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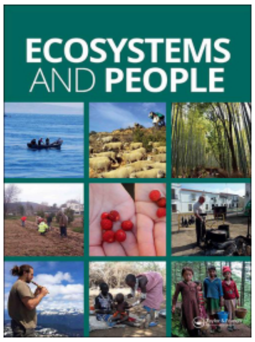

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Jiangxiao Qiu [a], Cibele Queiroz [b], Elena M. Bennett [c], Anna F. Cord [d,e], Emilie Crouzat [f,g], Sandra Lavorel [f], Joachim Maes [h], Megan Meacham [b], Albert V. Norström [b], Garry D. Peterson [b], Ralf Seppelt [d] and Monica G. Turner[i]

[a]School of Forest Resources & Conservation, Fort Lauderdale Research and Education Center, University of Florida, Davie, FL, USA; [b]Stockholm Resilience Centre, Stockholm University, Stockholm, Sweden; [c]Department of Natural Resource Sciences and McGill School of Environment, McGill University, Montreal, Canada; [d]Department of Computational Landscape Ecology, UFZ – Helmholtz Centre for Environmental Research, Leipzig, Germany; [e]Chair of Computational Landscape Ecology, Institute of Geography, Technische Universität Dresden, Dresden, Germany; [f]Laboratoire d'Ecologie Alpine, CNRS – Université Grenoble Alpes, Grenoble, France; [g]University of Grenoble Alpes, INRAE, LESSEM, Grenoble, France; [h]European Commission, Joint Research Centre, Ispra, Italy; [i]Department of Integrative Biology, University of Wisconsin-Madison, Madison, WI, USA

ABSTRACT

A key sustainability challenge in human-dominated landscapes is how to reconcile competing demands such as food production, water quality, climate regulation, and ecological amenities. Prior research has documented how efforts to prioritize desirable ecosystem services such as food and fiber have often led to tradeoffs with other services. However, the growing literature has revealed different and sometimes contradictory patterns in ecosystem service relationships. It thus remains unclear whether there are generalizable patterns across social-ecological systems, and if not, what factors explain the variations. In this study, we synthesize datasets of five ecosystem services from four social-ecological systems. We ask: (1) Are ecosystem service relationships consistent across distinct regional social-ecological systems? (2) How do ecosystem service relationships vary with land-use intensity at the landscape scale? (3) In case of ecosystem service tradeoffs, how does land-use intensity affect intersection points of tradeoffs along the landscape composition gradient? Our results reveal that land-use intensity increases magnitude of ecosystem service tradeoffs (e.g. food production vs. climate regulation and water quality) across landscapes. Land-use intensity also alters where provisioning and regulating services intersect: in high-intensity systems, food production and regulating services can be both sustained only at smaller proportions of agricultural lands, whereas in low-intensity systems, these services could be both supplied with greater proportions of agricultural lands. Our research demonstrates importance of considering multiple aspects of land uses (landscape composition and land-use intensity), and provides a more nuanced understanding and framework to enhance our ability to predict how land use alters ecosystem service relationships.

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Introduction

Sustaining ecosystem services and natural capital is fundamental to human society but challenged by anthropogenic modifications of the biosphere (Carpenter et al. 2009; Díaz et al. 2019). Humans have long managed our landscapes to produce desirable goods and services, such as food, fiber and timber products, to fulfil basic material needs (Imhoff et al. 2004; Ramankutty et al. 2008; Seppelt et al. 2014). However, these anthropogenic efforts to prioritize the supply of one or few services may negatively affect others due to tradeoff mechanisms (Rodríguez et al. 2006; Bennett et al. 2009; Cavender-Bares et al. 2015), thus compromising landscape multifunctionality (Mastrangelo et al. 2014; Hölting et al. 2019). Prominent examples include increased crop production at the expense of water quality (e.g. due to fertilizer use), carbon storage and water quantity tradeoffs (e.g. as a result of land-use change), and increased livestock production at the cost of soil carbon storage and biodiversity (e.g. at the high grazing intensity) (Rodríguez et al. 2006; Gerstner et al. 2014; Petz et al. 2014). Hence, understanding the land system multifunctionality and considering multiple ecosystem services holistically by addressing their interactions stands as a key challenge in landscape and natural resource management (Tallis and Polasky 2009; Qiu and Turner 2013; Ellis et al. 2019).

Over the past decade, a proliferation of research has revealed important relationships (i.e. tradeoffs and synergies) among provisioning, regulating and cultural services across a range of social-ecological systems and scales, as highlighted in several reviews and syntheses (e.g. Mouchet et al. 2014; Howe et al.

CONTACT Jiangxiao Qiu qiuj@ufl.edu School of Forest Resources & Conservation, Fort Lauderdale Research and Education Center, University of Florida, Davie, FL, USA

2014; Lee and Lautenbach 2016; Cord et al. 2017; Qiu 2019). However, different or even contradictory results have been reported. For example, Goldstein et al. (2012) showed tradeoffs between carbon storage and water quality across different land-use planning scenarios in O'ahu, Hawaii, whereas such tradeoffs were manifested as synergies in other regional watersheds in the U.S. (Nelson et al. 2009; Qiu and Turner 2013). Similarly, carbon storage and biodiversity were often characterized as synergies at national or global scales, but they showed mixed patterns and sometimes as tradeoffs at local scales (Anderson et al. 2009; Cimon-Morin et al. 2013; Palomo et al. 2019). Moreover, even the well-recognized tradeoffs between crop production and water quality can be context- and scale-dependent (Qiu et al. 2018b), evolve over time, and even shift towards synergies with proactive landscape management and policy interventions (Qiu et al. 2018a). Hence, it remains questionable whether patterns of ecosystem service relationships across distinct social-ecological systems can be generalizable. Such context- and scale-dependency also underlies the importance of addressing factors and mechanisms that could shape the patterns and dynamics of ecosystem service relationships (Cord et al. 2017; Spake et al. 2017; Vallet et al. 2018; Dade et al. 2018; Seppelt et al. 2020).

Among all drivers of global environmental changes, land use is arguably exerting the most significant impacts on nature and its life-supporting services (IPBES 2019). Here, land use is broadly defined to encompass the *composition* (i.e. amount) and *configuration* (i.e. spatial arrangement) of land-use elements (such as natural vs. agricultural covers), as well as their *intensity* (such as the amount of human inputs including fertilizer and pesticide, crop diversity, fallow length, tillage, and harvesting approach) (Van Asselen and Verburg 2012; Seppelt et al. 2016; Beckmann et al. 2019). All these different aspects of land use can affect the simultaneous supply of multiple ecosystem services and hence drive their relationships, either directly or indirectly via altering biodiversity and functional composition that underpin ecosystem functions and services (Bennett et al. 2009; Lavorel and Grigulis 2012; Chillo et al. 2018).

Mounting theoretical and empirical studies have investigated the effects of land use on ecosystem service relationships. Specifically, intensive land uses to promote a small set of provisioning services (e.g. food production) may be accompanied by declines in other services (e.g. biodiversity, water quality, soil retention) (Qiu and Turner 2013; Seppelt et al. 2016; Felipe-Lucia et al. 2018; Beckmann et al. 2019). In addition, if land-use change has negative effects on biodiversity, then a range of services that depends upon biodiversity (e.g. pollination and pest control) will be threatened (Isbell et al. 2011; Cardinale et al. 2012; Allan et al. 2015; Seppelt et al. 2020). Nonetheless, current understanding still remains patchy and is constrained to a particular set of services and/or systems. Moreover, few studies have investigated how different aspects of land use and their interactions affect ecosystem service relationships (e.g. response curves of multiple services to land-use gradients; Lindborg et al. 2017), especially in human-dominated landscapes where tradeoffs are more common. These knowledge gaps highlight the need for cross-study comparisons and a unified framework for synthesis (Meacham et al. 2016; Spake et al. 2017).

In this study, we propose three propositions (Figure 1) to demonstrate conceptually how land use could affect ecosystem services and their relationships, and test them by synthesizing datasets of ecosystem service indicators from deliberately selected regional social-ecological systems. We ask three research questions: **(1)** Are ecosystem service relationships consistent across distinct regional social-ecological systems? **(2)** How do ecosystem service relationships vary with land-use intensity at the landscape scale? **(3)** In case of ecosystem service tradeoffs, how does land-use intensity affect the intersection points of tradeoffs (i.e. where two services are provided at the same relative level) along the landscape composition gradient?

Proposed land-use effects on ecosystem service relationships

Previous regional and global assessments have suggested that, historically, human-domination of landscapes has increased provisioning services (e.g. food, fiber, and bioenergy products), and simultaneously reduced most regulating services (e.g. water and air purification, climate regulation, water flow regulation, and biodiversity) (Carpenter et al. 2009; Dittrich et al. 2017; Díaz et al. 2019). Hence, with the concept of 'space-for-time' substitution (Pickett 1989), it would be reasonable to expect that provisioning services could increase with the amount of human-transformation of landscapes (e.g. percent agricultural lands), and regulating services could exhibit the opposite pattern, leading to tradeoffs (***Proposition 1***, Figure 1(a)).

In addition, ecosystem service relationships could also vary with land-use intensity across different landscapes (i.e. areas of each case study region that range from several to thousands of km^2). Specifically, ecosystem service tradeoffs may be more pronounced in areas or landscapes with greater land-use intensity (e.g. indicated as higher human inputs such as nutrients, or higher prioritization of certain provisioning services) (Petz et al. 2014; Gong et al. 2019) (***Proposition 2***, Figure 1(b)). On the other hand, synergies among ecosystem services may decline

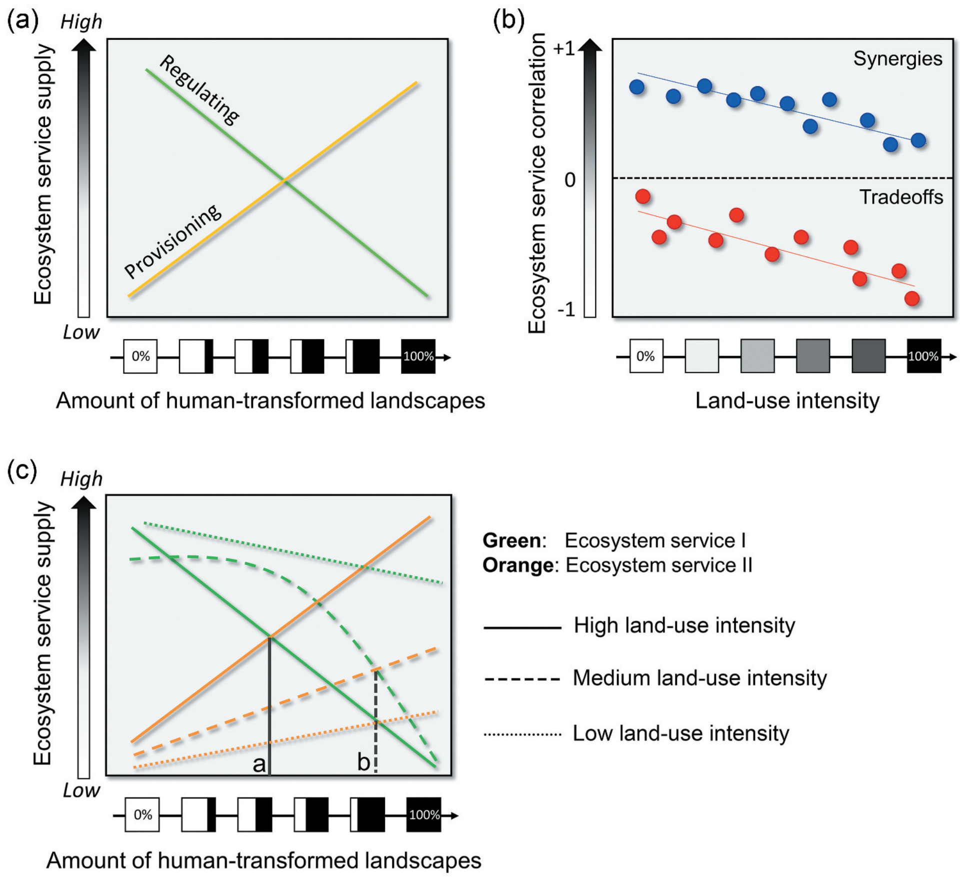

Figure 1. Propositions regarding land-use effects on ecosystem service relationships. In panel A, we anticipate that the supply of provisioning services would increase with the composition of human-transformed landscapes (e.g. percent agricultural lands), but regulating services would show the opposite pattern, resulting in a tradeoff relationship. In panel B, we expect that the magnitude of ecosystem service tradeoffs would increase whereas the magnitude of ecosystem service synergies would decline with the degree of land-use intensity across landscapes. In panel C, for ecosystem service tradeoffs, we further anticipate that the intersection points (i.e. where multiple services are supplied at the same relative levels) will occur at the lower proportion of human-transformed landscapes when these are managed with higher intensities (i.e. *intersection point a, Solid lines*). In contrast, the intersection points would occur at the greater proportion of human-transformed landscapes when these are managed with lower intensities (i.e. *intersection point b, Dash lines*). Under the situation of very low land-use intensity (i.e. *Dotted lines*), the two ecosystem services may not even intersect, indicating the likelihood of achieving balanced supply of multiple services even with the high proportion of human-transformed landscapes.

with increasing land-use intensity, since intensive anthropogenic activities could weaken or decouple synergistic relationships among services (Vallet et al. 2018; Qiu et al. 2018b; Santos-Martín et al. 2019) (***Proposition 2***, Figure 1(b)). However, whether these patterns are robust across distinct regional social-ecological systems has not been fully tested.

Some ecosystem service tradeoffs can be inevitable, for example, due to biophysical constraints that limit multifunctionality or cause inherent tradeoffs (Cord et al. 2017). Hence, it is intriguing, from both scientific and practical standpoints, to identify where and how tradeoffs among ecosystem services could be lessened (i.e. multiple services are balanced at same relative levels) through deliberate landscape management. Based on our conceptual diagram (Figure 1(c)), where two ecosystem services intersect along the landscape gradient may indicate such balancing points in tradeoffs where no service is maximized or prioritized at the expenses of another (i.e. both services were supplied at 'intermediate' levels). Hence, our final proposition (***Proposition 3***, Figure 1(c)) is centered on the intersection points of ecosystem service tradeoffs, inspired by Seppelt et al. (2016) who conceptualized 'biodiversity–agriculture production' tradeoffs as a function of landscape composition, landscape configuration, and land-use intensity. Assuming all other context-dependencies remain constant, we anticipate that the intersection points for ecosystem services tradeoffs would occur at a lesser proportion of human-transformed landscapes if these are managed with higher intensities (Figure 1(c), solid line). In contrast, the intersection points would occur at a greater proportion of human-transformed landscapes if these are managed with lower intensities (Figure 1(c), dash line). Under extreme conditions of very low-intensity land use, there even may be no intersection points (Figure 1 (c), dotted line). Explicitly testing these propositions and identifying the intersection points (or lack thereof) is a critical step to mitigate undesirable tradeoffs and balance the supply of diverse ecosystem services.

Materials and methods

We collated datasets from four well-studied regional social-ecological systems that quantified an equivalent suite of ecosystem service indicators (Table 1) and spanned the gradient of land uses and social-ecological conditions needed to test our propositions (Figure 2). Two provisioning services (crop and animal production), two regulating services (water quality and climate regulation), and one cultural service (outdoor recreation) were quantified in all selected study systems, except for climate regulation in the Norrström basin, Sweden. Our selection of services was based on: (1) their social-ecological importance; (2) the need to encompass a range of ecosystem service categories; and (3) most importantly, the availability, compatibility, and consistency of datasets across different studies. All datasets were contributed by the principal investigators of respective cases. Please refer to the original publications of

Table 1. Selected ecosystem services and their corresponding indicators collated from four regional case studies for this synthesis research.

	Biophysical indicators			
Ecosystem services	Norrström [1]	French Alps [2]	Montérégie [3]	Yahara [4]
Provisioning service				
Crop production	Wheat production	Major crop production	Percent land dedicated to crop production	Major crop production
Animal production	Livestock (cattle, pig and sheep) production	Major forage crop production	Pork production	Major forage crop production for livestock
Regulating service				
Water quality	Nutrient retention capacity	Nutrient retention capacity	Drinking water quality	†Phosphorus runoff to surface-water
Climate regulation	–	Carbon storage (above- and below-ground, dead organic matter, soil C)	Aboveground carbon sequestration	Carbon storage (above- and below-ground, dead organic matter, soil C)
Cultural service				
Outdoor recreation	Outdoor recreational areas	Recreational potential index	Percent forest lands for recreation	Recreational score

†Inverse indicator, where greater value of indicators represents low supply of service and vice versa. Inverse indicator was transformed prior to data analysis so that the value of indicator positively correlates with the supply of ecosystem services.
'–' indicates no data available for this ecosystem service.
References for datasets of ecosystem service estimates: (1) Norrström basin, Sweden (Queiroz et al. 2015); (2) French Alps, France (Crouzat et al. 2015); (3) Montérégie, Canada (Raudsepp-Hearne et al. 2010); (4) Yahara watershed, USA (Qiu and Turner 2013).

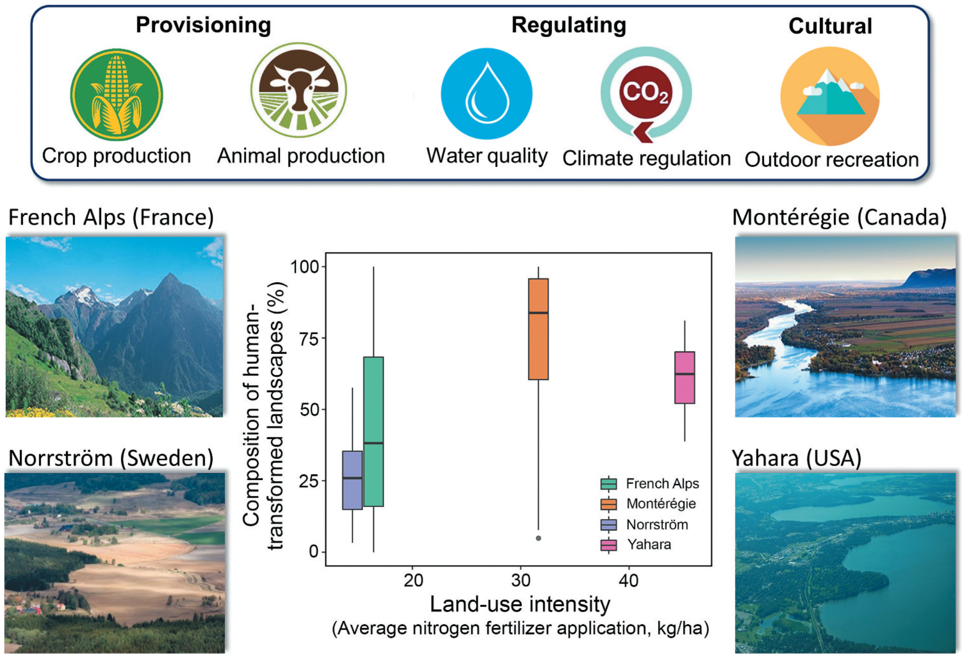

Figure 2. Land-use characteristics (i.e. landscape composition and land-use intensity) of all case studies and their supplied ecosystem services that are included in our synthesis.

each study for details on data source, quantification approach, and accuracy assessment for ecosystem services (Table 1) (Raudsepp-Hearne et al. 2010; Qiu and Turner 2013; Queiroz et al. 2015; Crouzat et al. 2015).

All ecosystem services were quantified using biophysical indicators that capture key ecological properties and processes that underlie the supply of each service (Qiu et al. 2019). It is worth noting that, for each given case, indicators of all ecosystem services were quantified independently (e.g. using independent data sources, methods, etc.) and therefore no underlying factors (e.g. land use/cover) would confound their relationships, with the exception of crop production in one case (i.e. Montérégie). Because indicators used to quantify ecosystem services were often determined by local contexts, specific researchers, and data availability, it is not surprising that the indicators generally differ across studies and systems (Feld et al. 2009; Reyers et al. 2013). Nonetheless, all indicators were comparable and contributed to different aspects of human well-being (Table 1). For example, crop and animal production were quantified using the amount of major crops and livestock produced; water quality was assessed with indicators reflecting the capacity of landscapes to retain nutrients that would otherwise contaminate water bodies; climate regulation was estimated using the amount of carbon stored in major pools; and outdoor recreation was quantified based on the primary factors contributing to the recreational uses, accessibility, or quantity of resources dedicated to providing recreational benefits to humans. Having a harmonized set of indicators across studies may be more ideal, but it is challenging. However, given the nature of these indicators and our understanding of the systems, we expect that our choices of indicators will minimally affect the correlations observed among services and thus our qualitative conclusions.

Prior to analysis, all indicators of ecosystem services were summarized to municipality, subwatershed, or equivalent units – a spatial scale at which land-use effects are manifested and where land management often takes place (Qiu and Turner 2015). For each case study, we then standardized indicators of all ecosystem services to 0–1 scale, and transformed as necessary so that higher values corresponded to greater service supply, following Qiu and Turner (2013). For each study, we also collected data on: (1) landscape composition (i.e. the amount of land use such as agricultural lands), whose data was contributed by each case study; and (2) land-use intensity (i.e. quantified using nitrogen fertilizer application), whose data was derived from a global dataset compiled by Potter et al. (2011). We did not consider landscape configuration because prior studies suggested that landscape composition played a dominant role in affecting these services (Qiu and Turner 2015; Lamy et al. 2016), and composition also constrains configuration (Gardner et al. 1987; Gustafson 1998). Moreover, with the appreciation of multiple aspects of land-use intensity (e.g. farm size, labor, harvest method and frequency, and chemical use) (Turner and Doolittle 1978; Rasmussen et al. 2018; Meyfroidt et al. 2018; Beckmann et al. 2019), we chose nitrogen fertilization as a proxy because: (1) it is a key indicator commonly used to analyze land-use intensity effects on the environment (Kleijn et al. 2009); (2) it has been widely used in our selected case studies to improve yields; and (3) it is publicly available.

To address our first question, we calculated the Spearman rank correlation for all possible combinations of ecosystem service pairs (i.e. 10 pairs total) and compared the magnitude and direction of relationships across case studies. Spearman rank correlation was chosen because of its robustness to non-normality and potential outliers (Li et al. 2017). To address our second question on how ecosystem service relationships vary with land-use intensity across landscapes, we first categorized the pair of ecosystem services into 'tradeoff' group if it is predominated by negative correlations, or as 'synergies' if predominated by positive correlations. We then plotted Spearman rank correlations against the land-use intensity indicator (mean nitrogen fertilizer application calculated in each case) with fitted linear regressions for each group (i.e. tradeoffs vs. synergies) of ecosystem service pairs. To address our third question, within each case study, we first plotted indicators of paired ecosystem services against percent agricultural lands and fitted with regression lines, and then determined where these two response curves intersected. We focused this analysis on selected pairs of provisioning vs. regulating services where tradeoffs were most dominant. Intersection points along the composition gradient of agricultural lands were further compared across regional social-ecological systems to test our proposition on how landscape-level land-use intensity affects intersection points of ecosystem service tradeoffs. To further test whether our results were robust to the spatial scale of analysis, we conducted a supplementary sub-regional analysis. Due to constraints on high-resolution nitrogen fertilizer data, we limited this analysis to the Yahara watershed (i.e. one of our case studies). Specifically, we first categorized all subwatersheds within the Yahara into high- or low-intensity groups using locally relevant threshold of mean nitrogen fertilizer of 40 kg N ha^{-1} yr^{-1}. We then plotted standardized ecosystem service indicators against percent agricultural lands to determine and compare the intersection points between two groups of high- vs. low-intensity subwatersheds. All analyses were performed in R statistics software 3.3 (R Core Team 2016).

Results

Ecosystem service relationships across social-ecological systems

Relationships between most pairs of ecosystem services varied across the four case studies included in our analyses (Table 2). For example, positive correlations were found between crop and animal production across most studies but not for the French Alps (Table 2). In addition, seemingly well-recognized tradeoffs between crop production and water quality services were only revealed in the Montérégie and Yahara watershed, whereas these two services showed as synergies in the French Alps and marginally positive in the Norrström basin. Similarly, animal production also exhibited context-dependent relationships with climate regulation and outdoor recreation services. Further, mixed correlations (either positive, negative, or no relationships) were found between water quality vs. climate regulation and outdoor recreation services (Table 2), with substantial variations across different regional landscapes.

Consistent relationships, nonetheless, did exist for certain pairs of ecosystem services. If not accounting for the insignificant correlations (at $\alpha = 0.05$), crop production showed consistent tradeoffs with climate regulation and outdoor recreation, and animal production showed consistent tradeoffs with water quality. Our analysis also revealed consistent synergies between climate regulation and outdoor recreation services across all included social-ecological systems.

Effects of land-use intensity on ecosystem service relationships

The magnitude of ecosystem service tradeoffs (i.e. negative Spearman correlations) increased with our indicator of land-use intensity (mean nitrogen fertilizer application) across all ecosystem service pairs and case studies ($P = 0.001$) (Figure 3). For certain pairs of ecosystem services (e.g. crop production vs. outdoor recreation), relationships even shifted from synergies towards tradeoffs as land-use intensity increased. However, no significant relationships were found between the magnitude of ecosystem service synergies (i.e. positive Spearman correlations) and land-use intensity ($P = 0.16$) (Figure 3).

Land-use intensity mediating intersection points of ecosystem service tradeoffs

Two provisioning services (crop and animal production) were positively associated with the proportion of human-transformed landscape (i.e. agricultural lands) across all studies (all $P < 0.05$) (Figure 4). Two regulating services (climate regulation and water quality) were negatively associated with percent agricultural lands across all studies (all $P < 0.05$) (Figure 4), except for water quality in the French Alps and Norrström basin.

Based on the simultaneous response curves of paired ecosystem services to percent agricultural lands, our results further revealed that land-use intensity altered where provisioning and regulating services intersected and were supplied at similar relative levels. For example, intersection points for 'crop production–climate regulation' tradeoffs occurred at ~35–40% of agricultural lands in the Yahara and Montérégie (both high-intensity systems), whereas these two services did not even intersect in the French Alps (a low-intensity system) (Figure 4). Similar patterns were observed for crop production and water quality (Figure 4): these two ecosystem services intersected at ~40–50% of agricultural lands in the Yahara and Montérégie, but did not even show as tradeoffs in the French Alps and Norrström basin (where these two services increased with the amount of agricultural lands). Tradeoffs of animal production vs. climate regulation and water

Table 2. Spearman rank correlations for all possible combination of pairs of ecosystem services across studies. Level of significance: *** p < 0.001, ** p < 0.01, * p < 0.05. Abbreviations for ecosystem services: Crop – Crop production; Animal – Animal production; Water – Water quality; Climate – Climate regulation; Recreation – Outdoor recreation.

Ecosystem service pairs	Norrström (N = 60)	French Alps (N = 2181)	Montérégie (N = 137)	Yahara (N = 21)
Crop vs. Animal	0.67***	−0.28***	0.46***	0.77***
Crop vs. Water	0.11	0.41***	−0.17*	−0.70***
Crop vs. Climate	–	−0.48***	−0.89***	−0.41*
Crop vs. Recreation	0.13	−0.33***	−0.69***	−0.55**
Animal vs. Water	0.07	−0.11***	−0.42***	−0.32
Animal vs. Climate	–	0.53***	−0.35***	−0.34
Animal vs. Recreation	−0.02	0.25***	−0.13	−0.54*
Water vs. Climate	–	−0.22***	0.09	0.73***
Water vs. Recreation	−0.22	−0.27***	0.07	0.68***
Climate vs. Recreation	–	0.48***	0.76***	0.70***

'–' indicates no available data.

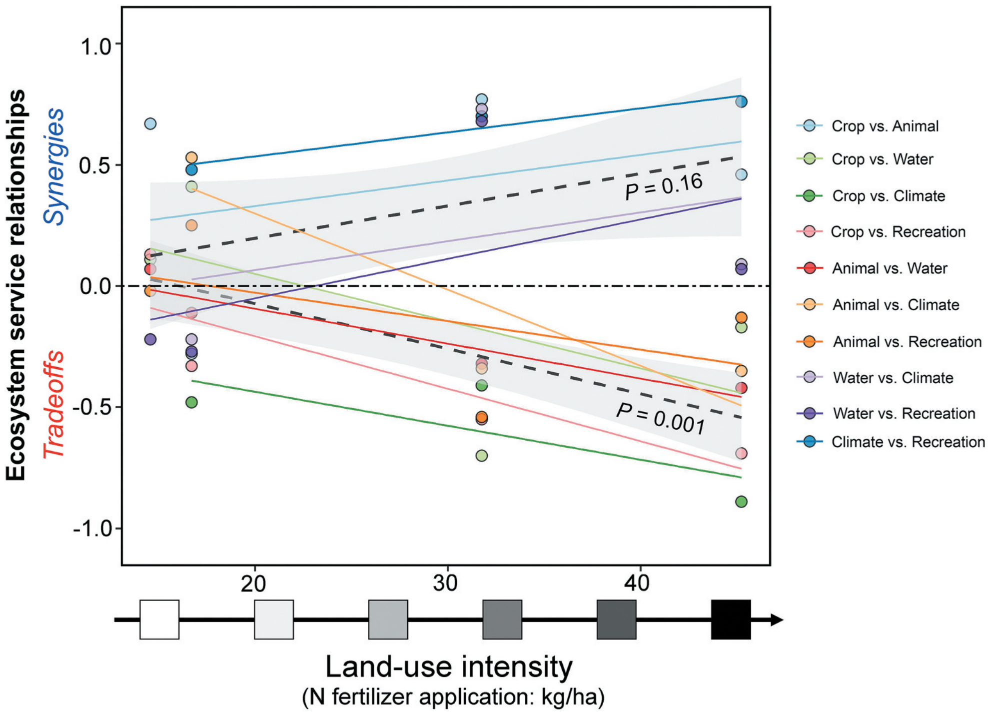

Figure 3. Ecosystem service relationships (i.e. tradeoffs or synergies quantified as the Spearman rank correlations) in response to land-use intensity across all possible combination of ecosystem service pairs and case studies. Pairs of ecosystem service relationships are color-coded, and fitted separately with linear regressions. Abbreviations of ecosystem services: Crop – Crop production; Animal – Animal production; Water – Water quality; Climate – Climate regulation; Recreation – Outdoor recreation. Black dashed lines are fitted linear regressions with significance tests.

quality services were similar to those of crop production: intersection points of tradeoffs occurred at the low proportion of agricultural lands in the high-intensity systems like Yahara, but in the low-intensity systems they did not even show as tradeoffs or occurred at the greater proportion of agricultural lands (Figure 4).

Supplementary sub-regional analysis in the Yahara watershed showed similar results (Figure 5). For each pair of tradeoffs between provisioning and regulating services, intersection points occurred at the smaller proportion of agricultural lands for subwatersheds characterized as low-intensity, or even did not intersect for the case of 'crop production–water quality' tradeoffs (Figure 5(b)). In contrast, for subwatersheds characterized as high-intensity, the intersection points for tradeoffs occurred at the much greater proportion of agricultural lands. In tandem, these results were thus robust at the two spatial scales of analyses.

Discussion

Our research reveals that while most ecosystem service relationships are context-dependent, the magnitude of ecosystem service tradeoffs (e.g. food production vs. climate regulation and water quality) increases with land-use intensity. Furthermore, for ecosystem service pairs with tradeoffs, we show that land-use intensity mediates the point along the landscape gradient where the two services intersect. With high-intensity land uses, food production and regulating services can be both sustained only with less dominance of agricultural lands at the landscape scale, whereas with low-intensity land uses, these services can be sustained with greater dominance of agriculture. Collectively, our synthesis supports the previously outlined three propositions and demonstrates the importance of considering multifaceted aspects of land use in driving ecosystem services and their relationships.

Overall magnitude and direction for the majority of ecosystem service relationships vary strongly across regional social-ecological systems, including those seemingly well-documented 'crop production–water quality' tradeoffs, and 'water quality–recreation' synergies (Vesterinen et al. 2010; Power 2010). Ecosystem service relationships occur due to: (1) responses to common drivers (e.g. management, nutrient, climate, biodiversity, etc.), and/or (2) interactions among services (Bennett et al. 2009; Cord et al. 2017). Hence, such context-specific ecosystem service relationships likely reflect the different social and biophysical drivers across case studies (Reyers et al. 2013; Bennett et al. 2015; Spake et al. 2017). For instance, high fertilizer and human inputs may be the primary driver for 'crop production–water quality' tradeoffs in Yahara and Montérégie (Raudsepp-Hearne et al. 2010; Qiu and Turner 2013). In contrast, less intensive management

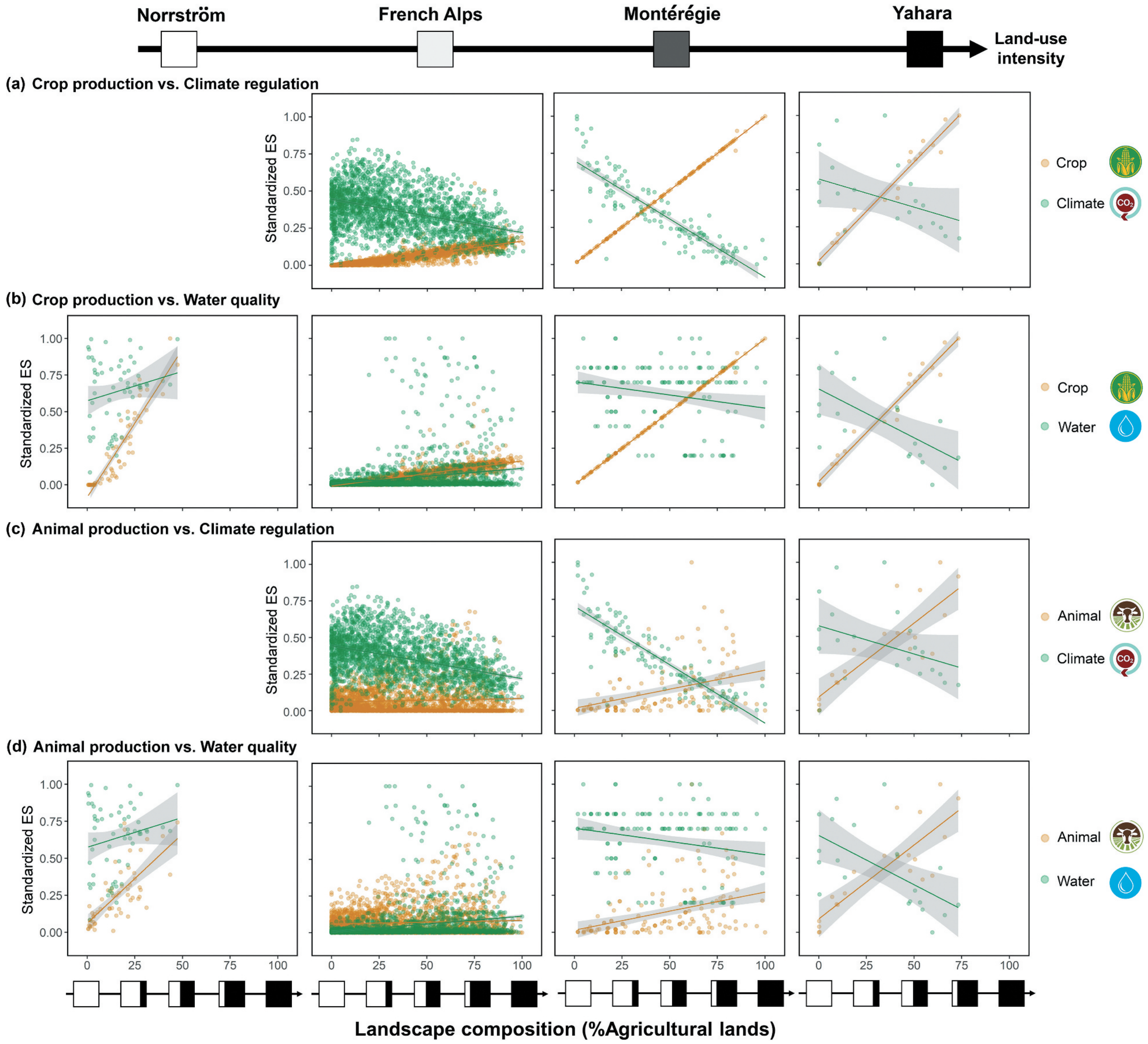

Figure 4. Intersection points for tradeoffs between provisioning vs. regulating ecosystem services examined in this analysis: (a) Crop production vs. Climate regulation; (b) Crop production vs. Water quality; (c) Animal production vs. Climate regulating; and (D) Animal production vs. Water quality. All ecosystem service indicators are standardized to scale of 0–1 (with zero as lowest and one as highest supply), and then plotted against the composition of agricultural lands (x-axes) for all case studies. All four cases (shown as column) are presented from left to right along the gradient of low-to-high intensity of land uses at the landscape scale. Abbreviations of ecosystem services: Crop – Crop production; Animal – Animal production; Water – Water quality; Climate – Climate regulation; Recreation – Outdoor recreation.

practices and overall low productivity (as compared to high industrialized production systems) in the French Alps may explain why this tradeoff does not occur in that region (Crouzat et al. 2015). Our results align with previous research revealing the context-dependent biodiversity-ecosystem service relationships (Duncan et al. 2015), as well as scenario-based studies showing the divergence and dynamics in ecosystem service relationships that is characterized by drastically different social-ecological factors (Koh and Ghazoul 2010; Goldstein et al. 2012; Oteros-Rozas et al. 2015, Pereira et al. in review, Felipe-Lucia et al. in review).

Our results also identify a small set of consistent tradeoffs among ecosystem services, such as crop production–climate regulation (i.e. carbon storage) and outdoor recreation, as reported previously (West et al. 2010; Turner et al. 2014; Lee and Lautenbach 2016; Qiao et al. 2019). These intrinsic tradeoffs could arise from: (1) biophysical processes (e.g. CO_2 emissions and carbon releases associated with agricultural production) linking services that are constant across systems (Bennett et al. 2009); or (2) responses to common drivers of land use, where increased cultivated lands for crop production reduces natural habitats that store more carbon and provide greater recreational opportunities (West et al. 2010; Renard et al. 2015). Our synthesis cannot rule out other factors (e.g. scale, methodologies) (Grêt-Regamey et al. 2014; Raudsepp-Hearne and Peterson 2016) and their relative importance for the consistency or context-dependence in

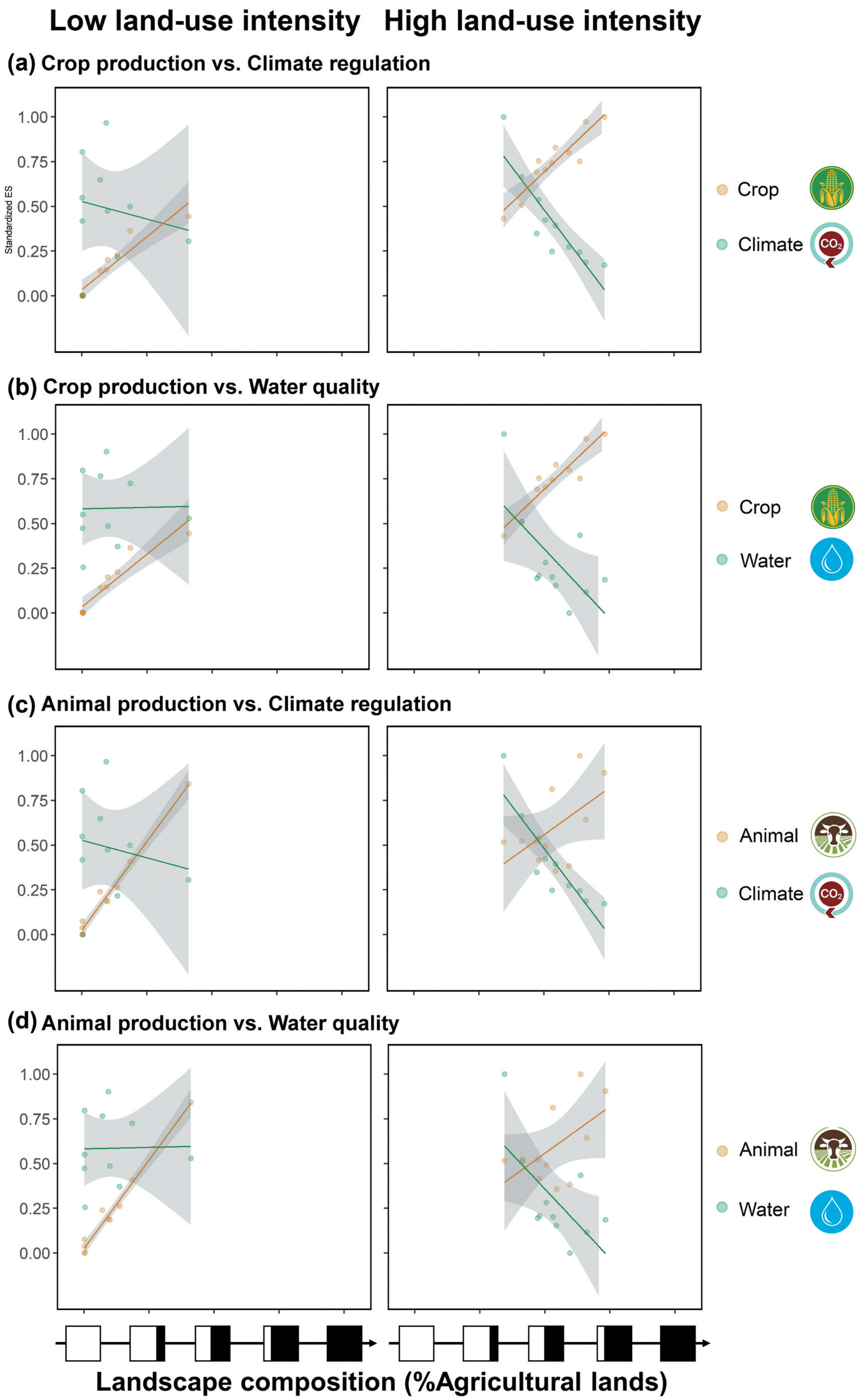

Figure 5. Intersection points for tradeoffs between provisioning vs. regulating ecosystem services in the Yahara watershed between two groups of low- vs. high-intensity subwatersheds: (a) Crop production vs. Climate regulation; (b) Crop production vs. Water quality; (c) Animal production vs. Climate regulating; and (d) Animal production vs. Water quality. All ecosystem service indicators are standardized to scale of 0–1 (with zero as lowest and one as highest supply), and plotted against the composition of agricultural lands (x-axes) of the subwatersheds. Abbreviations of ecosystem services: Crop – Crop production; Animal – Animal production; Water – Water quality; Climate – Climate regulation; Recreation – Outdoor recreation.

ecosystem service relationships. However, our results suggest caution for extrapolating findings from other studies and the need to identify context-specific ecosystem service relationships for local management.

Our results also demonstrate that land-use intensity could amplify existence and magnitude of tradeoffs between food production vs. regulating (water quality, climate regulation) and cultural services (outdoor recreation). Land-use intensity (quantified here by nitrogen fertilizer application) may alter ecosystem service tradeoffs through two possible pathways (Felipe-Lucia et al. 2018): (1) *biogeochemical*, where excess applications of nitrogen fertilizer for boosting crop yields can involve tradeoffs with water quality through nitrogen losses (e.g. via runoffs, subsurface drainage, leaching etc.) (Jaynes et al. 2001; Zhang et al. 2007; Power 2010; Mueller et al. 2014). These responses can also be nonlinear in some cases–i.e. fertilization application beyond a certain point would result in negligible increase in yields but substantial nitrogen losses (DeFries et al. 2004); and (2) *biological*, where nitrogen addition could drive biodiversity loss and shift functional composition of vegetation, especially in natural and semi-natural landscapes (Bai et al. 2010; Allan et al. 2015). Such alterations in biotic communities and plant functional traits can result in tradeoffs with services underpinned by species such as outdoor recreation and other cultural services (Lavorel and Grigulis 2012; Graves et al. 2017), as well as by diversity-driven ecosystem functions (Cardinale et al. 2012; Mitchell et al. 2013; Isbell et al. 2017). It is important to note that these are non-exclusive and non-exhaustive pathways. It is likely that both of them, or others that are not mentioned here, would act in concert, with often one pathway as dominant over others. Our findings also suggest that excessive nitrogen deposition, as identified in many regions worldwide (Vitousek et al. 1997; Galloway et al. 2008; Bobbink et al. 2010), may increase the historical 'background' (or baseline) magnitude of ecosystem service tradeoffs.

Our study further reveals interactive effects of multiple aspects of land uses on ecosystem service relationships. Seppelt et al. (2016) proposed a conceptual framework to synthesize multi-dimensional land-use effects (e.g. composition, configuration, and intensity) on the tradeoffs between agricultural production and biodiversity conservation. While focusing on multiple services, our results provide empirical support for this conceptual synthesis (Seppelt et al. 2016). On the spectrum of low-intensity systems, food production–regulating service tradeoffs can be balanced or even reversed; in other words, these services can be possibly achieved at relatively same levels with a high proportion of agricultural lands. In contrast, in high-intensity systems, food production and regulating services can only be balanced at the low amount of agricultural lands (Figure 4). Our findings on the intersection points suggest different land-use alternatives for mitigating tradeoffs and achieving multifunctionality in production landscapes: low input–high composition (of agricultural lands), vs. high input–low composition (of agricultural lands). These combinations of contrasting and multifaceted land-use effects have important management implications, especially when altering one aspect of land use is more challenging than another in different land-use archetypes (Václavík et al. 2013). For instance, in regions with intensive, large-scale cropping systems (e.g. Midwestern U.S., North China Plain), reducing agricultural lands (e.g. via restoring hedgerows and riparian buffers interspersed across the landscape) (Tscharntke et al. 2005; Kremen et al. 2007; Schulte et al. 2017) or decreasing land-use intensification at the landscape scale could help balance food production and other crucial regulating services. In contrast, in areas dominated by heterogeneous and often fragmented smallholder farming systems (e.g. Africa) where scarifying cultivated lands is not feasible, sustainable intensification (e.g. via proper uses of agro-chemicals or technologies) may help achieve food security, and bridge the gap between production goals, rural livelihoods and long-term environmental benefits (Garnett et al. 2013; Václavík et al. 2013; Vanlauwe et al. 2014; Zabel et al. 2019; Seppelt et al. 2020).

Our research has several limitations that suggest avenues for future investigations. First, due to data constraints, our analysis only used nitrogen input as the indicator for land-use intensity (Kleijn et al. 2009). This metric is reasonable for comparing land systems in developed economies that involve nitrogen fertilizer applications, but may be a poor proxy if we were intending to compare smallholder farming in Africa with those in Europe or North America. In addition, there are other agricultural inputs (e.g. water, labor, and pesticide) and management aspects (e.g. stocking density, tillage regimes, and disturbance frequency) that are also critical contributors to the full matrix of land-use intensity (Meyfroidt et al. 2018; Beckmann et al. 2019). Future research is thus needed to test whether our propositions are generalizable to other aspects of land-use intensity, and what the multiplicative effects of land-use intensity are, in conjunction with landscape patterns, for ecosystem service relationships. Second, our synthesis uses one contemporary snapshot of ecosystem service estimates from multiple case studies; we did not assess temporal dynamics. Yet it has been noted the need of embracing spatial-temporal dynamic perspectives in managing ecosystem services and their relationships (Renard et al. 2015; Qiu et al. 2018a). Hence, studies are especially encouraged to assess how effects of land use on ecosystem service relationships change over time, either from a retrospective (e.g. landscape legacy effects) (Dallimer et al. 2015; Tomscha and Gergel 2016; Ziter et al. 2017; Meter et al. 2018), or prospective (e.g. future climate and other environmental changes) (Motew et al. 2018; Qiu et al. 2018a) lens. Third, given the correlational nature of our research, more efforts such as seeking for multiple lines of evidence (Game et al. 2018; Qiu et al. 2018c) or using large-scale experimental manipulations (e.g. Schulte et al. 2017) and observations (e.g. Felipe Lucia et al., 2018) would be necessary, especially to address causal mechanisms that help predict land-use effects on ecosystem service relationships. Moreover, indicators of ecosystem services were standardized (to 0–1) so that they can be comparable across case studies. Such scaling, while imperative, could potentially affect intersection points and certain relationships that may depend on absolute ecosystem service values. Such standardization may also not capture how much absolute amount of ecosystem services is produced by a landscape and needed by its inhabitants. Further, if at all possible, it is crucial to use independent datasets (e.g. proxies unrelated to land use/cover) to quantify indicators of ecosystem services, and avoid potential confounding factors in interpreting effects of landscape pattern and land-use intensity on ecosystem service relationships. Finally, spatial scales (i.e. spatial unit of ecosystem service estimates) and landscape configuration are additional components of landscape pattern that differ across studies and could potentially alter ecosystem service relationships (Cavender-Bares et al. 2015; Qiu and Turner 2015; Raudsepp-Hearne and Peterson 2016). While we attempted to draw some insights regarding whether our results are robust to varying spatial scales of analysis, their effects need to be further addressed and teased apart as more consistent data across studies are available. It is important to note that our results were based on datasets from a small number of case studies, which might affect the extrapolation of our conclusions. Future attention on mechanism-driven, modeling-based factorial experiments, or establishment of research networks (e.g. Programme on Ecosystem Change and Society, and the Long-Term Socio-Ecological Research) (Balvanera et al. 2017; Angelstam et al. 2019) and databases for ecosystem services (Mitchell et al. 2015; Spake et al. 2017; Dade et al. 2018; Qiu 2019) may be promising to further disentangle the relative influences of land use on ecosystem service relationships. These coherent community efforts can also help test whether our propositions are generally applicable across scales and social-ecological contexts (Cavender-Bares et al. 2015).

Conclusions

Understanding how to manage production landscapes to feed a growing population while sustaining water, climate, and cultural ecosystem services vital for human society remains a grand challenge. We present a conceptual framework encompassing three propositions on how land use could affect ecosystem service relationships, contributing to an emerging literature that examines multi-faceted land-use effects on ecosystem services. Using a synthesis approach, our study empirically demonstrates the context-dependencies in ecosystem service relationships across distinct regional social-ecological systems. Overall, our results show that with high-intensity land uses, food production and regulating services can be both sustained only with less dominance of agricultural lands at the landscape scale, whereas with low-intensity land uses, these services can be sustained with greater dominance of agriculture. Our research reveals that land-use intensity enhances the tradeoffs among ecosystem services, and can interact with landscape composition to determine the response behaviors and intersection points in tradeoffs among food, water and climate regulation services.

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Data availability statement

All data used in this research will be made available upon requests.

Disclosure of potential conflicts of interest

No potential conflict of interest was reported by the author(s).

ORCID

Jiangxiao Qiu http://orcid.org/0000-0002-3741-5213
Cibele Queiroz http://orcid.org/0000-0003-1124-306X
Elena M. Bennett http://orcid.org/0000-0003-3944-2925
Anna F. Cord http://orcid.org/0000-0003-3183-8482
Emilie Crouzat http://orcid.org/0000-0001-5765-6543
Sandra Lavorel http://orcid.org/0000-0002-7300-2811
Joachim Maes http://orcid.org/0000-0002-8272-1607
Megan Meacham http://orcid.org/0000-0003-3626-967X
Albert V. Norström http://orcid.org/0000-0002-0706-9233
Garry D. Peterson http://orcid.org/0000-0003-0173-0112
Ralf Seppelt http://orcid.org/0000-0002-2723-7150

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