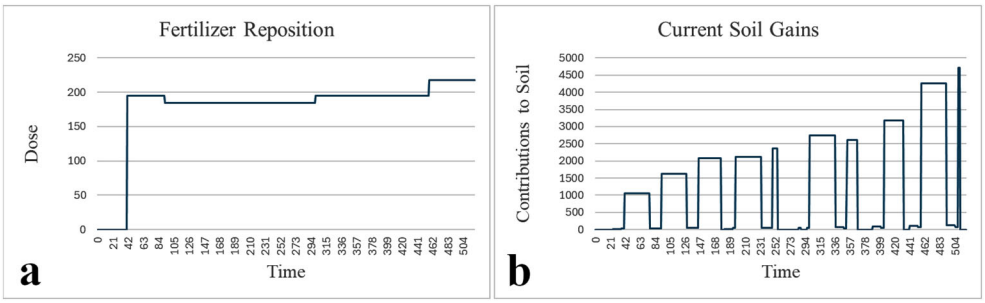


FIGURE 3
Evolution of external inputs and cumulative soil quality gains under fixed repositioning (dimensionless units). Simulation results for an initial soil quality index of 8,100 with a fixed 30% repositioning rate. **(a)** External fertilizer inputs over time. After an initial adjustment step, reposition values stabilize at a steady plateau. **(b)** Cumulative soil quality gains, showing a steep upward trend as synergistic feedback between endogenous SOM production and external reposition drives sustained soil improvement.

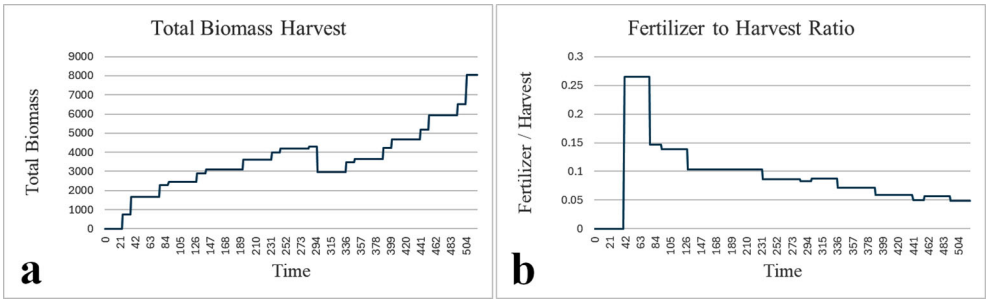


FIGURE 4
Total biomass harvested and fertilizer-to-harvest ratio under fixed repositioning (dimensionless units). Results correspond to the same simulation conditions as Figures 1-3. **(a)** Evolution of total biomass harvested—including *Ilex paraguariensis* and tree components—across the 10-year simulation. **(b)** Ratio of external fertilizer inputs to *I. paraguariensis* harvest, illustrating how rising total biomass reduces the proportional cost of inputs. The system reaches a critical inflection point where enhanced growth and biomass turnover accelerate SOM incorporation, reinforcing a self-sustaining cycle of fertility and productivity.

demonstrates the establishment of a virtuous cycle linking soil restoration, biomass accumulation, and long-term productivity.

Adaptive reposition strategy (25% with feedback)

This scenario examines an adaptive repositioning strategy that begins at 25% of extraction and automatically adjusts inputs in response to harvest feedback. Simulations start from fully restored soil (soil quality index = 8100, Soil 1) with a 40% harvest rate. Similar to the fixed-reposition case, the system initially exhibits a transient decline in fertility before endogenous SOM accumulation and feedback-regulated inputs jointly drive recovery. This gradual buildup initiates a positive feedback loop that elevates soil quality beyond its initial state and sustains higher annual harvest volumes (Figures 5–8). Although the high initial fertility temporarily declines —producing reduced early harvests (Figures 6a, b)—adaptive inputs, continuously calibrated to match extraction (Figure 7), progressively enhance biomass production (Figure 8a). By approximately year five, the cumulative effect establishes a self-reinforcing virtuous cycle

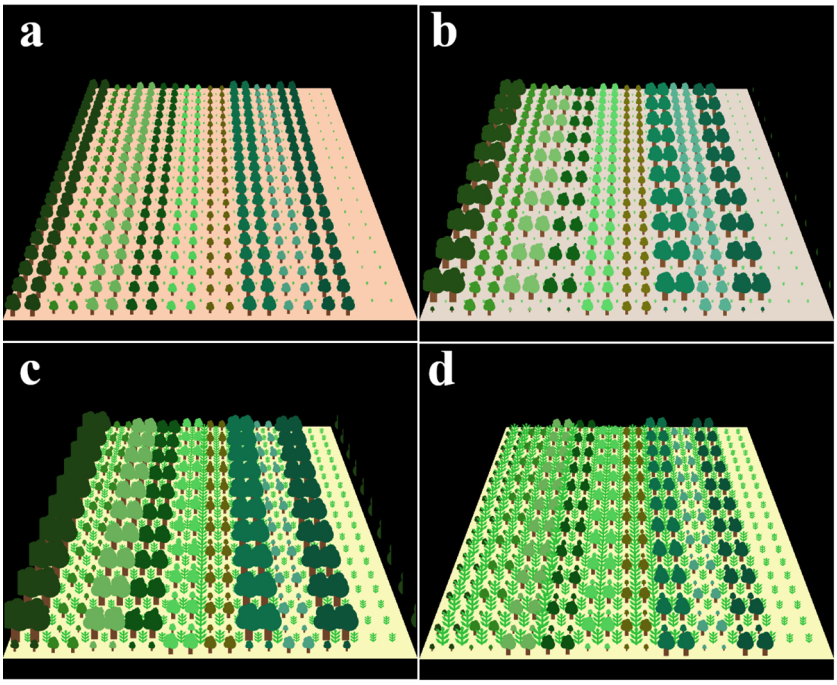


FIGURE 5
Snapshots of agroforestry system evolution over a 10-year simulation under adaptive repositioning. Simulation initialized with a soil quality index of 8100, a 40% harvest intensity, and a 25% adaptive repositioning strategy with self-adjusting feedback. **(a)** Initial phase (132 weeks, 2 years 7 months): early establishment before significant SOM accumulation. **(b)** Transition phase (232 weeks, 4 years 6 months): first thinning cycles completed; tree density reduced, and regrowth initiated. **(c)** Mature phase (440 weeks, 8 years 6 months): increasing heterogeneity as successive thinning cycles advance. *Ilex paraguariensis* plants in the control area (without trees) are smaller than consociated plants along tree rows. **(d)** Final state (520 weeks, 10 years): fully developed mosaic of regrowing trees and variable *I. paraguariensis* plant sizes at system equilibrium; the lines of plants consociated with recently thinned tree lines are significantly larger than plants within the control.

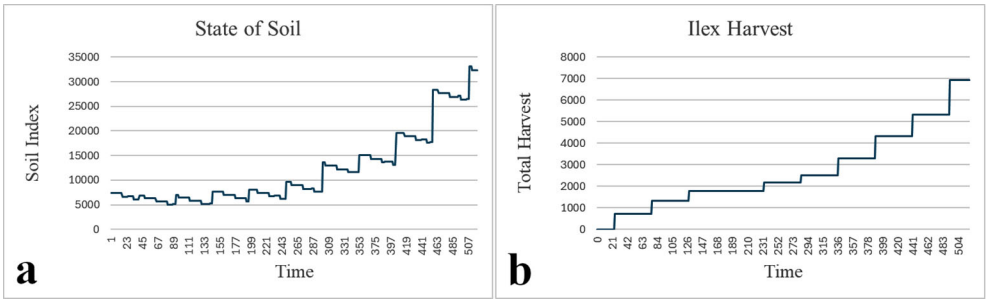


FIGURE 6
Evolution of soil quality and cumulative Ilex paraguariensis harvest under adaptive repositioning (dimensionless units). Simulations start with an initial soil quality index of 8100 and a 25% adaptive repositioning strategy. **(a)** Soil quality dynamics showing an initial decline followed by a steady, smooth recovery driven by feedback-regulated inputs. **(b)** Cumulative *I. paraguariensis* harvest displaying consistent yield growth and reduced inter-annual variability compared to fixed-input scenarios. Step size represents yield increments per harvest cycle.

linking soil improvement, plant growth, and yield stability (Figures 5, 6).

Initial Phase (0–3 years): During the establishment period, soil fertility declines along a controlled trajectory similar to the fixed strategy but with smaller amplitude. The soil index drops to *Soil 3* after about three years (132 ticks; Figures 5a, 6a), yet sequential fertilizer adjustments maintain robust plant growth. The fastest-growing tree species are marked to undergo a first thinning (50%), while *I. paraguariensis* continues to be harvested at reduced but steady increments (Figures 5b, 6b).

Transition Phase (3–5 years): The adaptive strategy produces a markedly superior soil trajectory compared with the fixed-input case, maintaining continuous fertility recovery through optimized feedback control (Figures 6a, 7). Soil quality improves steadily, reflecting a more efficient balance between endogenous and exogenous inputs. Biomass accumulation and harvest stability (Figures 5, 8) respond with a short delay to this improvement, revealing a lagged but coherent coupling between soil restoration and aboveground productivity.

Mature Phase (5–10 years): By the end of the simulation, total harvest reaches approximately 7,000 units—showing substantially stronger annual gains than the fixed-reposition scenario. Cumulative soil recovery approaches 25,000 units from its lowest point, following the most consistent upward trajectory across all simulations. The system exhibits remarkable uniformity in plant size, soil quality distribution, and yield variability, reflecting a stable equilibrium sustained by dynamic coupling between external fertilizers and endogenous SOM contributions (Figure 7). Locally produced SOM oscillates according to its characteristic half-life, generating subtle spatial patterns in *I. paraguariensis* growth; however, these variations are smoother under adaptive control, as feedback regulation dampens the amplitude of soil and growth fluctuations.

Figure 9 summarizes the comparative harvest performance across all consociated tree species, providing the quantitative foundation for model validation and demonstrating the ABM's ability to reproduce observed empirical patterns. Across all simulations starting from Soil 1, systems without repositioning exhibited continuous soil decline, whereas systems with 20–25% repositioning transitioned to increasing soil indices. In the absence of repositioning, soil fertility steadily declines, leading to eventual system collapse. However, even minimal repositioning—approximately 20–25% of extracted nutrients during cyclical harvest and thinning routines—enables the system to evolve

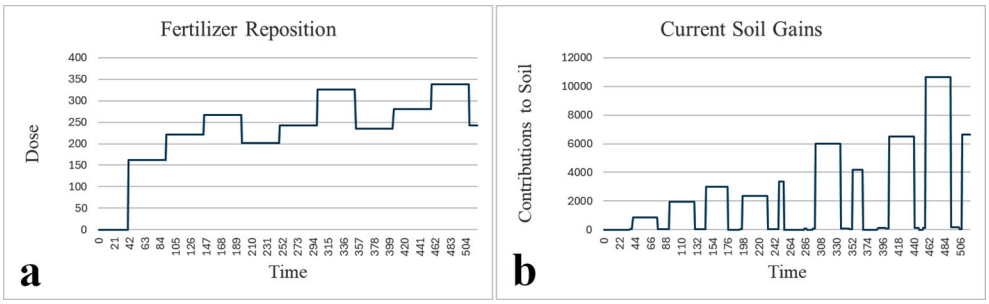


FIGURE 7
Evolution of external inputs and cumulative soil quality gains under adaptive repositioning (dimensionless units). Simulations begin with an initial soil quality index of 8100 and a 25 % adaptive repositioning strategy. **(a)** Temporal dynamics of external fertilizer inputs. After an early adjustment phase, input levels stabilize as feedback control maintains soil fertility. **(b)** Cumulative soil quality gains showing a continuous and accelerating increase over time, driven by the synergistic effect of endogenous SOM production and dynamically regulated external inputs.

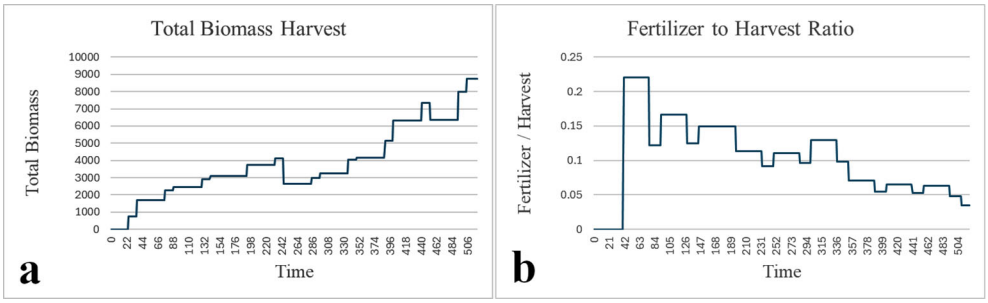


FIGURE 8
Total biomass harvested and external input ratio under adaptive repositioning (dimensionless units). Simulations start from the same initial conditions as in Figures 5-7 (soil index 8100, 40 % harvest, adaptive 25 % reposition). **(a)** Evolution of total biomass harvested (including *I. paraguariensis* and tree components) during the 10-year simulation. **(b)** Ratio of external fertilizer inputs to *I. paraguariensis* harvest. Increasing total biomass production progressively lowers the proportion of fertilizer required per unit yield, reflecting improved resource efficiency. The declining ratio marks the onset of a self-reinforcing feedback phase where harvested biomass contributes to SOM formation and further soil enhancement.

toward a self-sustaining, higher fertility state. In our investigation, while favorable initial soil conditions provide a head start, adaptive nutrient management remains crucial for maintaining productivity and resilience in the long term.

Comparative analysis of management strategies

A quantitative comparison of the two primary management approaches is presented in the Supplementary Materials. This quantitative comparison demonstrates the adaptive strategy's superior performance across several metrics, including higher overall productivity, increased biomass production, faster system recovery, and greater long-term soil restoration, while maintaining comparable harvest stability.

Comparative analysis of harvest yields by species

Our simulations, particularly for the 'Soil 1' initial condition with both fixed minimum and adaptive repositioning strategies, provide illuminating insights into the influence of individual tree species on *I. paraguariensis* harvest yields. As illustrated in Figure 9, distinct patterns emerged, with some tree species supporting higher *I. paraguariensis* harvest yields than the control (no trees), while others resulted in lower cumulative yields.

Notably, the model predicts that Toona, Cañafístola, Petiribi, and Anchico support higher harvest yields, a result consistent with observations from our real-life experimental field system (Comolli et al., 2024) over an 8-year period. This agreement strengthens the model's validity in capturing beneficial inter-species synergies. The case of Kiri in our simulations also coincides with the field system (Comolli et al., 2025b), where it was completely cut down after three years with its biomass contributing significantly to SOM. Our current model does not simulate this specific, dramatic, management intervention for Kiri, but the harvest biomass from this fast-growing species matches this result.

For Lapacho and Grevilea our simulations predict the lowest harvest volumes, which contradict the experimental results. These results are a consequence of the slower growth rate and biomass production for these species within the model. While in the experimental system Araucaria is correlated with the highest harvest volume (Comolli et al., 2024), our simulations predict a median harvest average. These contrasts suggest possible, significant and still uncharacterized synergies. Araucaria is known to have significant synergies with *I.* paraguariensis (Capellari et al., 2017;

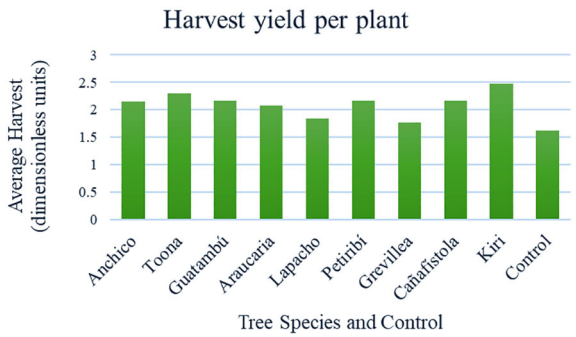


FIGURE 9
Total cumulative Ilex paraguariensis *harvest per plant by consociated tree species (dimensionless scaled units).* Each bar represents the simulated cumulative harvest per plant, averaged per sub-lot, over a 10-year simulation period. Simulations begin with an initial soil quality index of 8100 under an adaptive 20 % repositioning strategy. Values are expressed in dimensionless harvest units for relative comparison among consociated species and do not denote absolute mass (e.g., kg plant^{-1} or t ha^{-1}).

Fernandez et al., 1997; Day et al., 2011; Montagnini et al., 2011, 2006), perhaps due to mycorrhiza or to enrichment of key elements, which are outside the attributes included in our simulations. Guatambu produces high volumes of leaves and likely contributes to PAR reduction more than we account for in the model.

The remaining tree species in our simulations, which also resulted in slightly lower cumulative *I. paraguariensis* harvest, are consistent with field experiment outcomes. This pattern is primarily attributed to the complex interplay between shade competition and localized soil improvements from tree management, which collectively balance out to these observed yield differentials.

Discussion

We developed a computational Agent-Based Model (ABM) simulating 778 perennial individuals calibrated against a decade of measurements from a long-term multispecies agroforestry system. Using empirically derived allometric parameters and management rules, the model reproduces patterns in total harvest outcomes per consociated species, validating its predictive realism. These results demonstrate the value of ABMs as design and planning tools for agroforestry, landscape restoration, and climate-adaptive agriculture.

Comparative context and contribution

The increasing adoption of ABMs in ecology reflects their capacity to capture feedbacks, thresholds, and emergent properties that are difficult to represent with reductionist approaches. Conventional agricultural models—whether empirical, econometric, or differential-equation based—often assume homogeneous agents and linear responses, limiting their ability to describe nonlinear, spatially explicit dynamics typical of real agroecosystems (Dupraz et al., 2019; Rahman et al., 2023). In contrast, ABMs represent individual organisms and management units as autonomous agents, allowing local interactions to generate emergent, system-level behavior (Grimm et al., 2005, 2010; Railsback and Grimm, 2012; Spies, 2017).

Within agroforestry research, relatively few ABM studies have addressed multispecies interactions over long temporal horizons. Previous work has often emphasized human–environment decision dynamics (Berger and Schreinemachers, 2011; Burgess et al., 2019) or landscape/policy applications (Torralba et al., 2018; Liu et al., 2021; Page et al., 2013; Johnson and Salemi, 2022), and many approaches simplify crop–tree biophysical coupling (Dupraz et al., 2019; Soualihou et al., 2021; Millington and Wainwright, 2016). Our model advances this literature by directly integrating species-specific growth rates, canopy shading, and soil organic matter (SOM) dynamics measured in a long-term experimental system (Comolli et al., 2024, 2025a).

Across simulations, positive feedback loops emerge when biomass generated through harvest, thinning, and pruning is returned to the soil as SOM, increasing fertility and enhancing subsequent plant growth. This biomass–SOM–fertility coupling progressively stabilizes yields and reduces dependence on external inputs. These dynamics parallel field observations of soil recovery and yield maintenance in long-term agroforestry systems (Montagnini et al., 2006; Day et al., 2011; Comolli et al., 2023; Comolli et al., 2025b; Comolli et al., 2024, 2025a) and align with theoretical descriptions of agroecosystems as complex adaptive systems governed by reinforcing feedbacks (Levin, 1998; Holling, 2001; Paterno et al., 2024).

Model validation and ecological realism

Our agent-based model of an integrated multispecies agroforestry system demonstrates how computational approaches can elucidate complex ecological interactions in managed production landscapes. Grounding the model in empirically measured allometric parameters—including species-specific growth rates and photosynthetically active radiation (PAR)—ensures that relative plant sizes, competition intensity, and canopy interactions scale realistically. This empirical calibration enables faithful simulation of biomass production, management interventions, and their coupled effects on soil organic matter (SOM) dynamics, which underpin the model's predictive relevance and real-world applicability.

Although soil quality is represented using dimensionless indices rather than absolute physical units, the scaling of these indices is explicitly designed to reflect observed system behavior across degraded, intermediate, and restored soil states. This abstraction allows the model to highlight emergent patterns, nonlinear responses, and threshold effects that may be difficult to isolate in purely empirical studies. As with other agent-based and process-based approaches, this level of abstraction is not a limitation but a methodological choice that facilitates the identification of key knowledge gaps, the generation of quantitative hypotheses for field testing, and the prioritization of promising system designs for experimental evaluation (Grimm et al., 2005; Railsback and Grimm, 2012).

The model captures essential spatial dynamics by representing local interactions such as shade competition, differential SOM inputs from tree management, and species-specific effects on neighboring Ilex paraguariensis plants and their harvest yields. Importantly, simulations reproduce counterintuitive field observations—such as larger I. paraguariensis individuals occurring near fast-growing tree species rather than in full-sun control rows—a pattern documented empirically (Comolli et al., 2025b) but difficult to anticipate without computational modelling.

At the same time, the simulations expose clear knowledge gaps. While the model correctly reproduces relative yield advantages for several tree species, it underestimates the positive effects of Lapacho, Grevillea, and Araucaria observed in the field. This discrepancy points to additional ecological mechanisms not yet explicitly represented—such as phosphorus mobilization, mycorrhizal associations, or facilitative microclimatic effects—and highlights concrete directions for targeted empirical and modelling follow-up.

Critical thresholds and system dynamics

The simulations indicate that long-term sustainability in multispecies agroforestry systems depends on the presence of

critical thresholds in soil fertility and management intensity. Below these thresholds, productivity declines and self-reinforcing soil–plant feedbacks fail to establish; above them, the system converges toward a resilient equilibrium characterized by sustained biomass production and improving soil quality. In particular, the model identifies an inflection zone around a soil quality index of approximately 3,000–4,000 (corresponding to "Soil 4"–"Soil 3" conditions), below which continuous external inputs are insufficient to prevent long-term degradation.

Once this threshold is exceeded—either through prior restoration or adequate early fertilization—the system transitions to a regime dominated by endogenous SOM accumulation. In this regime, biomass inputs from harvest residues, thinning, and pruning amplify soil fertility gains, generating a positive feedback loop between productivity and soil quality. These dynamics suggest the possibility of developing empirically informed heuristics to guide site selection, initial restoration efforts, and early-stage management decisions.

Adaptive management strategies play a critical role in crossing and stabilizing these thresholds. In the simulations, feedback-regulated fertilization accelerates recovery by increasing inputs during early depletion phases and reducing them as endogenous SOM-driven fertility gains accumulate. This behavior mirrors resilience mechanisms observed in natural and managed ecosystems, where stability emerges from the balance between disturbance and recovery rates (Levin, 1998; Holling, 2001).

The model also exhibits hysteresis-like dynamics: once soil fertility falls below the viability threshold, restoring previous input levels is insufficient to recover productivity. Instead, a substantial initial investment in soil restoration is required to re-enter the self-sustaining regime. This result underscores the ecological and economic importance of preventing soil degradation beyond critical limits, as recovery costs and times increase sharply once thresholds are crossed.

Taken together, these threshold behaviors provide a conceptual bridge between empirical soil science and complex systems theory. They indicate that sustainable agroforestry systems operate within a bounded region of parameter space where soil fertility, biodiversity, and productivity co-evolve under adaptive feedback. Managing these thresholds thus emerges as a central design principle for both model-based planning and field implementation of resilient, long-lived agroecosystems.

Management implications and comparative strategies

Our simulations show that agroforestry performance is governed not only by input levels but by the timing and adaptability of management interventions. Across all evaluated metrics, adaptive repositioning—initiated at 25% of extraction and regulated by feedback—consistently outperforms fixed strategies in long-term productivity, soil restoration, and system recovery.

Adaptive management shortens the vulnerable establishment phase, enabling the system to recover from early soil depletion more than twice as fast as fixed-input strategies. Although fixed repositioning produces smoother short-term harvest trajectories, this apparent stability comes at the cost of lower cumulative productivity and slower soil recovery. In contrast, adaptive management accepts moderate temporal oscillations in exchange for faster stabilization, higher total biomass production, and substantially greater long-term yields.

These results reveal a fundamental trade-off between short-term input efficiency and long-term ecological resilience. Fixed strategies maximize harvest per unit of fertilizer, whereas adaptive strategies maximize total productivity, soil restoration, and system persistence. From a management perspective, the simulations suggest that responsiveness to system feedback—rather than static optimization—offers a more robust pathway toward sustainable agroforestry outcomes.

Importantly, the adaptive approach translates directly into actionable guidance: real-time adjustment of nutrient inputs during early depletion phases, followed by gradual reduction as endogenous SOM accumulation strengthens system fertility. Such feedback-driven strategies provide a practical framework for improving both economic viability and ecological performance in complex perennial agroecosystems.

System resilience and sustainability

A central emergent property of the model is the formation of self-reinforcing feedback loops linking biomass production, soil organic matter (SOM) accumulation, and plant growth. Through harvesting, thinning, and pruning, biomass is returned to the soil, increasing fertility and accelerating subsequent growth. Over time, this endogenous SOM production becomes the dominant driver of soil improvement, progressively reducing reliance on external inputs.

The inclusion of SOM decay—modelled with a finite half-life—introduces realistic temporal dynamics that prevent unrealistically smooth system trajectories. This turnover generates spatial and temporal heterogeneity in soil quality, which in turn supports resilience by providing multiple recovery pathways following disturbance. Rather than undermining stability, these controlled fluctuations contribute to long-term persistence by preventing nutrient lock-in and localized depletion, in agreement with natural systems (Pinho et al., 2012; Liu et al., 2018).

Together, these dynamics illustrate how sustainability in agroforestry systems arises not from static equilibria, but from adaptive cycling between growth, disturbance, and recovery. The model demonstrates that resilience emerges when management practices reinforce—rather than suppress—these natural feedbacks, allowing productivity and soil quality to co-evolve within a stable operational envelope.

Reciprocal species interactions and bidirectional feedbacks

A central implication of our results is that the focal crop, *Ilex paraguariensis*, does not merely respond to its associated tree species but actively reshapes their collective productive environment through feedbacks mediated by harvest, pruning,

and soil organic matter (SOM) dynamics. Tree species modify light availability, microclimate, and nutrient inputs to the crop, while the crop's biomass extraction and residue return—together with tree biomass converted to SOM through crop-driven management—reciprocally reorganize soil fertility gradients that govern tree regrowth and competitive balance. Productivity in this system therefore emerges as a self-reinforcing dynamic, a network property, rather than as an additive contribution of independent species. This explicitly demonstrates that agroforestry yield cannot be attributed to single-species performance alone, but instead to the structure of inter-species coupling and management-mediated feedback. Agroforestry systems function as mutualistic collectives rather than hierarchical arrangements. The model provides a computational framework for exploring how these reciprocal dependencies scale up to generate system-level properties like resilience, stability, and sustained productivity. Future empirical work should explicitly test these bidirectional couplings through controlled variation of tree and *I. paraguariensis* management regimes. The model situates agroforestry within the broader field of complex systems science, bridging empirical ecology, systems modelling, and sustainability policy.

Model limitations and future directions

While the present ABM captures essential biophysical feedbacks and emergent properties of multispecies agroforestry systems, it necessarily simplifies several ecological processes. The model does not yet explicitly represent microbial communities, mycorrhizal networks, faunal interactions, or detailed biogeochemical fluxes, all of which are known to influence nutrient cycling and ecosystem resilience. Future extensions could incorporate climate variability, pest–predator dynamics, and socio-economic feedbacks to enhance realism and broaden applicability across agroecological contexts. Importantly, the current formulation is intentionally minimal and empirically grounded, allowing it to expose causal structure and knowledge gaps that can guide targeted experimental and modelling efforts. Beyond its immediate relevance to yerba mate–based agroforestry, the framework developed here can be adapted to other multispecies agricultural systems and tree planting projects (Francini et al., 2024; Schwaab et al., 2021; Paterno et al., 2024; Johnson and Salemi, 2022; Spies, 2017).

Conclusion

This study shows that an empirically calibrated agent-based model can reproduce and explain key dynamics observed in a long-term multispecies agroforestry system. Using measured allometric parameters and documented management practices, the model accurately captures species-specific differences in *I. paraguariensis* harvest outcomes, soil organic matter (SOM) trajectories, and system recovery under contrasting management strategies.

Across simulations, adaptive nutrient repositioning consistently outperforms fixed-input strategies, yielding higher cumulative harvests, faster recovery from early soil depletion, and substantially greater long-term soil restoration. The model identifies a critical soil fertility threshold below which the system fails to recover and demonstrates that feedback-regulated management enables the system to cross this threshold efficiently, initiating a self-reinforcing cycle of biomass production, SOM accumulation, and yield stabilization.

Data availability statement

The complete simulation model (*EnsayoF_2.0.nlogo*) is provided in the Supplementary Materials and publicly available at https://github.com/lrcomolli/ABM-of-Inter-Species-Interactions-in-Agroforestry. Running this file in NetLogo (version 6.4.0, Northwestern University, Evanston, IL) reproduces all time series, plots, and figures presented in this article. Because the Agent-Based Model is deterministic, identical input parameters yield identical results; thus, the simulation code itself constitutes the complete, reproducible dataset.

Author contributions

LC: Visualization, Resources, Funding acquisition, Formal analysis, Validation, Project administration, Writing – original draft, Data curation, Supervision, Investigation, Writing – review & editing, Software, Conceptualization, Methodology. HF: Supervision, Data curation, Formal analysis, Conceptualization, Validation, Writing – review & editing.

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Conflict of interest

LC is president of El Rocio SA, an agricultural producer of yerba mate whose entire production is allocated as undifferentiated raw

green crop to the cooperative Productores Yerba Mate SCL. https://www.pipore.com.ar/.

The remaining author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The author LC declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fagro.2026.1657465/full#supplementary-material

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