RESEARCH PAPER

Using spatially-explicit plant competition models to optimise crop productivity in intercropped systems

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Abstract

Intercropping, by capitalizing on positive biodiversity−productivity relationships, represents a promising option to increase agricultural sustainability. However, the complexity and context-dependency of plant−plant interactions can make it challenging for farmers to find suitable crop combinations. Furthermore, intercropping is usually implemented with standard inter-row spacing and plant densities based on monoculture practices, which might not be the ideal configuration to maximize yield.

Here we present a spatially-explicit yield analysis method based on plant ecological interaction models that allowed to optimize crop species combinations and spatial configurations for maximal yield in intercropped systems. We tested this method with three crop species, namely oat, lupine, and camelina. In a first step, field experiments in which crop density and adjacent crop type were varied provided us with indications on which species would compete more with each other. The results showed us that oat and camelina strongly competed with each other. In addition, the distance experiments allowed us to understand how the changes in yield associated with the presence of neighbors vary with distance. This allowed us to find the sets of parameters (identity of neighbors, sowing density, distances between individuals) that optimise intercrop yield (measured as Land Equivalent Ratio [LER]) for the three considered species. Specifically, we show that alternating rows of species led to higher LERs than a homogeneous species mixing, and that 3-species combinations are not necessarily more performant than the best 2-species combinations. In addition, we show that increasing the density of oat is generally beneficial for LER, while increasing the density of lupine is not.

By modelling crop yield from simple and reproducible density and distance experiments, our results allow to optimize crop mixtures in terms of species combinations and spatial configurations, for maximal crop yield.

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Introduction

Intercropping is the agricultural practice of growing more than two crop species on the same field during a significant part of their life cycle (Vandermeer, 1992). By increasing crop diversity and consequently taking advantage of the positive relationship between biodiversity and ecosystem

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functioning (Brooker et al., 2021), crop mixtures have been recognized as a promising way to make agriculture more sustainable (Brooker et al., 2016; Martin-Guay et al., 2018; Tamburini et al., 2020). The benefits of intercropping for crop yield and various ecosystem services, such as nutrient cycling (Andersen et al., 2005), weed control (Ann Bybee-Finley et al., 2017), enhanced pollination (Montoya et al., 2020) or soil microbial diversity (Stefan et al., 2021), have been widely demonstrated (Bedoussac et al., 2015; Brooker et al., 2015; Tilman et al., 2002), with for instance increases in overall yield of up to 33% in intercropped systems in comparison to monocultures (Li et al., 2020).

In monospecific crop stands, sowing densities and intra- and inter-row distances are generally optimized to maximize population performance at the field scale (Weiner, 2017). Numerous studies have demonstrated that there is a well-known trade-off between optimal individual performance and optimal population performance in monocrop systems (Anten & Vermeulen, 2016; Denison, 2012). In particular, if row spacing is large, plants can access light, nutrients and space more easily (Jesch et al., 2018), which generally increases individual yield (Flénet et al., 1996), but also allows weeds to prosper (Fahad et al., 2015; Su et al., 2018). In contrast, if the row spacing distance is smaller, the increase in plant density might reduce individual yield but suppresses weeds and potentially increases population yield at the field scale (Weiner, 2017). Intercropped systems add a layer of complexity to this problem, as the goal might not only be to maximize population level yield, but also community (i.e. multi-species) level yield. In monocultures, optimal sowing densities and intra- and interrow distances are known to vary among species; for instance, maize has a standard sowing density of around 7.5 plants m^{-2} with a standard inter-row distance of approx. 0.75 m (Testa et al., 2016), while wheat, a smaller plant, has a standard sowing density of around 400 plants m^{-2} with a standard inter-row distance of approx. 12 cm (Olsen et al., 2006). Furthermore, interspecific interactions differ from intra-specific interactions; in particular, plant competition literature suggests that intraspecific competition is generally higher than interspecific competition, i.e. plants compete more strongly with individuals from the same species than with individuals from another species (Adler et al., 2018; Chesson, 2000). These elements suggest that optimal spacing might vary in an intercrop compared to a monocrop. However, there is little research on spatial configurations in intercrops, particularly when more than two species are considered. For instance, it remains unclear whether it would be more efficient for community-level yield to mix species as much as possible rather than keeping them in lines, as is often the case in intercropping systems due to practical constraints for mechanical sowing (Cheriere et al., 2020; Galanopoulou et al., 2019).

The ecological theory of coexistence suggests that interactions between species, and competitive interactions in particular, are core drivers of individual-, population- and community-level fitness (Chesson, 2000; Mayfield & Stouffer, 2017). Typically, individual-based growth models describe plant fitness as dependent on plant interaction intensity and density of surrounding individuals (Chesson, 1994; Hart et al., 2018). Plant interaction intensity between two individuals further depends on the identity of the two individuals, as well as the distance between them (Chesson, 1994; Purves & Law, 2002). Therefore, this framework allows to infer individual productivity based on the identity, density and distance of the surrounding plants.

In this project, we used this theory to predict optimal sowing patterns in intercropping systems. More specifically, we developed a spatially-explicit model of crop productivity based on the identity and abundance of an individual's neighbors and the distance between them. We used ecological interaction models based on density and distance to quantify the competitive abilities of the considered crops, and how these competition coefficients vary with distance (Hart et al., 2018; Vandermeer, 1986; Weiner et al., 2001). This model allowed us to find the spatial arrangement that maximizes either population-level yield, i.e. crop yield for each intercropped species, or community-level yield, i.e. the combined yield of all the species forming the intercrop. The latter can be expressed relative to the expected yield based on the corresponding monoculture yields using the Land Equivalent Ratio (LER). We focused on three species in this study, namely one cereal, oat (*Avena sativa),* one legume, lupine (*Lupinus angustifolius)*, and one Brassicaceae, camelina (*Camelina sativa).* We chose a cereal and a legume, because cereal-legume intercrops are generally very efficient combinations in intercropping due to complementary nitrogen acquisition strategies (Hauggaard-Nielsen et al., 2010). In contrast, intercrops with non-legumes are much less studied. In this case, we chose a member of the Brassicaceae family, which shows several promising aspects for successful intercropping (Engbersen et al. 2020), such as allelopathic activity (Engbersen et al., 2021; Rehman et al., 2019). By modelling crop yield from simple density and distance experiments, this research offers an easy way to optimize crop combinations and sowing patterns for minimal competitive interactions and maximal crop yield.

Materials and methods

Study site

The density and distance experiments took place in an outdoor experimental garden at the Aprisco de Las Corchuelas research station (39.8133 N, 6.0003 W, 350 m a.s.l.) in Torrejón el Rubio, Cáceres, Spain. The experimental garden consisted of 170 square boxes − or plots − of 0.25 m^2 with a depth of 40 cm. Beneath 40 cm the boxes were open, allowing unlimited root growth in the underlying soil. The boxes were embedded into larger beds of 10×1 m^2. Inside a bed, plots were separated from each other by metal frames.

Each box was filled down to 30 cm with standard, not enriched, agricultural soil coming from the local region. This soil was composed of 78% sand, 20% silt, and 2% clay, and contained 0.05% nitrogen, 0.5% carbon, and 253 mg total P/kg. The mean pH was 6.30.

The experimental garden was irrigated during the growing season in order to assure survival of the crops during drought periods. Irrigation was automated using soil moisture sensors (PlantCare Ltd., Switzerland); whenever a set dry threshold was reached, irrigation started and added water up to the set target value. During plant germination and establishment, i.e. until two months after sowing, the irrigation was configured for a dry threshold of soil moisture of 40% of field capacity, with a target of 60% of field capacity. After plants were properly established, irrigation was reduced to a dry threshold of 17% of field capacity, with a target of 25% of field capacity.

Crop species

We used three crop species belonging to three different phylogenetic groups with varying functional characteristics: *Avena sativa* (oat, cereal), *Lupinus angustifolius* (lupine, legume) and *Camelina sativa* (camelina, Brassicaceae). We chose these species because they are representative of three large groups of crops currently used in agriculture in Europe, namely cereals, legumes, and Brassicaceae. Cereals and legumes are commonly used in crop mixtures due to complementary use of nitrogen and facilitation in phosphorus uptake (Engbersen et al., 2021). Oat is a grass that usually reaches 70 cm in height, with a mean mass per seed of 0.024 g (Chen et al., 2020). Cereals are furthermore known to be strong competitors for soil nitrogen and are characterized by a high growth rate at early stages (Andrew et al., 2015). Lupine is a legume that grows to an average height of 55 cm, with a mean mass per seed of 0.16 g (Chen et al., 2020). As a legume, it is able to fix atmospheric N_2 and can also facilitate P mobilization by releasing carboxylates into

the rhizosphere (L. Li et al., 2003). Finally, camelina is a Brassicaceae, which generally grows to 50 cm with an average mass per seed of 0.00092 g (Chen et al., 2020). Furthermore, Brassicaceae are known to possess allelopathic activity, which can be beneficial to manage pests and diseases or even promote plant growth (Engbersen et al., 2021).

Interaction experiments

Two hypotheses were tested (Fig. 1): (A) the effect of increasing number and thus density of surrounding neighboring plants on the yield of a focal individual plant (with a solitary individual as a control); (B) the effect of increasing distance of eight neighboring plants on the yield of the focal individual plant. We compared results for both conspecific and heterospecific neighboring plants.

Density experiments (Fig. 1A). The density experiments consisted of one focal plant surrounded by none, one, two, four or eight neighboring individuals, either conspecific (i.e. of the same species) or heterospecific (i.e. of a different species). Neighbors were all planted at the same distance from the focal individual (8 centimeters). We chose this distance as it is the smallest of the standard between-row distances used for cereals (Boström et al., 2012). We measured yield of the focal plant at maturity.

Distance experiments (Fig. 1B). Distance experiments consisted of one focal individual surrounded by eight individuals, either conspecific or heterospecific, placed at four different distances from the focal (5, 8, 12 or 20 cm). We chose these distances to have both smaller and larger distances than the standard between-row distance used in the density experiment, and to accommodate the space constraints of the experimental beds. We measured yield of the focal plant at maturity.

Test communities (Appendix A:Fig.1). In order to validate the performance of our models, we set up test communities in similar beds adjacent to the previously described
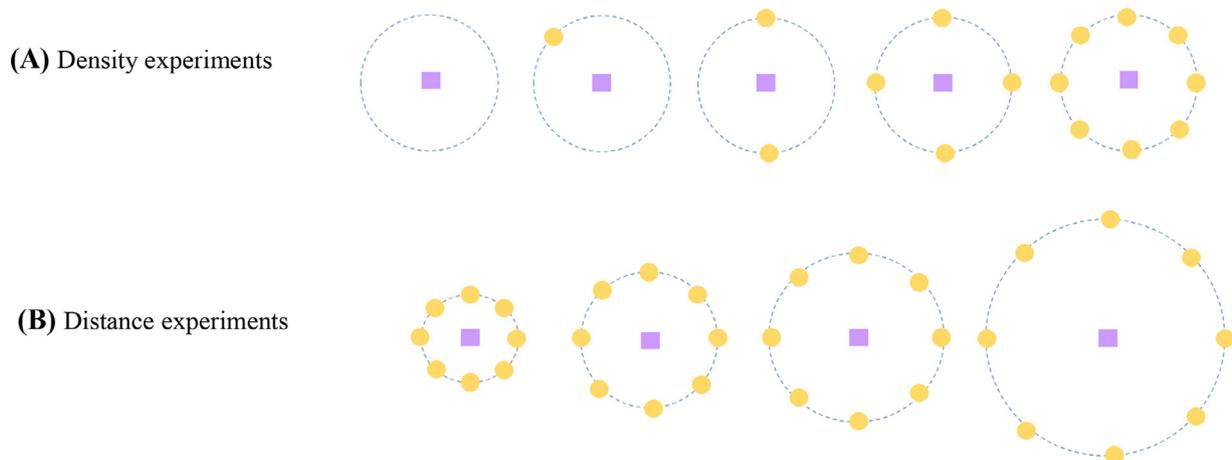
Fig. 1. Schematic representations of the density (A) and distance (B) experiments, with a heterospecific pair of species.

experiment, during the same growing period. These test communities consisted of (i) row alternations of 2 and 3 species with the same plant densities per species and with 8 cm row spacing, (ii) row alternations of 2 and 3 species with varying plant densities per species and with 8 cm row spacing, (iii) homogeneous mixing of 2 and 3 species with 8 cm within- and between-row spacing, and (iv) random arrangements of 3 species with 8 cm within- and between-row spacing (as illustrated in Appendix A:Fig.1). All the possible combinations of two species were planted (i.e. oat-lupine, oat-camelina, and camelina-lupine). In the plots with the same plant densities, all species had a density of 150 individuals.m^{-2}. In the varying densities plots, we kept lupine with 150 individuals m^{-2}, doubled the density of oat (300 individuals.m^{-2}), and tripled the density of camelina (450 individuals.m^{-2}), in order to get closer to field sowing densities in monocultures (i.e. 160 seeds.m^{-2} for lupine, 400 seeds.m^{-2} for oat, and 592 seeds.m^{-2} for camelina (Stefan et al., 2021).

We replicated the density, distance and test experiments two times and the single plant plots three times. Plots were fully randomized within and among the beds, with the single plots and the test plots separated from the density and distance plots in order to avoid potential shading of the single individuals. Sowing was conducted by hand on the 2nd and 3rd of February 2019. Germination was evaluated two weeks after sowing and missing individuals were then resown. After that, the number of individuals and focal plant growth were evaluated every week. Lupine individuals had a particularly low germination rate, due to pest presence. We therefore applied a systemic insecticide (Epik, SIPCAM INAGRA, S.A. [acetamiprid 20%]) three times on all the plots in order to allow germination and growth of the lupine individuals.

Until they reached the two-leaves stage, the dead lupine focal individuals that suffered obvious pest attacks (i.e. 6 out of 48) were replaced using a pool of extra individuals sown at the beginning of the experiment in a separate bed. After this, considering the size and phenological stage of the plants, replacing and transplanting focal individuals was stopped. Dead neighboring plants were still replaced using individuals from the extra pool. However, from May onwards, due to the large root system of the plants, transplanting individuals had a very low success rate. Therefore, a neighboring individual missing for more than half of the experiment was not taken into account for the final number of neighbors.

All plots were manually weeded weekly.

Data collection. Harvest was conducted manually in June − i.e. between 124 and 138 days after sowing − when the seeds of the focal plant species were mature. Aboveground biomass and grain yield of the focal plant was determined in each plot. Plants were clipped right above the soil surface, the focal individual was separated from the neighbors and seeds were separated from the vegetative parts. In the test communities, plants were sorted by species, and seeds were

separated from the vegetative parts. Seeds were threshed, sun-dried for five days and then weighed, while vegetative biomass was weighed after drying in an oven at 80°C for 72 h.

Data analyses

Productivity models and interaction coefficients

To describe the productivity of the focal plant, we used the Beverton-Holt model, which is used to describe annual plant competitive population dynamics in the field (Beverton & Holt, 2012; Hart et al., 2018):

$$Y_{A_{i,n}} = \frac{Y_{i,\ single}}{1 + \sum_{j=1}^{S} \alpha_{i,j} N_j} \tag{1}$$

where $Y_{A_{i,n}}$ is the productivity (often referred to as fecundity in the plant coexistence framework) (in grams) of the nth focal individual $A_{i,n}$ of species i in the presence of a specified set of neighbors; $Y_{i,\ single}$ is the intrinsic productivity (i.e. in the absence of competitors) (in grams) of an individual of species i; for $i \neq j$, $\alpha_{i,j}$ is the interspecific interaction coefficient that represents the direct impact (positive or negative) of species j on the focal individual of species i; N_j is the abundance of species j; and the summation sign indicates that the sum is taken of all species (S) surrounding the focal individual. If $N_i > 0$, $\alpha_{i,i}$ is included in the sum and therefore represents intraspecific competition.

α dependency on distance. Interaction coefficients have been shown to be strongly dependent on interplant distance; that is, as the interplant distance increases, the effect of competition (or facilitation) is expected to decrease. Therefore, the interaction coefficients were calculated as follows (Vandermeer, 1984, 1986):

$$\alpha_{i,j} = y_{i,j} \times distance_{A_{i,n}A_{j,m}}^{-z_{i,j}} \tag{2}$$

where $distance_{A_{i,n}A_{j,m}}$ is the distance in cm between the nth individual $A_{i,n}$ from species i and the mth individual $A_{j,m}$ from species j; $y_{i,j}$ is a constant representing the intensity of the interaction effect between species i and j, and $z_{i,j}$ a constant representing the rate at which that effect decreases with increasing interplant distance.

When combining Eqs. (1) and (2), we obtain the following spatially-explicit plant productivity model (see Appendix A:Fig. 2) for a schematic representation):

$$Y_{A_{i,n}} = \frac{Y_{i,\ single}}{1 + \sum_{j=1}^{S} \sum_{k=1}^{N_j} y_{i,j} \times distance_{A_{i,n}A_{j,k}}^{-z_{i,j}}} \tag{3}$$

The productivity − measured as grain yield − of species growing in isolation ($Y_{i,\ single}$) was determined by taking the average grain yield (in grams) of the three single individuals per species. Then, we used non-linear least squares (nls) models with the *stats* package in R (R Core Team, 2019) to fit the Eq. (3) to the grain yield data (in grams) of the focal
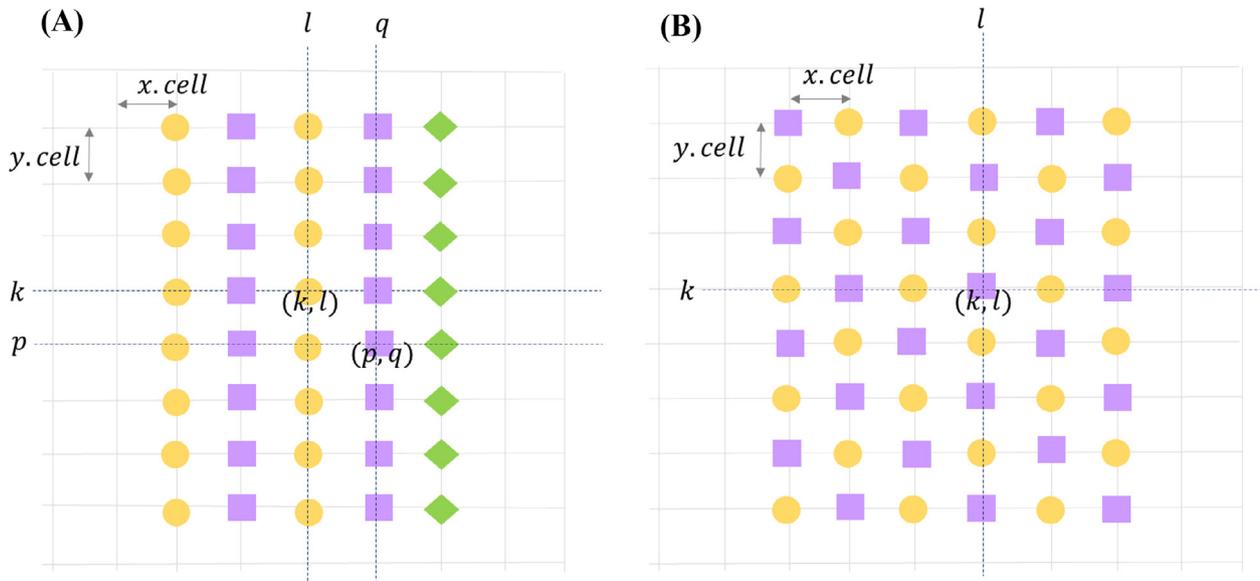
Fig. 2. Example of plant matrices showing a row configuration with three species (A) and a homogeneous mixture with two species (B). *(k,l)* designate the coordinates of an individual in the matrix; *x.cell* and *y.cell* represent the inter-column and inter-row distance.

individuals from the density and distance experiments to determine the y and z coefficients for each conspecific and heterospecific pairwise combination of species. Starting values for the nls models were defined by first fitting a nls Levenberg-Marquardt model (nlsLM, *minpack.lm* package) and reusing the obtained parameters as starting values for the nls model.

Model improvement with an intra-specific higher order interaction term. In cases where the fit of the model was poor ($R^2 < 0.50$) (Appendix A:Table 2), we tried adding the intra-specific second order interaction term $\beta_{ijj} \frac{N_j(N_j-1)}{2}$ to the denominator (Mayfield & Stouffer, 2017) and kept it if this term improved the fit of the model to the data points. This term represents the intraspecific crowding effect which occurs among N individuals of species j on the focal individual of species i, with the strengths of these effects given by β_{ijj}.

Species-level yield and LER simulations

We used the previously-described model in a spatially-explicit approach to calculate the yield per species at the field scale. In this study we consider up to three species, referred to in this example as A, B and C. For example, consider a matrix a of dimension $n \times m$ of individuals A, B and C (see example in Fig. 2). Each individual is defined by its position (k,l) in the matrix, as well as by its species identity value $a[k,l]$. In a first step, for each individual on location (k,l), we calculated its distances to every other individual at location (p,q), with p and q ranging from 1 to n and 1 to m, respectively, using the Euclidian distance $\sqrt{\left((q-l) \times x.cell\right)^2 - \left((p-k) \times y.cell\right)^2}$, where $x.cell$ and $y.cell$ represent the distance between the rows and

columns of the matrix a (Fig. 2). Then, for the individual (k, l), we selected all the neighboring individuals satisfied the condition that their distance to (k,l) was smaller than a predefined distance $(d.lim)$. Among the selected neighbors, we further selected only the eight closest neighbors − the Moore neighborhood (cf. Yitbarek & Vandermeer, 2017) − that were directly connected to individual *(k,l)* (i.e. without any other individual in the straight line between them and (k,l)). We chose to select these eight closest neighbors as including individuals further away did not improve the fit of our model (see section 2.4.3). Based on these selected neighbors, we calculated the yield of individual (k,l) using Eq. (3). This process was repeated for every individual in the plant matrix a. Finally, we summed the yield of each species; to avoid any edge effect at the boundary of the matrix, we only considered individuals that were not affected by the matrix boundaries (i.e. we excluded a buffer zone of potential edge effects ranging from rows $1 + buffer$ and $n - buffer$ to columns $1 + buffer$ and $m - buffer$). We then divided the obtained yield by the "area" $(n - 2 \times buffer) \times y.cell \times (m - 2 \times buffer) \times x.cell$ of the buffered plant matrix a to get a measure of yield in $g.m^{-2}$.

LER: The community-level yield was assessed by calculating the Land Equivalent Ratio (LER):

$$LER = \sum_{i=1}^{S} \frac{Yield_{species\ i,\ mix}}{Yield_{species\ i,\ mono}} \tag{4}$$

where $Yield_{species\ i,\ mix}$ represents the yield $(g.m^{-2})$ of species i in mixtures, and $Yield_{species\ i,\ mono}$ the yield $(g.m^{-2})$ of species i in monocultures. The ratio $Yield_{species\ i,\ mix}/Yield_{species\ i,\ mono}$ for a given species i represents its partial LER. We considered two options for $Yield_{species\ i,\ mono}$. Firstly, we simulated the monoculture yield with the spacing

that we used for our test communities (i.e. inter-row of 8 cm, intra-row of 5 cm). This constituted the standard monoculture yield. Secondly, we selected the highest monoculture yield among intra- and inter-row distances which varied from 5 to 20 cm in our model. This constituted the optimal calculated monoculture yield.

Model validation

We used our model to simulate the yield per species of the test communities from our field experiment, and subsequently compared the simulated values to the actual measured values using linear models for each species, with plot row as a random factor. We also used these comparisons to test different values of *d.lim* and subsequently selected the value of *d.lim* for which the linear model coefficients were significant and closest to one. We also performed sensitivity analyses for each model parameters, by determining how a variation of each parameter value by 5% (+5% and -5%) affected the final yield results.

Considered configurations

We considered four types of spatial plant configurations for our simulations (see Appendix A:Fig. 1): row alternation with equal densities of species, homogeneous mixing, row alternation with different densities of species and random placement. We simulated every pair of two-species mixtures and the 3-species mixture for all the configurations above, except for the random placement where we only considered the 3-species mixture. For the row alternation with three species, we added an extra combination in the following pattern: oat-lupine-camelina-lupine. Finally, the density variations were followed as indicated in Appendix A:Table 1. We simulated species-level yield and LER (standard and optimal) for each of these configurations with inter- and intra-row distance varying from 5 cm to 20 cm, i.e. the distances covered by our experiments.

Results

Growth model coefficients

The coefficient of determination, R^2, for the growth models estimating individual reproductive productivity as a

function of neighborhood identity and distance was generally high, i.e. higher than 0.70 for seven out of nine combinations (Fig. 3, Appendix A:Table 2). Only the fit of camelina with camelina was worse ($R^2 = 0.51$), while the fit of camelina with lupine was relatively poor ($R^2 = 0.34$).

Model validation with test communities

The estimated yield for the test communities based on the individual growth models was significantly correlated with the observed yield in the case of oat (linear regression coefficient: 0.262, *p*-value = 0.0033) and lupine (linear regression coefficient: 0.255, *p*-value = 0.045), but only marginally significant in the case of camelina (linear regression coefficient: 0.802, *p*-value = 0.0785) (Fig. 4). Results from the sensitivity analyses were consistent with the model validation, with low variations in response to the 5% changes for the majority of parameters (Appendix A:Table 3). The only notable exception involved camelina associated with oat and lupine associated with lupine, which showed a high variation in response to the 5% changes in the second parameter (Appendix A:Table 3).

Simulations and optimizations

Optimized monocultures

For each simulated monoculture, we determined the optimal inter- and intra-row distance for maximal yield at the field scale (Table 1, Appendix A:Fig.3). Oat and camelina reached the maximum population yield at the smallest simulated distance (5 cm), i.e. the highest densities encompassed in the scope of this study (400 individuals.m^{-2}). This increase in density from 250 to 400 individuals.m^{-2} led to an increase in population yield of 27% for oat and 131% for camelina compared to the standard density (8 cm). The optimal spatial parameters for lupine were inter- and intra-row distances of 6 and 6 cm, respectively, which corresponds to a density of 278 individuals.m^{-2}. This allows for an increase in yield of 4.7% compared to the standard density of 250 individuals.m^{-2}.

Table 1. Standard and optimal inter-row and intra-row distances (in cm), and corresponding population level yield (in g.m^{-2}) for monocultures of each species. Numbers in brackets indicate the lower and upper bounds of the yield responses to a +/-5% variation in the model parameters.

Species monoculture	Standard inter-row distance (cm)	Standard intra-row distance (cm)	Standard yield (g.m^{-2})	Optimal inter-row distance (cm)	Optimal intra-row distance (cm)	Optimal yield (g.m^{-2})
Oat	8	5	153 [139;167]	5	5	195 [179;211]
Camelina	8	5	184 [175;196]	5	5	425 [408:451]
Lupine	8	5	813 [679;974]	6	6	851 [718;1004]
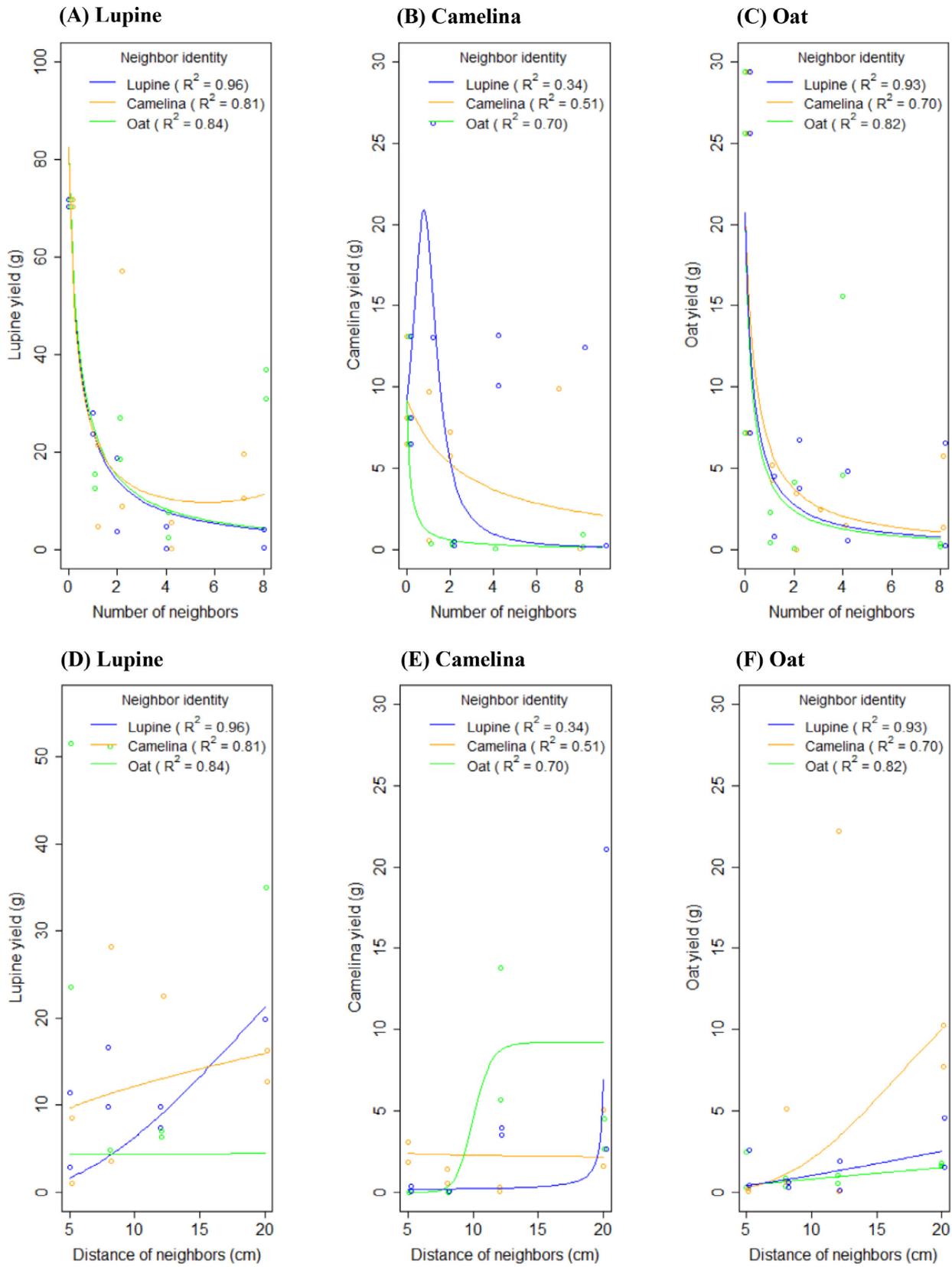
Fig. 3. Yield-density (A,B,C) and yield-distance (D,E,F) curves obtained with the equations from AppendixA:Table 1, showing the yield of lupine (A,D), camelina (B,E), and oat (C,F).

Table 2. Optimal inter-row and intra-row distances (in cm) for all species combinations and spatial configurations. Numbers in brackets indicate the lower and upper bounds of the yield responses to a +/-5% variation in the model parameters.

Species combination	Type of configurations	Density	Optimal inter-row distance (cm)	Optimal intra-row distance (cm)	Standard total yield (g.m^{-2})	Optimal total yield (g.m^{-2})	Yield increase (%)
Oat-Camelina	Row	Equal	11	5	172 [118;301]	548 [378;959]	219
Oat-Lupine	Row	Equal	5	5	467 [392;560]	709 [595;850]	52
Camelina-Lupine	Row	Equal	5	6	538 [451;645]	841 [706;1009]	56
Oat-Camelina	Homogeneous	Equal	10	10	98 [67;171]	158 [109;276]	61
Oat-Lupine	Homogeneous	Equal	5	5	506 [425;607]	832 [699;998]	64
Camelina-Lupine	Homogeneous	Equal	5	5	579 [486;694]	938 [787;1125]	62
Oat-Camelina	Row	2:1	11	5	247 [170;432]	545 [376;953]	121
Oat-Lupine	Row	2:1	5	5	395 [331;474]	600 [504;720]	52
Camelina-Lupine	Row	2:1	5	5	742 [623;890]	1044 [877;1252]	41
Oat-Camelina-Lupine	Row	Equal	12	5	385 [265;673]	506 [349;885]	31
Oat-Camelina-Lupine	Homogeneous	Equal	5	5	361 [249;631]	625 [431;1093]	73
Oat-Camelina-Lupine	Row	2:1:1	10	5	451 [311;789]	608 [419;1064]	35
Oat-Camelina-Lupine	Row	3:2:1	10	5	372 [256;651]	550 [379;962]	48
Oat-Camelina-Lupine	Random	Random	5	8	442 [305;773]	474 [327;829]	7
Oat-Lupine-Camelina-Lupine	Row	Equal	5	5	462 [388;554]	708 [594;859]	53
Oat-Lupine-Camelina-Lupine	Row	2:1:1	5	5	526 [441;631]	763 [641;915]	45
Oat-Lupine-Camelina-Lupine	Row	3:2:1	5	5	533 [448;640]	696 [584;835]	31

Optimized mixtures

Using the model simulations, we determined spatial configurations (i.e. homogeneous vs. row pattern) and sowing densities (optimal inter- and intra-row distances) that maximized community-level yield for each mixture (Table 2, Appendix A:Fig. 4−6). Increases in total yield in these optimized configurations compared to the ones we used in the test communities ranged from 7% for the 3-species random placement to 219% for the oat-camelina row pattern.

In all the row configurations, the optimal intra-row distance was generally small (almost always 5 cm), while the optimal inter-row distance showed more variability. In particular, the optimal inter-row distance between oat and camelina was larger than between oat and lupine or camelina and lupine: it was either 10 (in homogeneous mixing), 11 (in 2-species row pattern) or 12 cm (in 3-species row pattern). When looking at the homogeneous mixing, the optimal inter- and intra-row distances were the smallest possible in the case of oat-lupine (5 cm), camelina-lupine (5 cm), and the three species mixtures (5 cm) but larger for the oat-camelina mixture (10 cm).

LER gain

Next, we compared the yield of mixtures to those of monocultures using LER. Increases in LER when the
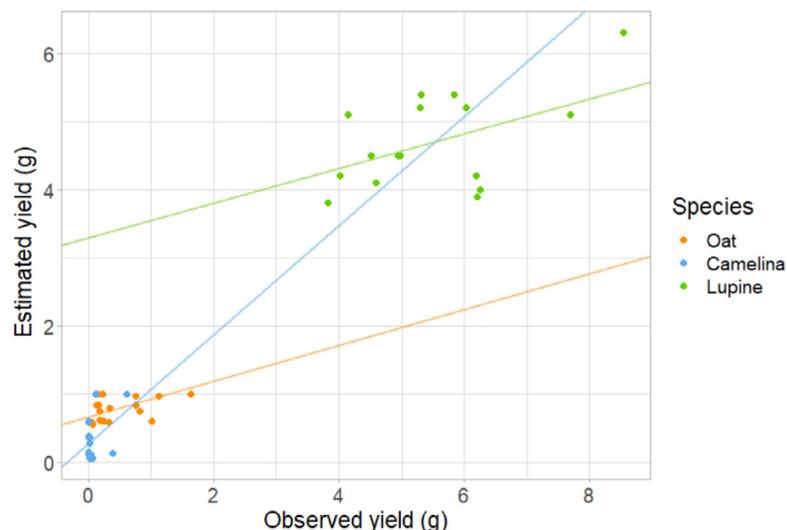
Fig. 4. Comparisons between the estimated and observed yields per individual in the test communities (in g).

Table 3. Standard and optimal LERs for each species combination and spatial configuration. Standard monoculture and mixture refer to the yield simulated with the spacing that we used for our test communities; optimal monoculture and mixture refer to the highest selected yield among intra- and inter-row distances varying from 5 to 20 cm.

Species combination	Type of configurations	Density	LER (standard mix/ standard mono)	LER (standard mix/ optimal mono)	LER (optimal mix/ standard mono)	Optimal LER (optimal mix/ optimal mono)	Increase in LER (%)
Oat-Camelina	Row	Equal	1.06	0.72	3.10	1.59	50
Oat-Lupine	Row	Equal	1.03	0.90	1.40	1.25	21
Camelina-Lupine	Row	Equal	0.86	0.70	1.28	1.08	25
Oat-Camelina	Homogeneous	Equal	0.62	0.44	0.94	0.57	-8
Oat-Lupine	Homogeneous	Equal	0.96	0.86	1.53	1.37	43
Camelina-Lupine	Homogeneous	Equal	0.98	0.77	1.77	1.30	33
Oat-Camelina	Row	2:1	1.42	0.79	3.05	1.51	6
Oat-Lupine	Row	2:1	1.01	0.87	1.42	1.22	21
Camelina-Lupine	Row	2:1	0.90	0.69	1.31	1.67	85
Oat-Camelina-Lupine	Row	Equal	1.06	0.78	2.06	1.15	8
Oat-Camelina-Lupine	Homogeneous	Equal	0.82	0.66	1.06	0.97	18
Oat-Camelina-Lupine	Row	2:1:1	1.32	0.89	2.21	1.38	4
Oat-Camelina-Lupine	Row	3:2:1	1.46	0.88	2.19	1.33	-9
Oat-Camelina-Lupine	Random	Random	1.05	0.78	1.23	0.84	-20
Oat-Lupine-Camelina-Lupine	Row	Equal	0.90	0.75	1.28	1.09	21
Oat-Lupine-Camelina-Lupine	Row	2:1:1	0.88	0.66	1.25	1.27	44
Oat-Lupine-Camelina-Lupine	Row	3:2:1	0.93	0.63	1.25	1.41	51

mixtures were spatially optimized compared to the distances used in the test communities ranged from 8% for the 3-species random placement to 142% for the camelina-lupine row pattern (Table 3).

We show that for almost all species combinations (except oat-lupine), the maximum LER of the row pattern is higher than the maximum LER of the corresponding homogeneous mixture (Fig. 5). This means that mixtures are more advantageous for productivity when crops are arranged in a row alternation than when they are completely mixed. For instance, the alternation of rows for oat-camelina led to a 2.8 times higher LER than the homogeneous pattern. Similarly, for the 3-species mixture, the LER for row alternation was 1.2 times higher than for the homogeneous mixing. The only exception is the oat-lupine mixture, where the homogeneous mixture led to a slightly higher LER (+10%) than the row alternation with the same density of species.

Moreover, we found that increasing plant density did not necessarily lead to more efficient crop mixtures (Fig. 5). For instance, in the case of camelina-lupine, reducing sowing density of lupine from 200 to 100 seeds.m^{-2} led to a 55% increase in LER. This was also the case for the 3-species mixture oat-camelina-lupine, where decreasing the densities of both lupine and oat from 66 to 33 seeds.m^{-2} increased LER by 20%. Similarly, for the oat-lupine-camelina-lupine mixture, reducing the density of lupine from 200 to 100 seeds.m^{-2} and the density of oat from 100 to 50 seeds.m^{-2} led to a 16% LER increase. Further reducing the density of lupine to 66 seeds.m^{-2} increased LER by 11%.

Finally, 3-species mixtures did not show higher LER than 2-species mixtures; specifically, oat-camelina and camelina-

lupine were able to reach higher LERs than the three species together (+13% for oat-camelina and +18% for camelina-lupine). The mixture of oat-lupine reached a similar LER value than the 3-species mixture.

When decomposing LER into partial LERs (Fig. 5), in most cases the increase in total LER was substantially driven by an increase in the contribution of camelina. This is notably true for the oat-camelina mixture, where the partial contribution of camelina increased by 420% in the optimized row pattern (i.e. 11 cm inter-row) compared to the homogeneous mixing. Similarly, in the 3-species mixtures, the contribution of camelina went from almost 0 in the homogeneous mixing to 0.73 in the optimized row pattern. On the contrary, the partial contribution of oat to total LER remained mostly similar across mixture combinations and spatial configurations. Finally, the relative contribution of lupine was generally high in the camelina-lupine mixture, as well as in the three species homogeneous mixture and the oat-lupine-camelina-lupine with equal densities. Then it drastically decreased by up to 88% in the other 3-species configurations, in favor of the increase of the partial contribution of camelina.

Discussion

This study demonstrates that models from plant coexistence theory can be used to optimize crop species combinations and spatial configurations in intercropped systems. While the density experiments gave us some clues on which species would perform well together, the distance
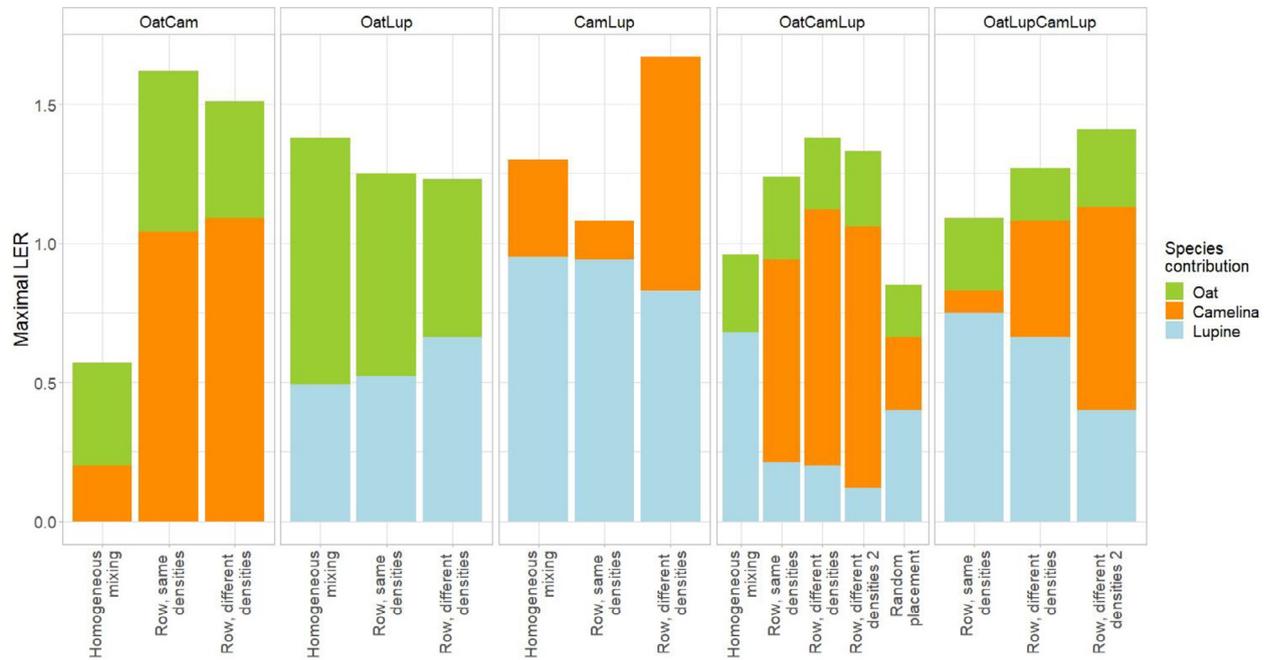
Fig. 5. Maximum land equivalent ratios (LER) observed for each species combination and spatial configuration. The densities considered in the graph refer to the ones shown in Appendix 1:Table 1. OatCam: oat-camelina; OatLup: oat-lupine; CamLup: camelina-lupine; OatCamLup: oat-camelina-lupine; OatLupCamLup: oat-lupine-camelina-lupine.

experiments allowed us to understand how the changes in yield associated with the presence of neighbors varied with distance. Based on these elements, we were able to find the sets of parameters (identity of neighbors, sowing density, distances between individuals) that would optimise intercrop yield (measured as LER) in terms of species combinations and spatial configurations.

Crop combinations

Our results from the density and distance experiments provided indications as to which species benefit from growing together. In particular, we demonstrated that oat and camelina strongly compete with each other: the yield-density curve of camelina with oat indeed decreased rapidly and steeply (Fig. 3B). However, the distance curve (Fig. 3E) suggests that there may be a limit after which the competitive effect of oat on camelina is weaker. This indicates that oat and camelina individuals must be far from each other (i.e. separated by more than 11 cm in our case) for a successful mixture (Appendix A:Fig.4A-B-C). Few previous studies have investigated the case of oat-camelina intercropping; in one study of camelina intercropped with wheat and with lupine, it was shown that camelina yields were lower in the wheat mixture than in the lupine mixture (Paulsen, 2007). The authors of this study used interrow distances (6.5 and 12.5 cm) and crop densities (100 seeds.m^{-2} for lupine, 400 for wheat, and 360 for camelina) which are comparable to what we did in our experimental design. They showed that

when wheat and camelina were grown in close proximity (6.5 cm), yields of intercropped camelina only reached between 2 and 20% of its yield in monoculture; however, when the interrow was doubled (12.5 cm), camelina yields increased and reached 12−66% of its monoculture yields (Paulsen, 2007). Their findings are therefore consistent with our results and further suggest that cereals are strong competitors of camelina, and that cereal-camelina intercrops may benefit from larger interrow distances.

On the contrary, promising crop combinations include camelina-lupine and oat-lupine. First, the yield-density curve of camelina with lupine neighbors suggests that there may be some facilitative effects at a low density of lupine (Fig. 3B). This has the potential to be highly beneficial for the species-level yield of camelina in the case of a lower density of lupine, which we can see in our camelina-lupine LER simulations (Fig. 5). Furthermore, the optimal LERs were quite high (Fig. 5); in his study, Paulsen (2007) similarly showed that intercropping of lupine and camelina with an interrow distance of 6.5 cm increased the total relative yields (ranging between 1.10 and 1.97), notably thanks to a strong development of camelina in the mixture (Paulsen, 2007). This is consistent with our findings and suggests that camelina-lupine is a successful mixture.

In the case of the oat-lupine combination, the two yield-density curves look very similar (Fig. 3A−C), which could indicate that competition between the species is symmetrical (Weiner et al., 2001). Furthermore, the yield-distance curve of lupine surrounded by oat (Fig. 3D) suggests that lupine and oat could perform well in close proximity. Indeed, our

simulation results show that LER for oat-lupine is highest when the distance between individuals from the two species is smallest (Appendix A:Fig. 4D−E-F). It is also the only mixture where the homogeneous mixing performs as well as the row configuration (Fig. 5). This suggests that oat is not a strong competitor of lupine and that there may be a high level of niche differentiation between the two species, which makes oat-lupine a promising crop combination. Intercropping lupine with cereals has indeed been demonstrated as a well-performing mixture in several studies, with LERs generally higher than 1 due to a complementary use of resources, particularly nitrogen (Engbersen et al., 2021, with similar crop densities and interrow distances).

Surprisingly, contrary to the diversity-productivity relationship (Loreau & Hector, 2001), the 3-species mixtures did not perform more efficiently than the best two-species mixtures (Fig. 5). Reasons for this lack of increase might be that going from two species to three species is not a substantial enough increase in crop diversity. It may also be that the three species are too similar in terms of growth strategies, or that our model fails to predict plant growth when more than two species are considered (see below).

Optimal spatial configurations

Our simulations show that, except oat-lupine, all combinations perform better in a row pattern than in a homogeneous mixing (Fig. 5); this may be because individuals are directly surrounded by more conspecific neighbors in the homogeneous mixing than in the row pattern. Since plants generally compete more strongly with individuals from their own species than with individuals from a different species (Adler et al., 2018), they tend to benefit from being surrounded by more heterospecific neighbors than conspecific neighbors. This is consistent with a recent meta-analysis showing that net biodiversity effects (i.e. the increase in yield in mixtures compared to monocultures) were significantly greater in alternate-row than in homogeneously mixed intercrops across climatic conditions and species mixtures (Li et al., 2020). Likewise, a recent study demonstrated that alternating rows were more successful in increasing soybean production while also controlling weed invasions than homogeneous mixing (Cheriere et al., 2020).

Furthermore, our results highlight the trade-off between density and productivity, i.e. between a few highly productive plants and many less productive individuals, also known as the constant yield law (Weiner et al., 2001; Weiner & Freckleton, 2010). This is illustrated by the fact that although individual yield is maximal when plants are further apart from one another, increasing the number of plants can compensate for this decrease in individual yield and lead to higher community yields. However, our results show that the strategy to increase density for higher yields has its limit (Fig. 5): in our case, we show for instance that decreasing the density of lupine by a factor of 2 or 3 can be beneficial

for LER (up to + 29%). This is in agreement with previous research on intercropping with legumes, where legumes usually have a much lower density than the other intercropped species (Bulson et al., 2020). On the contrary, in the two-species mixtures, decreasing the density of oat did not translate to an increase in LER. This is consistent with most of the cereal intercropping research, which shows that increasing the density of the cereal in mixtures generally leads to higher LERs (Bulson et al., 2020; Yu et al., 2016). Cereals are indeed commonly considered to be strong competitors, notably due to their high growth rate at early life stages and high uptake of nitrogen (Andrew et al., 2015). Furthermore, among the three species we considered in this study, cereals have the longest history of breeding for higher population yield, which is achieved by decreasing, not increasing, individual fitness (Denison, 2012; Weiner, 2017). Thus, we believe that cereals are adapted to reach high population-level yield, which can explain why they can withstand high densities without hindering their performance.

Model performance and limitations

When comparing the simulated monoculture yields with actual average yields from the local region, we found similar values for oat, with yields ranging from 1100 to 1600 kg. ha^{-1} ("Boletin Oficial Del Estado," 2020; Sánchez-Martín et al., 2014), in line with our simulations (1530 kg. ha^{-1}, Table 1). Local yields for lupine were generally smaller than what we simulated (8130 kg. ha^{-1}) and only reach up to 3000 kg.ha^{-1} in the field (López-Bellido et al., 1994, 2000). However, this study only considered *Lupinus albus*, which is a different species, and sowing densities were much smaller than what we did (between 20 and 60 seeds.m^{-2}). In another study, Lema (2005) investigated yields of single plants of *Lupinus angustifolius* and obtained seed yields averaging 30 g per plant (Lema et al., 2005). In our experiment, single lupines yielded an average of 70 g per plant (Fig. 3). This suggests that lupines were particularly productive in our experimental setting; we suggest that growth could have been boosted by the insecticide application, or that our sandy soil with low organic matter was well adapted for this plant (Lema et al., 2005). Furthermore, our simulations are consistent with results from a crop diversity experiment performed in 2018 with the same crop varieties, sowing densities, and experimental conditions, where the yield of lupine and camelina in monocultures had an average of 8840 kg. ha^{-1} and 1160 kg. ha^{-1}, respectively (Stefan et al., 2021). This emphasizes the potential of simple ecological models to accurately describe plant-plant interactions in crop systems characterized by plants growing in rows.

Our simulated values correlated reasonably well with the experimental values for lupine and oat, but not with camelina (Fig. 4). We believe this is because our model fails to completely capture the behavior of camelina when surrounded by lupine. Indeed, the R-square for the growth

model was particularly low (0.34, Appendix A:Table 2), which could be due to the potential facilitation occurring at low density of lupine, particularly in the case of one and four lupine neighbors (Fig 3B). This highlights the limitations of classical ecological models, which were not designed to integrate complex or facilitative behaviors (Bruno et al., 2003). More complex models including higher-order interactions might improve model fits (Martyn et al., 2020). In this study, our model only considered first-order interactions (representing the direct effect of neighbors) and intraspecific second-order interactions (representing the indirect effect of intraspecific crowding) when it improved the fit of the model. Interspecific higher-order interactions, which capture the indirect effects of all heterospecific pairs of species, were not added to the presented simulations in this study. Including interspecific higher order interactions would require more experiments, notably with combinations of three species (Levine et al., 2017; Mayfield & Stouffer, 2017). Thus, more experiments and replications are needed to confirm the observed interactions and to improve the models. In particular, we advocate for a higher number of replicates and an expansion of the number of density-distance combinations (i.e. repeating the distance experiments for each density treatment). Finally, interaction coefficients are strongly dependent on local abiotic conditions, such as climate or soil parameters (Hart & Marshall, 2013). Thus, the value of the interaction coefficient, but also how it changes with distance, is expected to vary under different abiotic conditions (Holzapfel et al., 2006). Our findings are therefore hard to extrapolate to different climates or species. However, Paulsen (2007) found similar results in an experiment run in northern Germany, which has a different climate, with notably higher monthly precipitation (around 70 mm per month). Furthermore, the behavior of wheat was largely comparable to oat, which suggests that our findings may be applied − with caution − to species from the same family. In any case, we emphasize the importance of studying plant−plant interactions over a range of conditions (Callaway, 1998). This highlights the need to test and validate our model under different environmental conditions to determine how the competition coefficients might be affected, and whether this changes the conclusions for optimal spatial configurations.

While the adoption of intercropping practices on large scales are nowadays still hindered by technical constraints, such as ill-adapted machines, solutions are emerging to increase the practicability of sowing and harvesting crop mixtures (Hong et al., 2020). For mechanized agriculture, row intercropping remains the most relevant option, as it can make use of available machinery to sow in lines (Cheriere et al., 2020). Machines designed to sow intercropped rows, such as interseeders or precision seeders, already exist for wide-row crops, notably for corn or soy (Bybee-Finley & Ryan, 2018; Cortez et al., 2018; Mondani & Karparvarfard, 2016; Prakash et al., 2020). Trials are running to develop such machines for narrow-row crops (Technology Agency of the Czech Republic, 2020); in practice, narrow-row intercrops can still be sown with a double seeder passage (Paulsen, 2007). Intercropped species can then be harvested simultaneously with a standard combine harvester and seeds sorted later on, provided that the intercropped species are ripe at the same time (Loïc et al., 2018). Evidently, in real situations, plants cannot be as perfectly aligned as described in our experimental setting; likewise, a perfect homogeneous pattern may not be achievable, but seeds can be randomly mixed by broadcasting. Nonetheless, the bulk of our findings can be applied on farm, and this approach, based on simple and reproducible density and distance experiments, represents a promising way to optimize crop mixtures in terms of both species combinations and spatial configurations.

Authors' contributions

L.S. and C.S. conceived the study with input from N.E. L. S. and N.E. collected the data; L.S. assembled and analyzed the data with the help of C.S.; L.S. and C.S. wrote the paper. All authors discussed data analyses and results.

Data accessibility

Data is available online: 10.5281/zenodo.6552717.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j. baae.2022.05.004.

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