Received: 5 April 2021 | Accepted: 19 November 2021
DOI: 10.1111/1365-2664.14092

Journal of Applied Ecology
BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Economic and not ecological variables shape the sparing–sharing trade-off in a mixed cropping landscape

Hila Segre[1,2] | Yohay Carmel[3] | Assaf Shwartz[1]

[1]Faculty of Architecture and Town Planning, Technion - Israel Institute of Technology, Haifa, Israel

[2]Plant Ecology and Nature Conservation Group, Wageningen University, Wageningen, The Netherlands

[3]Faculty of Civil and Environmental Engineering, Technion - Israel Institute of Technology, Haifa, Israel

Correspondence
Hila Segre
Email: hilasegre@gmail.com

Funding information
Ministry of Agriculture and Rural Development, Grant/Award Number: 14-34-0001; Israel Nature and Parks Authority; Nekudat Hen Foundation

Handling Editor: Lorenzo Marini

Abstract

1. The framework of land sparing versus land sharing provides a useful analytical tool to address the crop-production/biodiversity trade-off. Despite multiple case studies testing the sparing–sharing trade-off, this framework still lacks the ability to identify the conditions in which sparing, or sharing, would be the preferred strategy for pareto-optimizing both food production and biodiversity. Under some conditions, ecosystem services may create a positive feedback between biodiversity and crop production, affecting the optimization.
2. This study aims to identify the conditions and the relevant variables that determine the preferred land use strategy in terms of maximizing both biodiversity and food production, while accounting for positive feedback of ecosystem services in this analysis. We used a simulation model with data from a mixed cropping landscape (100 km^2) covering seven crop types, five taxonomic groups, three biodiversity metrics and 23 bioindicators to explore the variables shaping the biodiversity–production trade-off and ecosystem services underlying it. We explored a continuum of sparing large semi-natural patches to sharing by maintaining uncultivated field margins of varying size.
3. Land sparing outperformed land sharing in 62% of the scenarios and it was economically more predictable. The optimization was shaped by costs, associated with crop type, rather than by landscape composition and configuration, biodiversity metric, taxonomic group or bioindicator.
4. Landscape configuration and taxonomic group results corroborate the notion that land sharing benefits mainly small organisms, and that the common width of field margins in many agri-environmental policies (10 m) is not cost-effective compared to land sparing.
5. Land sharing was the optimal strategy whenever it resulted in minimal costs, despite contributing little to biodiversity. Yet, when field margins were >20 m wide (small-scale sparing), land sharing maintained higher biodiversity and was at least as cost-effective as sparing.
6. *Synthesis and applications*. Our model highlights the importance of socio-economic variables compared to ecological variables in selecting land-management strategy to pareto-optimize both food production and biodiversity. Considering opportunity costs alongside economic benefits from ecosystem services in various

cropping systems may therefore improve the cost-effectiveness of biodiversity conservation policies in agricultural landscapes.

KEYWORDS
biodiversity conservation, cost-effectiveness, ecological corridors, ecosystem services, land management, semi-natural habitat, wildlife friendly farming, yield gap

1 | INTRODUCTION

Rapid population growth during the last decades has significantly increased the proportion of land used for food production at the expense of natural habitats, resulting in massive habitat loss, fragmentation and biodiversity decline (Tilman et al., 2017). Reducing the impact of food production on biodiversity is at the heart of the land sparing versus land sharing (LSLS) debate (Green et al., 2005). Land sparing favours intensive agriculture, which is more productive, requires less land for cultivation, and potentially allows for more land to be spared for natural habitats (Phalan et al., 2011). Contrary to land sparing, land sharing favours extensive farming techniques, allowing for both production and biodiversity on the same land (Tscharntke et al., 2012). Although there is a lively discussion over LSLS, the number of studies that tested this theory empirically is small and results are so far equivocal (Kremen, 2015; von Wehrden et al., 2014; but see Luskin et al., 2018 for tropical forestry systems).

The dependency on species traits and landscape context makes it challenging to generalize beyond a specific context. In order to apply the best strategy across spatial scales and taxa, there is a need for more general approaches (Bennett, 2017). Empirical and theoretical analyses show that mixed strategies perform better than implementing sparing or sharing alone (Butsic & Kuemmerle, 2015; Legras et al., 2018; Troupin & Carmel, 2014). Mixed allocation of sparing and sharing might be more easily applied by planners and policymakers than choosing one strategy, even if it is not the optimal solution of the biodiversity–production trade-off (Grau et al., 2013). Rather than a global test of the superior strategy, the major question is, therefore, under which circumstances would either strategy better utilize the landscape for greater biodiversity and crop production (Fischer et al., 2008; Shackelford et al., 2015).

To date, the sparing–sharing framework has mostly focused on production versus biodiversity, ignoring other socio-economic factors relevant for policy-makers (Fischer et al., 2014, 2017). For instance, land sparing may involve higher inputs resulting in lower sustainability, and land sharing may provide a range of ecosystem services from services supporting production to cultural services (Barral et al., 2015; Tscharntke et al., 2012). Considering the feedback of biodiversity on yield by exploring ecosystem services and disservices, and the contexts under which this feedback occurs or fails to promote higher yields can help make the LSLS debate more relevant for policy (Ekroos et al., 2014; Grass et al., 2019; Seppelt et al., 2020).

The effects of landscape composition (e.g. amount and type of semi-natural and crop habitats) and configuration (e.g. field size and edge density) on biodiversity, yield and ecosystem services are increasingly studied (e.g. Dainese et al., 2019; Sirami et al., 2019). These relationships are complex and may differ between crop types and cropping system, affecting both biodiversity conservation and yield (Pywell et al., 2015; Segre et al., 2020; Seppelt et al., 2020). For instance, small-holder farms with small fields may benefit sensitive species compared to industrial large fields (Law & Wilson, 2015) and areas with high productivity tend to be intensively cultivated, increasing conservation costs (Naidoo & Iwamura, 2007). The biodiversity–productivity trade-off may also shift with taxonomic group. Arthropod pollinators may benefit from sparing of small patches such as field margins, while large mammals may require sparing of large contiguous patches (Ekroos et al., 2016). Finally, the optimal strategy (LSLS) depends on the focal species' affinity to farmed and natural habitats ('winners and losers' in the sparing–sharing terminology) and it is also scale dependent (Fischer et al., 2014; Green et al., 2005). Therefore, LSLS framework should incorporate biodiversity-yield feedback (e.g. via ecosystem services) under different contexts of biodiversity indicators and cropping systems, and explicitly target scales in which land is allocated to sparing and sharing (this extent may vary among global or regional policies; Fischer et al., 2014).

The goal of this study is to understand the relative importance of the variables that affect the sparing–sharing trade-off and determine the optimal strategy that jointly maximizes ecological and agricultural benefits at a regional scale. We employed scenario modelling based on real-life data to compare landscape planning strategies in different contexts. Our model compares a range of scenarios from sparing of large semi-natural patches to sharing based on maintaining uncultivated field margins of varying width in multiple crop types. Instead of the classic LSLS production–biodiversity trade-off we explicitly model the effect of land management on biodiversity and production. This implicitly incorporates potential feedback of biodiversity on yield via ecosystem services (i.e. we do not assume that land sharing has lower yields). We tested the effect of the following variables on the LSLS trade-off: (a) cropping system composition and configuration (crop type, field size and field shape), (b) size of spared land (ranging from narrow field margins to large patches) and (c) the specific taxonomic group and diversity measure used to estimate biodiversity. Our approach offers a mechanistic understanding of the variables that influence the LSLS trade-off, while integrating ecosystem services into the sparing–sharing framework and considering multiple crops, species and a range of LSLS scenarios.

2 | MATERIALS AND METHODS

2.1 | Study area and data collection

The study was conducted in Harod valley (northern Israel), an intensive agriculture area of approximately 100 km^2 that separates two large ecoregions and several nature reserves and therefore it was designated as a national ecological corridor (Figure S1 in Supporting Information). Our model was based on data from Segre et al. (2019), and we provide the full description of site selection and data collection methods in Appendix S1. Permission to sample in agricultural plots was obtained from the relevant landowners, sampling of fauna and flora was coordinated with the Israeli Nature and Parks Authority. No ethical approval was required for this work. During the agricultural season of 2015–2016, we conducted biodiversity surveys of plants, birds, butterflies, ground-dwelling and plant-associated arthropods in four habitats (*n = 88*): fields, orchards, field margins and semi-natural habitats (Appendix S1). We visited each plot multiple times in the spring (all species groups), summer (all arthropod groups) and fall (butterflies, ground-dwelling arthropods and birds). In each visit we recorded all plant species, abundance of all present species of birds, butterflies and ground-dwelling arthropods (the latter was identified to the lowest recognizable taxonomic unit, see Appendix S1), and abundance of all sub-orders present of plant-associated arthropods.

We studied a total of seven arable crops (rain-fed wheat, irrigated wheat, tomatoes and watermelon), and orchards (olives, almonds and citrus). We surveyed and interviewed 12 farmers in the region, obtaining profit and loss reports, as well as the revenue and profit for a total of 47 plots during the same season as the ecological surveys. Revenue and profit were reported in NIS (1 USD = 3.84 NIS) per unit area (0.1 ha). We calculated the percentage of uncultivated margins covered by natural vegetation within a radius of 10 m around each plot, which best reflects the immediate field margins, where most damage or benefit to crops is expected (see Appendix S1). We also calculated field size and perimeter as estimates of field configuration. We used the estimated profit or loss to calculate both costs of sparing and sharing as well as economic benefits from ecosystem services.

2.2 | Cost-effectiveness metric

We compared sparing land by converting cultivated land to natural habitats (e.g. riparian area for streams and grasslands), and sharing land by maintaining uncultivated field margins with natural vegetation (e.g. no application of herbicide and tilling). Costs model specification and detailed calculations can be found in Appendix S2. The model and data analysis were built in R software version 3.5.3 (R Core Team, 2017). We used a cost-effectiveness measure, previously developed in Segre et al. (2019), to measure the ecological effectiveness of each strategy (i.e. species richness and population size) relative to the costs (i.e. revenue). We first fitted an ANCOVA model to the revenue data in order to estimate the crop-specific effect of percentage of uncultivated margins on total revenue ha^{-1}, controlling for plot size as fixed effect and landowner as random effect. Variance was modelled separately for each crop type due to heteroscedasticity ('gls' R package NLME). We calculated the costs of **sparing** (converting cultivated land to natural habitats, 'loss-of-opportunity'), as the potential profit from cropland that is lost when the land is not cultivated (i.e. baseline revenue at the intercept for each crop type) summed over all crops in the landscape. We excluded additional costs due to damage to adjacent crops, because the interface between fields and natural habitats is small and the land spared is marginal land characterized by low profit (Pywell et al., 2012).

The cost of **sharing** (maintaining uncultivated field margins) is the profit–loss correlated with field margins (e.g. caused by pest damage), which is the decrease in revenue of each crop type when field margins are present, summed over all crops in the landscape. We neglect field margins' effect on production costs (e.g. higher herbicide applications), since production costs for the modelled crops were robust to maintaining uncultivated field margins (Segre et al., 2019). Field margins may further provide ecosystem services that increase yield in our system as we previously showed (e.g. increasing the abundance of natural enemies compared to pests and providing pest and weed control in tomato crops Segre et al., 2019, 2020). Thus, we assume that increased revenue is the result of beneficial ecosystem services (i.e. when field margins increase farmer's revenue, then they have no costs). We assume that establishing field margins does not require additional area to be removed from production, since there are numerous non-productive road and field verges which are tilled or applied with herbicide to prevent dispersal of weeds and pests into the fields.

We assessed the ecological effectiveness using three measures: species richness (per visit and yearly total) and the geometric-mean abundance of all species (GMA; Santini et al., 2017). We calculated the effect size of sparing and sharing strategies on all three measures, using a set of regression models fitted separately to each taxonomic group. Some species may be more sensitive than others to farming intensity, therefore, we divided the five species groups to additional functional groups related to their life-history traits, conservation status and distribution, and we fitted separate regression models to GMA of functional groups (except for plants, for which we used richness). We fitted generalized linear models to the total richness per year and GMA of plant-associated arthropods data, and generalized linear mixed-effects models with site as a random effect to the richness and GMA per visit data (R packages STATS, GLMMTMB, STATMOD). We used Poisson error distribution for the richness measures and gamma or tweedie for GMA to account for zero inflation. Fixed variables included four habitats (arable, orchard, field margin and semi-natural), field margins width interaction for field margins habitat, and additional taxon-specific variables that were found influential in Segre et al. (2019, i.e. landscape, habitat and climate properties). The model specification and detailed calculations for the effectiveness analysis can be found in Appendix S3.

Cost-effectiveness was then calculated as the ratio of the unscaled biodiversity effectiveness (response ratio) to the costs. For each scenario, either sparing or sharing was selected as the preferred scenario, based on their cost-effectiveness values. The equilibrium line of cost-effectiveness of both strategies is:

$$\mathrm{COST}_{\mathrm{sparing}}/\mathrm{COST}_{\mathrm{sharing}} = \mathrm{EFF}_{\mathrm{sparing}}/\mathrm{EFF}_{\mathrm{sharing}}$$

Therefore, any increase in sparing costs must be accompanied by an increase in the same ratio in sparing effectiveness; otherwise sharing will become more cost-effective, and vice-versa.

2.3 | Scenarios

We used a spatially implicit simulation model in which every scenario represents a proportion of each crop type in the landscape (to a total of 100%), field size, field shape and field margins width to implement as land sharing, and we modelled all possible combinations of these variables (Figure 1). For each scenario we calculated the economic costs and the ecological effectiveness of sparing and sharing, and chose the most cost-effective strategy. We used per visit richness averaged over all species groups for the base scenario. The effects of biodiversity measures (i.e. taxonomic groups, functional groups and year total richness or GMA) were tested in a separate sensitivity analysis (SA). Input variable values were selected to represent constant change of 33% between scenarios, to evaluate model sensitivity across input variables (Table S3). Crop combinations included the seven local crop types with relative proportion of each crop type ranging from 0% to 100% of the total area, and constant change of 33% in Jaccard dissimilarity (Appendix S4). Attributes of fields and field margins were based on the range of actual values in the study area and were derived from our datasets (Table S3).

We calculated three indices for each scenario: effectiveness ratio ($\mathrm{EFF}_{\mathrm{sparing}}/\mathrm{EFF}_{\mathrm{sharing}}$), which is the effectiveness of sparing relative to sharing, costs ratio ($\mathrm{COST}_{\mathrm{sparing}}/\mathrm{COST}_{\mathrm{sharing}}$), which is the cost of sparing relative to sharing, and the strategy selected (sparing or sharing). We also calculated the proportion of scenarios for which each strategy was selected. We used a constrained correspondence analysis (CCA) with the three above-mentioned scenario-specific indices as constrained variables to test how crop composition affected the model results, which crop types were associated with the selection of each strategy and whether the cause was high effectiveness or high costs of one strategy compared to the other.

2.4 | Sensitivity analysis

We tested if the decision to spare or share land is sensitive to the input variables of our model using a local SA. In a local SA, all variables are kept constant, and only one variable is changed at a time, in order to filter variables that are not influential in the model ('Factor's Fixing', Morris, 1991; Saltelli & Tarantola, 2004). Using this method, we quantified local effects of variables on model output at different values, and computed two sensitivity measures: the mean effect across all values was used to assess the effect of a given variable in the model, and the standard deviation was used to identify nonlinearity or interactions. This method combines advantages of both local and global SAs. It is computationally simple like other local SA methods, yet it averages effects across the input space of the model and can identify nonlinear effects and interactions, similar to

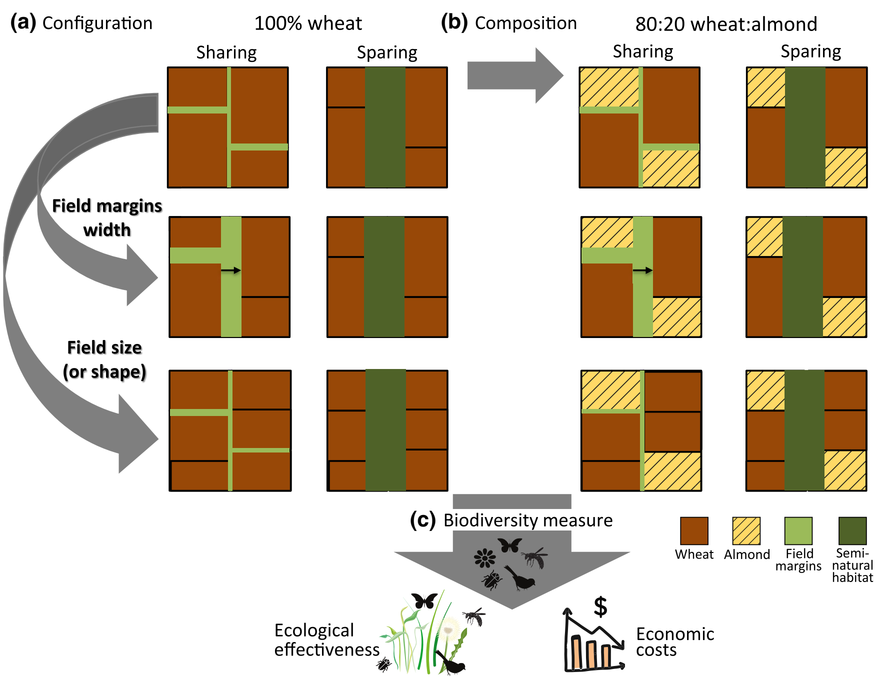

FIGURE 1 A representation of the model scenarios. We modelled different cropping system configuration (a) by varying the width of the field margins and the size or shape of the fields, crop composition (b) by assigning different proportion of the land to different crops (represented by the yellow and brown parcels), and calculated the ecological effectiveness for multiple species groups (c)* and the economic costs for both sparing and sharing. * The basic scenario included one biodiversity measure, followed by sensitivity analysis for changing the biodiversity measure

global SA. For each input variable, we recorded the change in cost-effectiveness of sparing and sharing for a single change in its value (e.g. increasing field size) and calculated the mean and standard deviation of this change across all input values. The change in cost-effectiveness was calculated proportional to the starting point, that is, the change in cost-effectiveness divided by the original value. The decision variable (sparing or sharing) is binomial, so change in model results was calculated as the proportion of scenarios in which the selected strategy changed in response to the change in the input variable.

We also conducted a SA, to evaluate model sensitivity to the specific choices of the diversity metric and bioindicator (taxonomic and functional groups). We ran all the scenarios for each combination of diversity metric (per visit richness, year total richness, GMA), taxonomic group (plants, birds, butterflies, arthropods, and all taxa combined) and additional scenarios for functional groups (Appendix S5). We then recorded the proportion of scenarios in which the selected strategy changed in response to the change in the diversity metric, that is, using GMA or total richness instead of per visit richness. We repeated this SA with all taxonomic and functional group, for example, using birds richness instead of multi-taxa richness and using migrating birds GMA instead of all bird species GMA respectively. Finally, we tested if explicitly including ecosystem services (e.g. biological pest control), influences the balance between sparing and sharing, but results were similar to the model assuming implicit benefits via increased yields and therefore not presented here (see Appendix S6).

3 | RESULTS

3.1 | Scenario results

We evaluated a total of 73,920 scenarios, covering a wide range of the possible parameter values of crops, field margins width, field size and perimeter. Sparing (converting cultivated land to semi-natural habitats) was selected as the preferred strategy in 0.62 of the cases, while sharing (maintaining uncultivated field margins with natural vegetation) was the preferred strategy in 0.38 of the cases. The frequency of scenarios favouring sparing versus sharing was slightly affected by field and field margin configuration. Large and quadrate fields with narrow field margins favoured sparing, while small and narrow fields with wide field margins resulted in more sharing scenarios as the cost-effective solution (Figure 2). For example, field margins 10 m wide, which are a common standard in many EU countries, resulted in sharing being favoured in only 0.27 of all scenarios across all field sizes. In contrast, for field margins of 23.5 m wide, sharing was preferred in 0.51 of the scenarios.

The type of crops strongly affected model results. The three CCA axes represent our three model outputs (Figure 3; Table S4): axis 1 corresponds to the ratio between sparing and sharing effectiveness for biodiversity, axis 2 corresponds to sharing strategy and axis 3 corresponds to the ratio between sparing and sharing costs. The total variance explained by the three constraining axes was 0.19, with the first axis responsible for 0.11 of that proportion. Arable crops show higher effectiveness ratio, that is, higher effectiveness of sparing land compared to sharing land with field margins. Watermelon, tomato and citrus crops were positively correlated with cost ratio; tomato and citrus crops were highly correlated with sharing while watermelon was associated with sparing (Table 1). The selection of sharing and sparing strategies is parallel to the costs ratio axis and not related to the effectiveness ratio, although the variability among crops in the landscape is also related to the effectiveness ratio (i.e. fields and orchards; Figure 3; Table S4).

3.2 | Sensitivity analysis

The preferred strategy in different scenarios was quite robust to field configuration (size and shape) and field margin width. The sensitivity of the model to all three variables was low, with only 0.04–0.08 of the scenarios changing the model's decision of sparing or sharing (Table 1). Cost-effectiveness of sharing decreased with increasing field size and increased with increasing field perimeter and field margins width. In contrast, the preferred strategy was sensitive to the crop type, with 0.15 probability to change strategy with change in crop composition (Table 1; Figure S5). Specifically, watermelon had a high impact, when the proportion of watermelon in the land was >20%, the strategy was stable and the chance of changing the preferred strategy was very low (Figure S6). Cost-effectiveness of both sharing and sparing were sensitive to the change in crop type proportions; cost-effectiveness of sharing decreased on average when almond or watermelon proportions increased. In contrast, cost-effectiveness of sharing increased when other crops increased

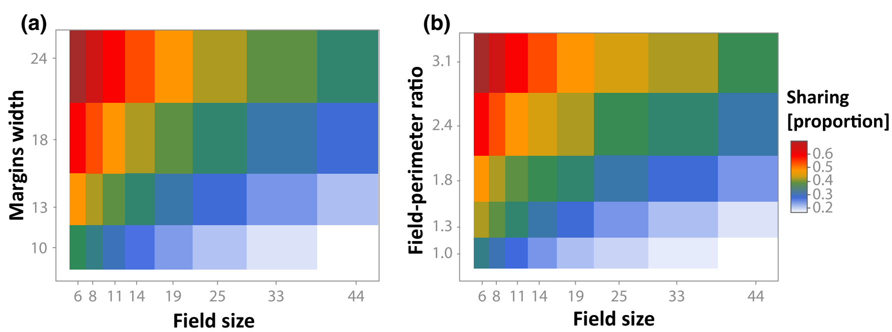

FIGURE 2 Proportion of scenarios which selected sharing as the cost-effective strategy at different combinations of (a) field margins width (m) against field size (ha), and (b) field perimeter ratio against field size (ha)

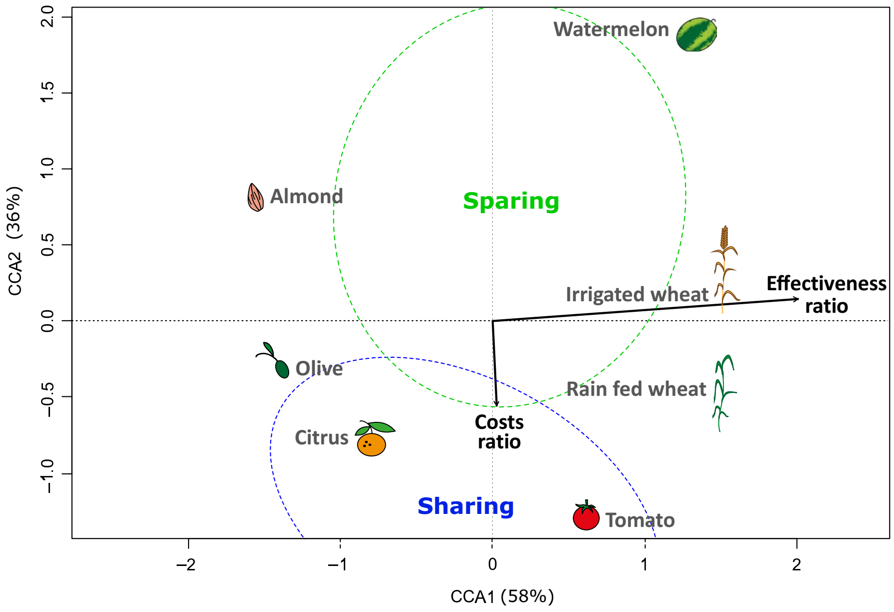

FIGURE 3 Results of the constrained correspondence analysis of crop composition, showing the effect on effectiveness ratio and cost ratio between sparing and sharing, and the selection of sparing and sharing strategies (green and blue, correspondingly)

their proportions (Table 1). Cost-effectiveness of sparing decreased when proportions of almonds, citrus and tomato crops increased, and vice versa (Table 1).

3.3 | Biodiversity metrics

The preferred strategy was very robust to biodiversity metric. Only 0.03 of the scenarios changed the selected strategy on average, when using GMA or total richness instead of richness per visit (Table 1; Figure 4), with highest sensitivity for plant-associated arthropods. Sensitivity to the specific taxonomic group was slightly higher, with 0.08 probability of changing strategy when switching to a different taxonomic group (Table 1). The most sensitive taxonomic group was butterflies (0.12). Cost-effectiveness of both sparing and sharing increased when plants were used as the biodiversity measure, whereas butterflies increased the cost-effectiveness of sharing but decreased the cost-effectiveness of sparing. Choosing any of the other taxa as biodiversity indicator decreased cost-effectiveness of both strategies. Finally, choosing birds and plants as biodiversity indicator slightly increased the proportion of sparing scenarios, while the three arthropod groups increased the proportion of sharing scenarios (Figure 4). The selection of functional group changed 5% of the scenarios, with large differences among taxonomic groups (Table 1). However, the sensitivity to functional group was correlated and usually smaller than the sensitivity to the taxonomic group (see Appendix S5 for the full descriptions of the results).

4 | DISCUSSION

The growing need for food supply highlights the dire trade-off between agricultural production and biodiversity conservation. Numerous studies of this trade-off examined the impact of various production methods and land management practices on ecological benefits, particularly biodiversity (e.g. Egan & Mortensen, 2012; Hodgson et al., 2010). Our study assessed varying parameters at both ends of the trade-off simultaneously and affirmed that economic considerations, rather than ecological considerations, dominated the production–biodiversity trade-off. Thus, the selection of the best strategy at the landscape scale depended mostly on the costs related to specific crop types rather than on the differences in biodiversity outcome. This finding corroborates the proposition of Ekroos et al. (2014) that farmland productivity affects opportunity costs and service provisioning benefits, thus favouring land sharing in areas with high productivity. Accounting for both agricultural yield and biodiversity, sparing was the favourable solution across a range of field and field margin attributes and diversity measures, as previously claimed (Phalan, 2018). Although sparing was favoured in 62% of the scenarios, it was also very stable in terms of costs, and therefore performed well in the remaining 38% of scenarios. This was not the case for land sharing for which any costs incurred to the farmers outweighed the benefits to biodiversity (see also Law & Wilson, 2015). Sharing was only preferred when costs were negligible or when sharing provided ecosystem services that increased yields, whereas in the other 62% of the scenarios it inflicted high costs on the farmers.

Farm and field characteristics can alter the effectiveness of agro-ecological practices (Concepción et al., 2012) and the provision of ecosystem services (Segoli & Rosenheim, 2012) that drive benefits from land sharing. In our model, large fields reduced the cost-effectiveness of sharing, because we assumed that the revenue loss that field margins inflicted on crops was uniformly distributed within the field. Hence, equal damage per unit area in large fields resulted in higher total damage than in small fields. Uniform damage is not necessarily realistic since field margins may have a stronger effect on crop production in field edges than in field centre (Segre et al., 2020; Tschumi et al., 2016). Incorporating this assumption into the model

TABLE 1 Sensitivity analysis results for all model input variables. Proportion of scenarios changing the selected strategy (strategy changed) and relative change in cost-effectiveness (CE) of sharing and sparing (mean ± *SD*) for each change in the input variables. Change in continuous variables is 33% for each step

Variable	Strategy changed	CE sharing	CE sparing
Crop type (total)	0.15 ± 0.11	+22.11 ± 525.31	+0.04 ± 0.32
Almond	0.11 ± 0.06	−0.21 ± 0.07	−0.26 ± 0.06
Citrus	0.16 ± 0.03	+730.15 ± 1241.04	−0.03 ± 0.01
Irrigated wheat	0.15 ± 0.02	+0.67 ± 0.07	+0.49 ± 0.23
Olive	0.17 ± 0.06	+1.11 ± 0.16	+0.02 ± 0
Rain-fed wheat	0.19 ± 0.1	+5.58 ± 3.36	+0.6 ± 0.36
Tomato	0.16 ± 0.01	+781.89 ± 1329.98	−0.04 ± 0.01
Watermelon	0.13 ± 0.26	−0.35 ± 0.23	+0.01 ± 0
Field size (ha)	0.04 ± 0.01	−0.13 ± 0.02	0
Margins width (m)	0.08 ± 0.01	+0.36 ± 0.04	0
Perimeter ratio	0.07 ± 0.01	+0.33 ± 0.04	0
Biodiversity metric (total)	0.03 ± 0.03	0.13 ± 0.34	0.24 ± 0.54
Total richness			
Butterflies	0.01	−0.19 ± 0.06	−0.22 ± 0.05
Birds	0.03	+0.08 ± 0.02	−0.04 ± 0
Ground-dwelling arthropods	0.03	+0.02 ± 0.01	+0.11 ± 0.01
Geometric-mean abundance			
Butterflies	0	0.20 ± 0.07	0.18 ± 0.07
Birds	0.04	−0.14 ± 0.02	0.09 ± 0.02
Ground-dwelling arthropods	0.01	0.06 ± 0.02	0.10 ± 0.01
Plant-associated arthropods	0.08	0.85 ± 0.27	1.49 ± 0.37
Taxonomic group (total)	0.08 ± 0.02	0.00 ± 0.46	0 ± 0.71
Plants	0.07	+0.77 ± 0.38	+1.37 ± 0.4
Butterflies	0.12	+0.01 ± 0.16	−0.35 ± 0.13
Birds	0.06	−0.47 ± 0.03	−0.31 ± 0.04
Ground-dwelling arthropods	0.07	−0.19 ± 0.09	−0.37 ± 0.11
Plant-associated arthropods	0.07	−0.13 ± 0.17	−0.33 ± 0.16
Functional group	0.05 ± 0.05	0.28 ± 0.68	0.33 ± 0.63
Plants (total)	0.06	0.38 ± 0.73	0.52 ± 0.74
Annuals	0.06	0.13 ± 0.05	−0.13 ± 0.02
Perennials	0.13	0.02 ± 0.12	1.29 ± 0.04
Woody	0.14	−0.54 ± 0.13	0.04 ± 0.3
Composites	0.02	1.95 ± 0.64	1.73 ± 0.59
Legumes	0.03	0.94 ± 0.09	1.22 ± 0.1
Graminoids	0.10	−0.13 ± 0.13	−0.42 ± 0.08
Mediterranean	0	0.63 ± 0.17	0.65 ± 0.17
Irano-Turanian	0.01	0.15 ± 0.08	0.08 ± 0.08
Euro-Siberian	0.02	0.28 ± 0.14	0.18 ± 0.13
Birds (total)	0.01	0.13 ± 0.45	0.19 ± 0.5
Red List	0.04	0.21 ± 0.55	0.5 ± 0.65
Non-nesting	0.01	−0.1 ± 0.19	−0.03 ± 0.19
Nesting	0	0 ± 0	0 ± 0
Ground nesting	0.01	−0.22 ± 0.29	−0.25 ± 0.27
Cavity nesting	0.01	0.14 ± 0.11	0.1 ± 0.1

(Continues)

TABLE 1 (Continued)

Variable	Strategy changed	CE sharing	CE sparing
Tree nesting	0	0.77 ± 0.44	0.81 ± 0.45
Butterflies (total)	0.11	0.4 ± 1.03	0.25 ± 0.53
Migratory	0.15	−0.37 ± 0.03	0.1 ± 0.05
Non-migratory	0.08	0.23 ± 0.03	−0.06 ± 0.02
Mediterranean	0.07	−0.24 ± 0.05	−0.02 ± 0.06
Non-Mediterranean	0.13	1.98 ± 0.84	0.99 ± 0.63
Ground-dwelling arthropods (total)	0.06	0.14 ± 0.23	0.21 ± 0.49
Herbivores	0.12	0.19 ± 0.22	0.87 ± 0.35
Predators	0.10	0 ± 0.11	−0.28 ± 0.07
Detritivores	0.03	0.01 ± 0.14	−0.07 ± 0.14
Omnivores	0	0.34 ± 0.22	0.32 ± 0.2

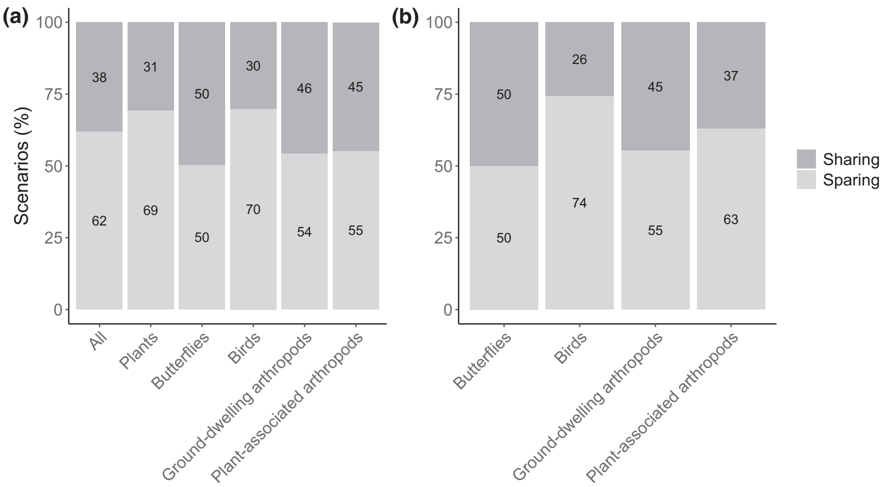

FIGURE 4 Proportion of the scenarios resulting in sparing or sharing for all groups, plants, butterflies, birds, ground-dwelling arthropods in falling traps and plant-associated arthropods in vacuum samples with (a) per visit richness and (b) geometric-mean abundance

would have increased the proportion of scenarios which selected sharing as the cost-effective strategy in larger field sizes, but including this possibility in our model without rigid numbers would be speculative. Future research should seek to overcome this limitation by establishing the yield distance from margin relationships and integrate them in the models.

However, sensitivity to field size was relatively low, and these spatial effects may thus have little effect on the overall favourability of each strategy. Contrary to field size, field margins width and field perimeter ratio increased the cost-effectiveness of sharing, because they reduced the interface between the field and field margins and the risk to crop production. As a result, implementing few wide field margins outperformed the option of implementing many narrow field margins. Large-scale interventions such as wide field margins or set asides can be considered as small-scale sparing. This demonstrates the importance of advancing a multi-scale continuum approach of sparing–sharing instead of the dichotomous scale-insensitive traditional framework (Ekroos et al., 2016; Grass et al., 2019). In that regard, the scale of our study allowed to explore a fraction of this continuum (i.e. different levels of land sharing) and research in larger scale is still needed to cover the full range of options.

The most influential variable in our model was crop composition, consistent with previous studies showing that productivity and cropping system are major variables affecting the sparing–sharing trade-off (Ekroos et al., 2016; Law & Wilson, 2015). As reviewed by Law and Wilson (2015), most sparing–sharing models and empirical studies either study a single type of crop (large monocultures), or ignore the effect of crop type in their analysis. The effects of land use intensification on biodiversity and yield vary among production systems, with especially high variability within harvested crop systems (Beckmann et al., 2019). Here we used a mixed-crop landscape and found that this may be explained by large differences in opportunity costs (i.e. crop profitability and land value) and production losses which drive the ultimate gain from land sparing and land sharing. A recent analysis showed that for small holders land use decisions are prone towards high profitability, reducing landscape multifunctionality threatening biodiversity and livelihood (Grass et al., 2020). Land sharing should preferably be promoted in cropping systems that exhibit a smaller trade-off between productivity and biodiversity. In ecological hotspots, if both goals cannot be achieved together, land sharing may be supported using incentives. Yet, in many regions, landscapes include a diversity of crops along spatial and temporal scales. This adds to the complexity and favours the sparing approach, which may be less dependent on this complexity. Although we did not directly model temporal scale such as crop rotation, we did incorporate different crops into our simulated landscapes. This can be viewed as either spatial variation of crops across the landscape or crop rotation in time, therefore our conclusions may fit both scenarios.

Cost-effectiveness of sparing was substantially more stable than cost-effectiveness of sharing. This makes sharing a high-risk solution that may explain the mixed results obtained in many studies (Grau et al., 2013). Large budgets are directed towards agro-ecological practices (Batáry et al., 2015; Pe'er et al., 2014); thus, more effort should be directed to assess the cost-effectiveness of these practices in different cropping systems (Ansell et al., 2016). We note that the high sensitivity of sharing costs must be interpreted with caution, since it reflects the differences between seven crops in a particular area. The ecological effectiveness of sparing compared to sharing varied between arable fields and orchards due to differences in their baseline biodiversity. However, the favoured strategy was dictated by the costs ratio, so crops that incurred no sharing costs (i.e. tomato and citrus) favoured sharing whereas crops with high sharing costs (i.e. watermelon) favoured sparing and negatively affected the cost-effectiveness of sharing. These effects were non-linear; the probability to change strategy sharply decreased in medium proportions of watermelon in the landscape. Possibly, revenue loss in watermelon was very large, causing extremely high sharing costs when watermelon composed over 20% of the crops. Just as density-yield functions vary among species, the yield-density feedback can vary among crop types, and we may not assume a uniform positive feedback. Indeed, there are indications that some crops benefit more than others from agro-ecological practices aiming to provide ecosystem services (Balzan et al., 2016; Pywell et al., 2015). Depending on the cropping system, land sparing may be favourable to land sharing.

Our approach slightly differs from the classic sparing–sharing framework (Green et al., 2005), which has merits and weaknesses. The cost-effectiveness measure maximizes both farmers' profit and biodiversity, rather than maximizing biodiversity for a selected production target. Thus, our scenarios may result in different yields, as long they retain the same biodiversity gain per unit cost, which could theoretically result in compensation for the yield loss elsewhere. However, such displacement effects are complex and translating increasing yields to spared land requires planning and economic incentives (Phalan, 2018). Such incentive policies are usually planned at national or regional scales. Our approach has an advantage of better informing policy makers about cost-effective land management subsidies at the regional scale which can help bind together changes in yield and sparing land (Ansell et al., 2016).

The biodiversity metric and taxonomic group used in the analysis affected the choice between sparing and sharing, as previously suggested (Fischer et al., 2014). Arthropods, and several bioindicator groups such as non-migratory butterflies, were the main beneficiaries from field margins, and they contributed to higher cost-effectiveness of land sharing relative to land sparing whereas birds and plants (especially perennials) favoured sparing. The choice between abundance-based measure (GMA) and species richness was far less influential than the choice of bioindicators. We chose these measures rather than assessing individual species for two reasons. First, densities of many species, especially the rare species, are too low to assess their response. Furthermore, densities are more susceptible to fluctuations over time (particularly herbaceous plants and arthropods which constitute four of our groups), while overall richness is relatively stable. Our results were consistent with previous assessments in regards to the preferences of the species groups towards sparing and sharing (Hodgson et al., 2010; Phalan et al., 2011). Despite the ecological differences between taxonomic groups, both biodiversity metric and taxonomic group had smaller effect on the choice between sparing and sharing compared to the economic variables. It is therefore concerning that socio-economic factors are rarely discussed relative to other landscape variables (Kremen, 2015).

Ecosystem services and disservices link the ecological processes with the economic outcomes. Although the effect of biodiversity-based ecosystem services on yield is inconsistent (Bommarco et al., 2013; Dainese et al., 2019), the sparing–sharing framework has long been criticized for ignoring these possibly positive feedbacks (Tscharntke et al., 2012). Our model assessed the effect of land management on biodiversity and crop production independently rather than linking them by means of yield-density function, therefore allowing for negative and positive feedbacks on crop production. This may not be the case for ecosystem services that support societal benefits rather than crop production, as for example carbon sequestration and recreation, which may need to be explicitly accounted for since they do not affect crop yield (Kremen & Miles, 2012). Our model demonstrates how economic assessments can optimize for complex relations between biodiversity, ecosystem services and disservices and crop production to provide a more solid base for policy design. We only show this proof-of-concept for production-supporting ecosystem services, but future studies should quantify these complex relations empirically and incorporate more services and disservices into the sparing–sharing framework.

5 | CONCLUSIONS

Economic implications of sparing and sharing, driven by the crop type, outweighed the effect of spatial configuration and ecological effects in determining the sparing–sharing optimization. Understanding the socio-economic factors can advance the sparing–sharing debate, and substantially improve the robustness of sparing–sharing assessments. Our results emphasize the importance of socio-economic factors in the design of multi-functional landscapes (Fischer et al., 2017). The high costs of conservation in productive lands and the bias towards low-value land is a well-known problem in conservation (Shwartz et al., 2017), yet, it seems that expanding conservation efforts towards production areas to minimize this bias may suffer from the very same problem. Adopting a crop-specific strategy and allocating croplands to sharing or to sparing according to their specific cost-benefit, can provide a robust solution that promotes both biodiversity and crop production. Promoting such strategies requires profound understanding of the cost-effectiveness of biodiversity conservation strategies (Wätzold et al., 2010). We highlight several trade-offs between bioindicators as well as crop types, which call for careful selection of targets. Still, our results suggest that land sparing is favoured over a wide range of conditions, and it is less sensitive to landscape and economic context. Land sharing may complement land sparing where synergies between crop production and biodiversity occur, but more experimental evidence of such synergies is needed.

ACKNOWLEDGEMENTS

We thank Tamar Keasar, Yaron Ziv and Niv DeMalach for helping to improve the manuscript. This work was supported by Nekudat Hen Foundation, Israeli Ministry of Agriculture and Israel Nature and Parks Authority. We also wish to thank David R. Williams and an anonymous reviewer for their constructive comments that improved this article. Vector graphics for plants and animals were downloaded from www.freepik.com.

CONFLICT OF INTEREST

The authors have no conflict of interest.

AUTHORS' CONTRIBUTIONS

All authors conceived the idea for the paper; H.S. and A.S. collected the data; H.S., A.S. and Y.C. developed the simulation model and H.S. analysed the data; H.S. wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.msbcc2g04 (Segre et al., 2021).

ORCID

Hila Segre https://orcid.org/0000-0002-3354-4675
Yohay Carmel https://orcid.org/0000-0002-5883-0184

REFERENCES

Ansell, D., Freudenberger, D., Munro, N., & Gibbons, P. (2016). The cost-effectiveness of agri-environment schemes for biodiversity conservation: A quantitative review. *Agriculture, Ecosystems and Environment*, *225*, 184–191. https://doi.org/10.1016/j.agee.2016.04.008

Balzan, M. V., Bocci, G., & Moonen, A. C. (2016). Landscape complexity and field margin vegetation diversity enhance natural enemies and reduce herbivory by Lepidoptera pests on tomato crop. *BioControl*, *61*(2), 141–154. https://doi.org/10.1007/s10526-015-9711-2

Barral, M. P., Rey Benayas, J. M., Meli, P., & Maceira, N. O. (2015). Quantifying the impacts of ecological restoration on biodiversity and ecosystem services in agroecosystems: A global meta-analysis. *Agriculture, Ecosystems and Environment*, *202*, 223–231. https://doi.org/10.1016/j.agee.2015.01.009

Batáry, P., Dicks, L. V., Kleijn, D., & Sutherland, W. J. (2015). The role of agri-environment schemes in conservation and environmental management. *Conservation Biology*, *29*(4), 1006–1016. https://doi.org/10.1111/cobi.12536

Beckmann, M., Gerstner, K., Akin-Fajiye, M., Ceaușu, S., Kambach, S., Kinlock, N. L., Phillips, H. R. P., Verhagen, W., Gurevitch, J., Klotz, S., Newbold, T., Verburg, P. H., Winter, M., & Seppelt, R. (2019). Conventional land-use intensification reduces species richness and increases production: A global meta-analysis. *Global Change Biology*, *25*(6), 1941–1956. https://doi.org/10.1111/gcb.14606

Bennett, E. M. (2017). Changing the agriculture and environment conversation. *Nature Ecology and Evolution*, *1*(1), 1–2. https://doi.org/10.1038/s41559-016-0018

Bommarco, R., Kleijn, D., & Potts, S. G. (2013). Ecological intensification: Harnessing ecosystem services for food security. *Trends in Ecology & Evolution*, *28*(4), 230–238. https://doi.org/10.1016/j.tree.2012.10.012

Butsic, V., & Kuemmerle, T. (2015). Using optimization methods to align food production and biodiversity conservation beyond land sharing and land sparing. *Ecological Applications*, *25*(3), 589–595. https://doi.org/10.1890/14-1927.1.sm

Concepción, E. D., Díaz, M., Kleijn, D., Báldi, A., Batáry, P., Clough, Y., Gabriel, D., Herzog, F., Holzschuh, A., Knop, E., Marshall, E. J. P., Tscharntke, T., & Verhulst, J. (2012). Interactive effects of landscape context constrain the effectiveness of local agri-environmental management. *Journal of Applied Ecology*, *49*, 695–705. https://doi.org/10.1111/j.1365-2664.2012.02131.x

Dainese, M., Martin, E. A., Aizen, M. A., Albrecht, M., Bartomeus, I., Bommarco, R., Carvalheiro, L. G., Chaplin-Kramer, R., Gagic, V., Garibaldi, L. A., Ghazoul, J., Grab, H., Jonsson, M., Karp, D. S., Kennedy, C. M., Kleijn, D., Kremen, C., Landis, D. A., Letourneau, D. K., … Steffan-Dewenter, I. (2019). A global synthesis reveals biodiversity-mediated benefits for crop production. *Science Advances*, *5*(10), eaax0121. https://doi.org/10.1126/sciadv.aax0121

Egan, J. F., & Mortensen, D. A. (2012). A comparison of land-sharing and land-sparing strategies for plant richness conservation in agricultural landscapes. *Ecological Applications*, *22*(2), 459–471. https://doi.org/10.1890/11-0206.1

Ekroos, J., Ödman, A. M., Andersson, G. K. S., Birkhofer, K., Herbertsson, L., Klatt, B. K., Olsson, O., Olsson, P. A., Persson, A. S., Prentice, H. C., Rundlöf, M., & Smith, H. G. (2016). Sparing land for biodiversity at multiple spatial scales. *Frontiers in Ecology and Evolution*, *3*(141), 1–11. https://doi.org/10.3389/fevo.2015.00145

Ekroos, J., Olsson, O., Rundlöf, M., Wätzold, F., & Smith, H. G. (2014). Optimizing agri-environment schemes for biodiversity, ecosystem services or both? *Biological Conservation*, *172*, 65–71. https://doi.org/10.1016/j.biocon.2014.02.013

Fischer, J., Abson, D. J., Bergsten, A., French Collier, N., Dorresteijn, I., Hanspach, J., Hylander, K., Schultner, J., & Senbeta, F. (2017). Reframing the food-biodiversity challenge. *Trends in Ecology & Evolution*, *32*(5), 335–345. https://doi.org/10.1016/j.tree.2017.02.009

Fischer, J., Abson, D. J., Butsic, V., Chappell, M. J., Ekroos, J., Hanspach, J., Kuemmerle, T., Smith, H. G., & Wehrden, H. (2014). Land sparing versus land sharing: Moving forward. *Conservation Letters*, *7*(3), 149–157. https://doi.org/10.1111/conl.12084

Fischer, J., Brosi, B., Daily, G. C., Ehrlich, P. R., Goldman, R., Goldstein, J., Lindenmayer, D. B., Manning, A. D., Mooney, H. A., Pejchar, L., Ranganathan, J., & Tallis, H. (2008). Should agricultural policies encourage land sparing or wildlife-friendly farming? *Frontiers in Ecology and the Environment*, *6*(7), 380–385. https://doi.org/10.1890/070019

Grass, I., Kubitza, C., Krishna, V. V., Corre, M. D., Mußhoff, O., Pütz, P., Drescher, J., Rembold, K., Ariyanti, E. S., Barnes, A. D., Brinkmann, N., Brose, U., Brümmer, B., Buchori, D., Daniel, R., Darras, K. F. A., Faust, H., Fehrmann, L., Hein, J., … Wollni, M. (2020). Trade-offs between multifunctionality and profit in tropical smallholder landscapes. *Nature Communications*, *11*(1). https://doi.org/10.1038/s41467-020-15013-5

Grass, I., Loos, J., Baensch, S., Batáry, P., Librán-Embid, F., Ficiciyan, A., Klaus, F., Riechers, M., Rosa, J., Tiede, J., Udy, K., Westphal, C., Wurz, A., & Tscharntke, T. (2019). Land-sharing/-sparing connectivity landscapes for ecosystem services and biodiversity conservation. *People and Nature*, *1*(2), 262–272. https://doi.org/10.1002/pan3.21

Grau, R., Kuemmerle, T., & Macchi, L. (2013). Beyond 'land sparing versus land sharing': Environmental heterogeneity, globalization and the balance between agricultural production and nature conservation. *Current Opinion in Environmental Sustainability*, *5*(5), 477–483. https://doi.org/10.1016/j.cosust.2013.06.001

Green, R. E., Cornell, S. J., Scharlemann, J. P. W., & Balmford, A. (2005). Farming and the fate of wild nature. *Science*, *307*(5709), 550–555. https://doi.org/10.1126/science.1106049

Hodgson, J. A., Kunin, W. E., Thomas, C. D., Benton, T. G., & Gabriel, D. (2010). Comparing organic farming and land sparing: Optimizing yield and butterfly populations at a landscape scale. *Ecology Letters*, *13*(11), 1358–1367. https://doi.org/10.1111/j.1461-0248.2010.01528.x

Kremen, C. (2015). Reframing the land-sparing/land-sharing debate for biodiversity conservation. *Annals of the New York Academy of Sciences*, *1355*(1), 52–76. https://doi.org/10.1111/nyas.12845

Kremen, C., & Miles, A. (2012). Ecosystem services in biologically diversified versus conventional farming systems. *Ecology and Society*, *17*(4), 40. https://doi.org/10.5751/ES-05035-170440

Law, E. A., & Wilson, K. A. (2015). Providing context for the land-sharing and land-sparing debate. *Conservation Letters*, *8*(6), 404–413. https://doi.org/10.1111/conl.12168

Legras, S., Martin, E., & Piguet, V. (2018). Conjunctive implementation of land sparing and land sharing for environmental preservation. *Ecological Economics*, *143*, 170–187. https://doi.org/10.1016/j.ecolecon.2017.07.006

Luskin, M. S., Lee, J. S. H., Edwards, D. P., Gibson, L., & Potts, M. D. (2018). Study context shapes recommendations of land-sparing and sharing; a quantitative review. *Global Food Security*, *16*, 29–35. https://doi.org/10.1016/j.gfs.2017.08.002

Morris, M. D. (1991). Factorial sampling plans for preliminary computational experiments. *Technometrics*, *33*(2), 161–174. https://doi.org/10.1080/00401706.1991.10484804

Naidoo, R., & Iwamura, T. (2007). Global-scale mapping of economic benefits from agricultural lands: Implications for conservation priorities. *Biological Conservation*, *140*(1–2), 40–49. https://doi.org/10.1016/j.biocon.2007.07.025

Pe'er, G., Dicks, L. V., Visconti, P., Arlettaz, R., Báldi, A., Benton, T. G., Collins, S., Dieterich, M., Gregory, R. D., Hartig, F., Henle, K., Hobson, P. R., Kleijn, D., Neumann, R. K., Robijns, T., Schmidt, J., Shwartz, A., Sutherland, W. J., Turbé, A., … Scott, A. V. (2014). EU agricultural reform fails on biodiversity. *Science*, *344*(6188), 1090–1092. https://doi.org/10.1126/science.1253425

Phalan, B. (2018). What have we learned from the land sparing-sharing model? *Sustainability*, *10*(6), 1760. https://doi.org/10.3390/su10061760

Phalan, B., Onial, M., Balmford, A., & Green, R. E. (2011). Reconciling food production and biodiversity conservation: Land sharing and land sparing compared. *Science*, *333*(6047), 1289–1291. https://doi.org/10.1126/science.1208742

Pywell, R. F., Heard, M. S., Bradbury, R. B., Hinsley, S., Nowakowski, M., Walker, K. J., & Bullock, J. M. (2012). Wildlife-friendly farming benefits rare birds, bees and plants. *Biology Letters*, *8*(5), 772–775. https://doi.org/10.1098/rsbl.2012.0367

Pywell, R. F., Heard, M. S., Woodcock, B. A., Hinsley, S., Ridding, L., Nowakowski, M., & Bullock, J. M. (2015). Wildlife-friendly farming increases crop yield: Evidence for ecological intensification. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1816), 20151740. https://doi.org/10.1098/rspb.2015.1740

R Core Team. (2017). *R: A language and environment for statistical computing*. Retrieved from https://www.r-project.org/

Saltelli, A., & Tarantola, S. (2004). *Sensitivity analysis in practice: A guide to assessing scientific models*. John Wiley & Sons, Ltd. https://doi.org/10.1002/9780470057339.vas015

Santini, L., Belmaker, J., Costello, M. J., Pereira, H. M., Rossberg, A. G., Schipper, A. M., Ceaușu, S., Dornelas, M., Hilbers, J. P., Hortal, J., Huijbregts, M. A. J., Navarro, L. M., Schiffers, K. H., Visconti, P., & Rondinini, C. (2017). Assessing the suitability of diversity metrics to detect biodiversity change. *Biological Conservation*, *213*, 341–350. https://doi.org/10.1016/j.biocon.2016.08.024

Segoli, M., & Rosenheim, J. A. (2012). Should increasing the field size of monocultural crops be expected to exacerbate pest damage? *Agriculture, Ecosystems and Environment*, *150*, 38–44. https://doi.org/10.1016/j.agee.2012.01.010

Segre, H., Carmel, Y., Segoli, M., Tchetchik, A., Renan, I., Perevolotsky, A., Rotem, D., & Shwartz, A. (2019). Cost-effectiveness of uncultivated field-margins and semi-natural patches in Mediterranean areas: A multi-taxa, landscape scale approach. *Biological Conservation*, *240*, 108262. https://doi.org/10.1016/j.biocon.2019.108262

Segre, H., Carmel, Y., & Shwartz, A. (2021). Data from: Economic and not ecological variables shape the sparing–sharing trade-off in a mixed cropping landscape. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.msbcc2g04

Segre, H., Segoli, M., Carmel, Y., & Shwartz, A. (2020). Experimental evidence of multiple ecosystem services and disservices provided by ecological intensification in Mediterranean agro-ecosystems. *Journal of Applied Ecology*, *57*(10), 2041–2053. https://doi.org/10.1111/1365-2664.13713

Seppelt, R., Arndt, C., Beckmann, M., Martin, E. A., & Hertel, T. W. (2020). Deciphering the biodiversity-production mutualism in the global food security debate. *Trends in Ecology & Evolution*, *35*(11), 1011–1020. https://doi.org/10.1016/j.tree.2020.06.012

Shackelford, G. E., Steward, P. R., German, R. N., Sait, S. M., & Benton, T. G. (2015). Conservation planning in agricultural landscapes: Hotspots of conflict between agriculture and nature. *Diversity and Distributions*, *21*(3), 357–367. https://doi.org/10.1111/ddi.12291

Shwartz, A., Davies, Z. G., Macgregor, N. A., Crick, H. Q. P., Clarke, D., Eigenbrod, F., Gonner, C., Hill, C. T., Knight, A. T., Metcalfe, K., Osborne, P. E., Phalan, B., & Smith, R. J. (2017). Scaling up from protected areas in England: The value of establishing large conservation areas. *Biological Conservation*, *212*, 279–287. https://doi.org/10.1016/j.biocon.2017.06.016

Sirami, C., Gross, N., Baillod, A. B., Bertrand, C., Carrié, R., Hass, A., Henckel, L., Miguet, P., Vuillot, C., Alignier, A., Girard, J., Batáry, P., Clough, Y., Violle, C., Giralt, D., Bota, G., Badenhausser, I., Lefebvre, G., Gauffre, B., … Fahrig, L. (2019). Increasing crop heterogeneity enhances multitrophic diversity across agricultural regions. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(33), 16442–16447. https://doi.org/10.1073/pnas.1906419116

Tilman, D., Clark, M., Williams, D. R., Kimmel, K., Polasky, S., & Packer, C. (2017). Future threats to biodiversity and pathways to their prevention. *Nature*, *546*, 73–81. https://doi.org/10.1038/nature22900

Troupin, D., & Carmel, Y. (2014). Can agro-ecosystems efficiently complement protected area networks? *Biological Conservation*, *169*, 158–166. https://doi.org/10.1016/j.biocon.2013.11.009

Tscharntke, T., Clough, Y., Wanger, T. C., Jackson, L., Motzke, I., Perfecto, I., Vandermeer, J., & Whitbread, A. (2012). Global food security, biodiversity conservation and the future of agricultural intensification. *Biological Conservation*, *151*(1), 53–59. https://doi.org/10.1016/j.biocon.2012.01.068

Tschumi, M., Albrecht, M., Bärtschi, C., Collatz, J., Entling, M. H., & Jacot, K. (2016). Perennial, species-rich wildflower strips enhance pest control and crop yield. *Agriculture, Ecosystems and Environment*, *220*, 97–103. https://doi.org/10.1016/j.agee.2016.01.001

von Wehrden, H., Abson, D. J., Beckmann, M., Cord, A. F., Klotz, S., & Seppelt, R. (2014). Realigning the land-sharing/land-sparing debate to match conservation needs: Considering diversity scales and land-use history. *Landscape Ecology*, *29*(6), 941–948. https://doi.org/10.1007/s10980-014-0038-7

Wätzold, F., Mewes, M., van Apeldoorn, R., Varjopuro, R., Chmielewski, T. J., Veeneklaas, F., & Kosola, M. L. (2010). Cost-effectiveness of managing Natura 2000 sites: An exploratory study for Finland, Germany, the Netherlands and Poland. *Biodiversity and Conservation*, *19*(7), 2053–2069. https://doi.org/10.1007/s10531-010-9825-x

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Segre, H., Carmel, Y., & Shwartz, A. (2022). Economic and not ecological variables shape the sparing–sharing trade-off in a mixed cropping landscape. *Journal of Applied Ecology*, 59, 779–790. https://doi.org/10.1111/1365-2664.14092