Completing the land-sharing strategy: reaching human-wildlife coexistence through alternative resource management

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"Conservation is a state of harmony between men and land. By land is meant all of the things on, over, or in the earth. Harmony with land is like harmony with a friend; you cannot cherish his right hand and chop off his left. That is to say, you cannot love game and hate predators; you cannot conserve the waters and waste the ranges; you cannot build the forest and mine the farm. The land is one organism. Its parts, like our own parts, compete with each other and co-operate with each other. The competitions are as much a part of the inner workings as the co-operations. You can regulate them—cautiously—but not abolish them."

"We shall never achieve harmony with land, any more than we shall achieve absolute justice or liberty for people. In these higher aspirations the important thing is not to achieve, but to strive."

Leopold, Aldo (c. 1938): Round River, Oxford University Press, New York, 1953.

Biography

I was born in El Salvador (1985). I am a biologist from the Universidad de El Salvador (2009). Since 2011 I have been part of the Laboratorio de Conservación Biológica at the Universidad de Chile, where I have defined my research interests which now lie in conceptual innovations for biodiversity and conservation science focusing on effective land-use strategies to reach compatibility between biodiversity conservation and human activities. I am specifically interested in human-wildlife coexistence in agroecological systems.

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Finally, I cannot claim these accomplishments as my own. I owe this to my family. They always supported me in any and all manners available to them. My brothers, Tito Peña and Fidel Peña financially supported me during my first year in Chile when I began my Master’s. Leaders in their own fields, to me they are paragons for following your convictions. One final note of gratitude is to my parents, Edmidlia Guzmán and Augusto Crespín. They showed me how accomplishing great things requires maximum effort and instilled in me compassion for life.

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Abstract

The land-sharing strategy implies co-occurrence of human beings and wildlife, which frequently results in loss of life or injury to people, damage to crops and predation of livestock. Consequently, wildlife is persecuted in retaliation. The existence of contrasting interests such as food security through livestock production on the one hand, and the need to protect threatened species on the other, lay the foundations for human-wildlife conflict.

After a decade of the introduction of "land-sharing" there is no formal analysis on the role of conflicts in the success of this strategy. This suggests that a review of the state of the art is necessary to identify gaps in the nature of human-wildlife conflicts in the framework of the strategy. To manage these conflicts, we must understand the underlying ecological basis of the predator's response to the choice of crops or livestock instead of their natural prey. The most frequent biological interaction that prevents coexistence is the predation livestock by carnivores and a factor that could explain it is the availability of natural prey. Predators choose the most profitable prey in relation to the cost and energy benefit incurred in the search and handling of prey. Therefore, if natural prey is scarce in relation to livestock, then livestock should be more profitable.

Within this framework, I first determined that coexistence between humans and wildlife has not been considered a requirement for the viability of land-sharing/sparing approaches. Second, I determined under what conditions the availability of natural prey decreases livestock predation, the underlying biological impediment of human-carnivore coexistence, by using data from the literature around the globe. I found that wild prey availability increases livestock predation rate, but open vegetation is a more important predictor. Third, I empirically tested availability of wild prey as an explanatory factor of livestock predation through field observations by comparing rates of ovine predation by foxes on fields with varying wild and domestic prey availability. I found that higher occurrences of hare decrease ovine kill rate. Finally, I discuss framing food production landscapes in a social-ecological systems context and suggest viewing manageable variables of conflict resolution as system parameters that define states of coexistence to aid in swifter conflict resolution planning.

GENERAL INTRODUCTION

The advent of agriculture initiated man-made shifts from natural landscapes to anthropogenic systems, which required space dedicated not only for living quarters, but also for crop and livestock production among other activities (Ellis et al. 2010). Agroforestry systems and livestock raising currently remain the leading practices of human encroachment and wildlife exclusion (Vitousek et al. 1997). Since its inception, civilization has sought to control the natural world and transform wilderness into a profitable economic activity (Leopold 1925). The consequence of such a paradigm is the steep decline of global biodiversity in the last 40 years beyond the background extinction rate (Ceballos et al. 2015), and according to the Living Planet Index, expressed in the halving in size of animal populations (McLellan et al. 2014).

The loss of biodiversity threatens human wellbeing by changing ecosystem processes and reducing the benefits obtained from them (Díaz et al. 2006). Therefore, halting the ongoing loss of biodiversity and protecting ecosystem processes are in the best interest of human society (Díaz et al. 2006). Traditional strategies for biodiversity conservation began by separating human activities from remnants of wilderness to avoid further human intervention. The most significant instrument of this approach are protected areas (Mace 2014). Sparing land from human activities, including the raising of livestock, is the business-as-usual approach of protecting a natural area, which is usually surrounded by intensively used lands, and thus hindering wildlife from using the protected area’s surroundings (Green et al. 2005). In fact, protected areas are an integral part of the world’s commitment to stop the loss of biodiversity through the Convention on Biodiversity (CBD), and are certainly necessary but ultimately insufficient (Simonetti 1998, Mora & Sale 2011). Carnivores, in particular, have large home ranges and require large areas to achieve viable populations, placing them in dire straits when confronted with restricted habitat availability such as the ones provided by protected areas (Redford & Robinson 1991, Simonetti & Mella 1997, Crespin & García-Villalta 2014). The fact that the remaining natural area is not enough to meet species' minimum population requirements necessitates considering expanding the area on which biodiversity can be conserved beyond protected areas, an approach which presents a conundrum: how to achieve biodiversity conservation in human-dominated landscapes, the very same source of biodiversity threats.

Today, the traditional focus on the separation of human activity from nature and the alternative view of nature and human society as one entity, have translated into two simultaneous and complementary approaches based on the amount and intensity of resource use: land-sparing and land-sharing (Green et al. 2005, Fischer et al. 2008). Transferring the interpretation of islands to protected areas from the seminal Theory of Island Biogeography (MacArthur & Wilson 1967), land-sparing assumes the matrix that immerses protected areas is uninhabitable (Wilson & Willis 1975). However, the surrounding anthropogenic matrix presents varying degrees of contrast with natural habitats regarding resources and physical structure, where low contrast matrixes might function as surrogate habitats by offering resources or similar structure to the original habitat (Fahrig 2003). Thus, land-sharing can be defined as anthropogenic use of low contrast land with regards to natural habitat that also functions as an alternative or complementary habitat depending on the resources available for wildlife (Green et al. 2005).

Accomplishing a land-sharing directive conveys the presence of wildlife on human-dominated lands. Such cohabitation of humans and wildlife generally results in interactions with adverse effects on both. Humans might suffer injury or loss of life, crop damage and livestock predation. Wildlife that threatens people or raid against crops or livestock on the other hand, is persecuted in retaliation, usually being killed by hunting or poisoning. Carnivores are a persecuted group, despite being species of conservation concern (Baker et al. 2008). The existence of contrasting interests: human safety and livestock productivity on one hand, and the need to protect threatened species on the other, settle the basis for a human-wildlife conflict (Woodroffe et al. 2005). A conflict is an incompatibility between competing interests where the fulfillment of one interest disallows the other (Young et al. 2010). We follow Redpath et al. (2013) who defines conflicts as “situations that occur when two or more parties with strongly held opinions clash over conservation objectives and when one party is perceived to assert its interests at the expense of another, recognizing that the competing opinions and interests giving rise to conservation conflicts transpire between people. Therefore, conservation conflicts are embedded in social-ecological systems (*sensu* Ostrom 2009), emerging from interactions (Lischka et al. 2018: “the spatial and temporal juxtaposition of human and wildlife activities where humans, wildlife, or both are affected”) between the ecological and social domains (Lischka et al. 2018), and more so when land is shared. Here, we operationalize the definition of conservation conflicts as “opposing interests between humans that result from the need of an affected party to eliminate biodiversity impacts, the negative effects of biodiversity on human wellbeing or *vice versa*” (*sensu* Young et al. 2010), hence rendering the end of a conflict as meeting of the needs for both parties involved. In the land-sharing context, conflicts arise when wildlife threatens the lives or livelihoods of humans, and the need to conserve species and the protection of humans and their property become incompatible (Woodroffe et al. 2005). Conflicting interests include the landowner’s right to produce crops and livestock while wildlife conservation interests lie in allowing wildlife to inhabit the same lands and satisfying both interests makes a sustainably managed productive matrix feasible. Therefore, the implementation and success of land-sharing might be attained by the avoidance of human-wildlife conflicts, thereby ensuring human-wildlife coexistence. Ecological coexistence entails the continued existence of species in predator-prey interactions or in competition. Instead, I approach human-wildlife coexistence from a social-ecological perspective and define it as the meeting of both wildlife conservation aims and the production of human food and services on the same land, by (a) enabling the fulfillment of both interests and avoiding the emergence of conflicts and (b) allowing natural wildlife dynamics to progress (such as predator-prey interactions) and societal needs to be met without incurring damages to human wellbeing or *vice-versa*.

Recognizing the perils of losing biodiversity and the provision of ecosystem services, world leaders have agreed, within the framework of the Convention on Biological Diversity, to meet the 20 Aichi Biodiversity Targets by 2020 (Convention on Biological Diversity 2010). Target 11 prescribes sparing 17% of land surface to protect biodiversity. Empirical data and models suggest that such an amount, even in a single large reserve will be insufficient to stem the loss of biodiversity. Current evidence indicates that at least 30% is needed (Svancara et al 2005). Since maintaining current biodiversity levels requires more land area, land-sharing plays a key role in complementing the already spared habitat.

Addressing the role of coexistence in land-sharing is therefore in urgent need of attention to comply with Aichi Target 7, which was created after gleaning the necessity of providing the conditions needed for the compatibility between conserving biological diversity and the production of goods and services for human society on the same land, all outside protected areas. Specifically, the Aichi Target 7 includes the desideratum that "By 2020 areas under agriculture, aquaculture and forestry are managed sustainably, ensuring conservation of biodiversity" (Convention on Biological Diversity 2010). In this regard, a challenge is to assess the conditions required in order to render a habitat suitable for both tenants: wildlife and production of goods.

Prior to this document and decade after the introduction of the land-sharing approach as a way to promote the production of goods for humans as well as the conservation of wildlife (Green et al. 2005), there was no formal analyses of the role of conflicts in affecting the success of this approach (Law & Wilson 2015). The implications of coexistence for achieving land-sharing had scarcely been addressed and an overview of the state of the art was needed to analyze gaps regarding the nature of these conflicts.

To manage human-wildlife conflicts that impede coexistence on human-dominated lands, I needed to understand the ecological basis underlying predator response for choosing crops or livestock instead of their natural prey. At the forefront of biological interactions preventing coexistence and land-sharing is the predation of carnivores upon livestock, since carnivores in particular fall in unwilling danger when “stealing” prey from their human owners (Baker et al. 2008), and a factor that might account for livestock predation is the availability of natural prey (Sacks & Neale 2007). Predators choose the most profitable prey when taking into account the energy expended seeking out and handling prey (MacArthur & Pianka 1966). Therefore, if natural prey is scarce then a livestock kill should be more profitable. Natural prey biomass should be sufficient to support local populations of predators, but if domestic prey biomass far exceeds that of natural prey, then predators will continue to prey on livestock attending to its high abundance, which reduces search time besides offering a large amount of resource (Polisar et al. 2003). Conditions that might affect the relation between natural prey availability and livestock predation include types of livestock, predator, and natural prey, their availability and vegetation, which might have a direct effect by modulating the cover of predators or the vulnerability of livestock to attack, but also have a distal effect on livestock predation by modulating the availability of natural prey. If availability of natural prey reduces livestock predation, then understanding and managing the factors that determine the density of natural prey can prevent livestock predation and facilitate the presence of native carnivores on farmlands.

Predators have historically relied on natural prey, so one might expect for higher availability of natural prey to decrease the rate of livestock predation; therefore, landscapes with a higher natural to domestic prey ratio should have lower rates of attacks on livestock. However, an alternative scenario is also feasible.

Predation upon livestock might increase as natural prey availability rises. Areas of high abundance of natural prey might attract carnivores. If livestock is raised in such areas, their syntopy might increase the likelihood of attacks upon livestock. These two scenarios denote prey switching, a particular expression of functional response, because the relative frequency with which natural prey is encountered relative to domestic prey will change through time allowing for new search images to form (Holling 1959).

Within this framework, I first determine whether coexistence between humans and wildlife has been considered a requirement for the viability of land-sharing/sparing approaches (Chapter 1). Because human-carnivore coexistence is pre-requisite for the implementation of land sharing, I expect that the ecological basis underlying the use of human-dominated landscape by carnivores to have been formally addressed in order to deal with the biological grounds for the occurrence or avoidance of conflicts. Second, I determine under what conditions if any, the availability of natural prey decreases livestock predation, the underlying biological impediment of human-carnivore coexistence, by using data from the literature around the globe (Chapter 2). Third, I empirically test the quality of availability of natural prey as an explanatory factor of livestock predation through field data by comparing rates of livestock predation on fields with varying natural and domestic prey availability (Chapter 3). Finally, I discuss identification of factors affecting human-wildlife coexistence in agroecological landscapes by framing them as parameters defining system states of coexistence in social-ecological systems (General discussion). This work aims at explaining the underlying biological factor that impedes human-carnivore coexistence, livestock predation, as a potential management tool to establish how land-sharing can be made into a realizable strategy.

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Chapter 1

Reconciling farming and wild nature: integrating human-wildlife coexistence into the land-sharing and land-sparing framework[1]

Abstract

Land has traditionally been spared to protect biodiversity; however, this approach has not succeeded by itself and requires a complementary strategy in human dominated landscapes: land-sharing. Human-wildlife conflicts are rampant in a land-sharing context where wildlife co-occur with crops or livestock, but whose resulting interactions adversely affect the well-being of land owners, ultimately impeding coexistence. Therefore, true land-sharing only works if coexistence is also considered an end goal. We reviewed the literature on land-sharing and found that conflicts have not yet found their way into the land-sharing/sparing framework, with wildlife and humans co-occurring without coexisting in a dynamic process. To successfully implement a land-sharing approach we must first acknowledge our failure to integrate the body of work on human-wildlife conflicts into the framework and work to implement multidisciplinary approaches from the ecological, economic and sociological sciences to overcome and prevent conflicts. We suggest the use of Conflict Transformation by means of the Levels of Conflict Model to perceive both visible and deep-rooted causes of conflicts as opportunities to create problem solving dynamics in affected socio-ecological landscapes. Reconciling farming and nature is possible by aiming for a transition to landscapes that truly share space by virtue of coexistence.

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Introduction

Emerging approaches that integrate biodiversity conservation and the production of goods through wildlife-friendly farming have yet to consider potential human-wildlife conflicts as a factor influencing conservation outside protected areas. Habitat loss is the leading cause behind the global decline of biodiversity (Sala et al. 2000). Traditional strategies for biodiversity conservation have relied on sparing land for nature, segregating human activities from remnants of wilderness to avoid further human intervention. However, while protected areas are certainly necessary, they are ultimately insufficient and biodiversity loss has not declined (Butchart et al. 2010; Mora and Sale 2011). A large fraction of species and ecosystems are not covered by protected areas, which further do not necessarily offer surfaces large enough to sustain viable populations of most large bodied species (Redford and Robinson 1991, Venter et al. 2014). Furthermore, the global siting of protected areas has so far been biased towards areas with lower maintenance costs than those with greater biodiversity representativeness (Venter et al. 2014). International collaboration has remained minimal, and lack of economic resources along with governance challenges result in many “paper parks”, especially in less wealthy countries (Di Minin and Toivonen 2015). Hence, wildlife is expected to survive beyond protected areas, and given these limitations, complementary approaches, such as wildlife-friendly farming, are required. Wildlife-friendly farming, or land-sharing between wildlife and agriculture, demands more area to satisfy production targets, but presumably allows wildlife to survive within these lands (Green et al. 2005; Fischer et al. 2008). Here, we aim to position the issue of coexistence by means of conflict reconciliation as necessary for land-sharing to work.

Conflicts and the food-biodiversity tradeoff

The need to rely on unprotected areas for wildlife conservation is reflected by the Aichi Biodiversity Target 7 of the Convention on Biological Diversity, which expresses the need of providing the conditions required for the compatibility between biological diversity and the production of goods and services for human society on the same land, demanding that “By 2020 areas under agriculture, aquaculture and forestry are managed sustainably, ensuring conservation of biodiversity” (Convention on Biological Diversity 2010). Also, there are cases in which sparing land might not be a realistic option attending to long-term disturbances that have reduced natural areas to a minimum extent, below that which is required for sustaining minimum viable populations of wildlife, such as in El Salvador whose largest protected area cannot sustain populations of 87% of its carnivores (Crespin and García-Villalta 2014). Under these scenarios, nations where natural area is diminished may find that protecting wildlife with a land-sharing approach might be the most viable option.

Land-sparing remains a cornerstone for conserving global biodiversity (DeFries et al. 2005). However, carnivore home ranges are large, placing them in dire straits when confronted with restricted amounts of habitat such as the ones provided by protected areas and thus are prime candidates to inhabit unprotected lands (Woodroffe and Ginsberg 1998), as expected in Aichi Biodiversity Target 7. Moreover, land-sharing can result in conflicts as nature spills over unto farmland, exemplified by carnivores that permeate through the borders between protected areas and farmsteads conspicuously more so than other taxa, directly affecting human livelihood when the production of livestock is in contention, such as in buffer zones around protected areas, where human-wildlife conflict is usually exacerbated (Rao et al. 2002, Patterson et al. 2004, Wang and MacDonald 2006).

The land-sparing/sharing framework has so far ignored potential ill consequences for biodiversity, carnivores included. Such consequences are due to the subsequent interactions between humans and wildlife that generally result in negative outcomes, such as injury or loss of life for humans and wildlife, crop damage and livestock predation (Baker et al. 2008). Ultimately, these losses render the need to conserve species and the protection of human interests in the same area to be at odds with each other in places where compensation schemes fail, or cultural norms do not accept any loss to wildlife (Woodroffe et al. 2005).

Sharing land: conflict laden co-occurrence or peaceful coexistence?

Despite the fact that achieving coexistence between human activities and wildlife outside protected areas is a requirement for land-sharing to be effective, conflicts have been a neglected component of such an approach. We support this claim with a literature review which we performed by collating and reviewing scientific papers up to September 2017 that dealt with land-sharing. We first targeted scientific articles registered on the Thomson Reuters Web of Science that cite Green *et al.* (2005), which formalized the land-sharing/sparing model (see also Law and Wilson (2015)). We then included articles on land-sharing which may not have cited Green et al. (2005), beginning with a search string using the keywords “land sharing OR wildlife friendly”, following up with a second search by adding “AND “conflict” to the string. Several filtering steps come into place. First, we excluded all articles that do not explicitly deal with land-sharing. Secondly, we identified a) articles that mentioned conservation conflicts in some capacity even when not dealing with them, b) studies which held any aspect of conservation conflicts as their aim. Finally, c) we assessed whether conflict resolution is suggested in each article as necessary for a shared land. We provide a list of the assessed studies as Supplementary Information.

We define conservation conflicts as opposing interests that result from the need of an affected party to eliminate biodiversity impacts, the negative effects of biodiversity on human wellbeing or *vice versa (sensu* Young et al. 2010). Conflicts generated at the ecosystem level generally focus around threats, such as habitat loss and the loss of ecological functions, and can be approached by land use strategies such as the land-sharing/sparing model. Conflicts that specifically occur at the community level have classically been perceived as human-wildlife conflicts, focusing on the impacts of single species on human livelihoods or of human actions on specific species populations. It is these interactions that occur between specific species and humans in agro-productive systems that emerge once land is shared. This results in agricultural stakeholders wanting to satisfy their interests by eliminating their perceived loss, while conservation needs demand the protection of the interacting species, forming conflicting interests between the wellbeing of both humans and wildlife. Therefore, there is an urgent need to determine if and how the land-sharing literature has included conservation conflicts as an article's aim, as part of the discussion or even gone so far as to offer possible methods of resolution.

Our literature review reveals that conflict resolution and achieving coexistence are not currently considered in research concerning land-sharing. We retrieved 210 articles dealing with land-sharing, and although 35 mention conflicts in some capacity, and one handles identifying conservation conflicts as an aim, none pertain to resolving conflicts and achieving coexistence as necessary to sharing land (Fig. 1). After more than a decade since the publication of the land-sparing/sharing model (Green et al. 2005), which also does not include conflict resolution as a prerequisite, the situation remains unchanged. The expanding literature has so-far managed conflicts separately from land-sharing or -sparing, and at most, has treated conflicts as areas of high biodiversity and potential high agricultural yield juxtaposition (Baudron and Giller 2014; Shackleford et al. 2015). Research so far has overlooked the resulting conflicts and their resolution.

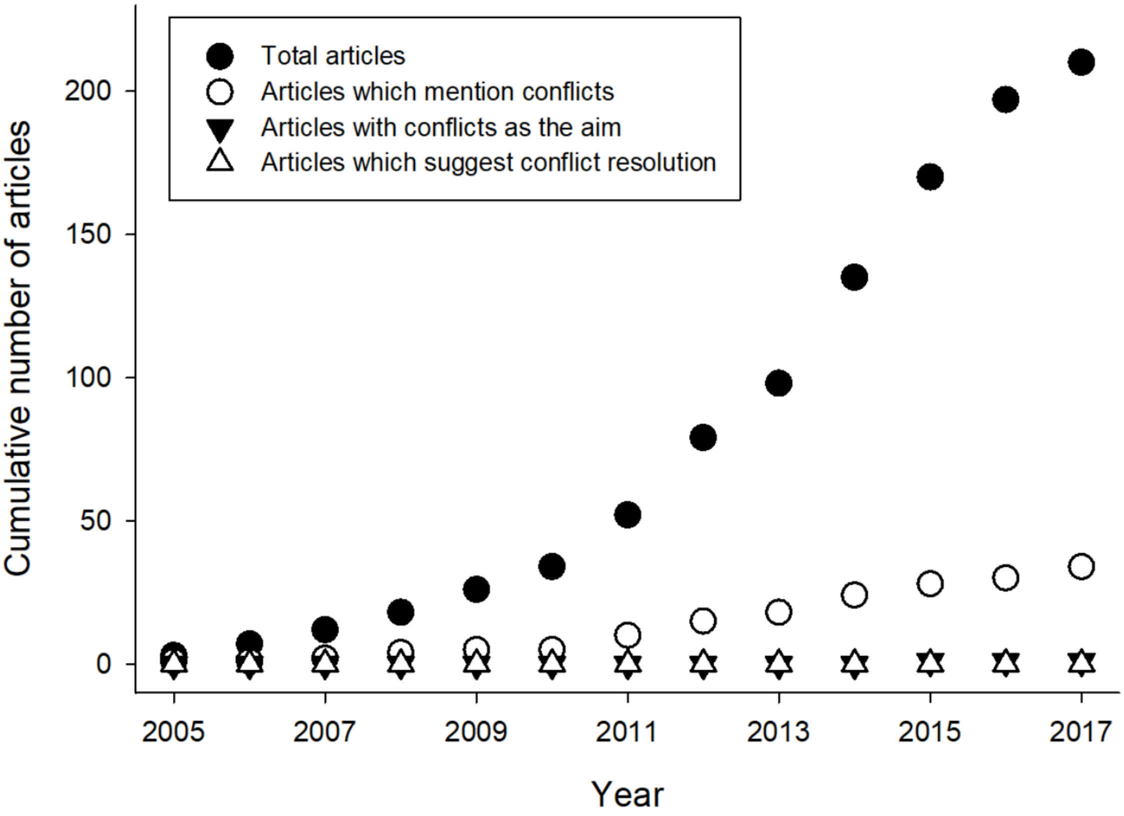

Figure 1. Cumulative number of articles that deal with land-sharing or sparing (●), mention conflicts in some capacity (○), identify conservation conflicts as an aim (▼), or suggest conflict resolution and coexistence as necessary to sharing land (Δ).

Advances in ecological research have skimmed just shy of integrating conflict resolution into land-sharing since the model's inception. Mattison and Norris (2005) pushed for a holistic approach towards the effects of land-use change on biodiversity and a context dependent decision towards sharing or sparing land. Recently, Fischer et al. (2017) shifted the emphasis of agriculture from yield-only towards food security which when coupled with the state of biodiversity, means managing socio-ecological dynamics. Both mention conflicts pertaining to land-use: potential gains for either conservation or social purposes, and impingements on social rights or biodiversity wellbeing. When considering research on conflict-prone species or systems, we have also missed the mark. For example, Lerner et al. (2017) discuss reconciling food production and conservation in relation to cattle production and include land-sharing as a potential fostering of ecosystem services but obviate the possible presence of predators, such as carnivores, that might prey on cattle and cause potential conflicts. Bouyer et al. (2015) implicitly integrate coexistence into the land-sharing strategy by assessing the tolerance of the Eurasian lynx (*Lynx lynx*) to use shared lands, finding that it has the potential to inhabit shared lands if tolerated by people. Even when pondering the beneficial consequences of land-sharing such as for use in biological corridors for carnivores, potential sources for conflicts have been overlooked (see Crespin and Garcia-Villalta 2014). Although 17% of published articles on land-sharing mention conflicts, only one includes conflicts as part of its aim. Shackelford et al. (2015) identified conservation conflicts in agricultural contexts as places of juxtaposition between food production and wildlife conservation. All in all, no article outright suggests the resolution of a conflict in a land-sharing context.

Why are land-sharing and conflicts uncoupled?

Demand for food production has risen consistently as global human population has grown, and so have its impacts on biodiversity, giving way to the two competing solutions, sparing land by intensifying production, or wildlife-friendly farming but decreasing yield (Green et al. 2005). The research that followed focused mainly on comparing the effectiveness between both strategies regarding biodiversity, with land-sparing frequently considered a more promising option *ceteris paribus*, although authors generally point out that their results are context-dependent (Phalan et al. 2011, Hulme et al. 2013). All efforts so far have been directed towards determining whether one strategy is superior to the other, with little regard to the consequences of implementing either. The most likely cause behind conflicts having been passed over in land-sharing is precisely the context in which experiments have so far been immersed. Notably, other dimensions besides ecological context are missing from the sparing versus sharing debate, such as governance, where policy and implementation stakeholders prefer one strategy over the other (sparing and sharing, respectively), indicating that these decisions should be positioned in a socio-ecological context (Jiren et al. 2017).

Until now, coexistence in a shared-land scenario has been taken as a given, which should not be surprising. Most research on land-sharing has centered around birds, butterflies, ants, other arthropods, trees and other plants (Balmford et al. 2015, Goulart et al. 2016), which are taxa commonly not engaged in human-wildlife conflicts, while the most well-known cases worldwide involve large mammalian carnivores (Graham et al. 2005). The majority of assessed agro-productive systems in land-sharing are croplands and agroforestry systems (Goulart et al. 2016). Evidently, conflict prone taxa and systems, such as carnivores and animal husbandry, have not been as well researched in the land-sharing context. Both make tough models to work with. Carnivores generally have large home-ranges and tend to be hard to track. Livestock also move about, while keeping count and determining cause of death, especially when extensively managed, may not always be possible and lead to self-report bias when depending on stakeholder data. Avoiding conflict-prone species in the name of feasibility may explain why conflicts, their resolution, and coexistence in general, have been neglected by the land-sharing literature. On the other hand, simple oversight by researcher bias towards particular taxa may be to blame on behalf of researchers of land-use strategies, while human-wildlife conflict specialists with a more focused mindset on explaining livestock predation might overlook land use strategies such as land-sharing. Basing the selection of the biodiversity component and agro-productive system assessed on ease of measurement has led to addressing biodiversity composition but forfeiting the inclusion of structure and function components, from which interactions such as predation of crops and livestock are derived.

Integrating conflicts and the land-sharing approach

Acknowledging the failure to unify the body of work on human-wildlife conflicts with the coexistence that is required to successfully implement the land-sharing approach, is the first step to overcoming it. From an ecological standpoint, framing interactions between humans and wildlife by applying community theory to human-dominated landscapes can help describe the problem and pinpoint explicit factors available for future research (Chapron and López-Bao 2016). If farmland is to be shared, a minimum level of predation is to be expected even after reducing, mitigating or compensating predation. Therefore, to avoid the persecution of wildlife, a minimum level of tolerance must exist on behalf of stakeholders (Dickman 2011, Oriol-Cotterill et al. 2015). Whilst compensation schemes may ease immediate monetary losses, this minimum threshold of tolerance may be hard to determine due to the non-monetary losses accrued by farmers, such as the loss of selected breeds, their genetic characteristics, potential gain in the form of future cohorts, and the time and energy invested in them. In fact, while most affected stakeholders approve compensation as a management strategy, compensation does not always increase tolerance (Naughton-Treves et al. 2003). Also, top-down strategies emanating from management may be perceived as disempowerment by local communities, creating enmity that is then directed towards wildlife, ultimately lowering tolerance (Dorresteijn et al. 2016). Indeed, beyond the visible impacts of direct injury and economic losses, the hidden impacts of human-wildlife conflicts in general are poorly understood and often ignored, residing in the form of psychological trauma, the interruption of daily living activities, and unfulfilled food security (Barua et al. 2013).

Resolving conservation conflicts in a land-sharing context requires understanding why conflicts arise in the first place. The ecology and underlying biological causes behind the emergence of conflicting interests in shared lands, loss of crops and livestock by biodiversity, can be generalized to whenever wildlife co-occurs with human used resources, but reconciling interested parties for any conflict will require addressing its unique socio-economic context (Young et al. 2010).

Incentives such as profits, can cause changes in land uses that threaten conservation interests (Hanley 2015). Unpolished and unclear property rights can also lead to conflicting interests, such as in scenarios reminiscent of the *Tragedy of the Commons* (Hardin 1968), where everyone may have the incentive to add a small increase to their own profit. Translating the tragedy to conflicts, wildlife is interpreted as the common good. Egotistical sentiments and actions, such as thinking that killing just those individuals that affect one's own livestock should not inflict major damage on wildlife, may be mirrored by multiple stakeholders of a landscape's wildlife, from which large-scale problems may ensue (Hanley 2015). Market failures may also cause conflicts when biodiversity as a public good, be it forest cover or wildlife, lacks incentive to be maintained on farmed land, particularly when the market incentivizes activities that maximize individual gains (Hanley et al. 2007). Lastly, the market also fails when externalities emerge, such as the unforeseen consequences from eliminating the wildlife that prey on livestock or crop which may trigger loss of ecological interactions that lack redundancy, and result in other species populations or ecosystem functions ultimately being affected in tandem (Hanley 2015).

Profit incentives, misused property rights and market failures need not remain a hindrance to coexistence. Incentives can be shifted towards conservation milestones, since outcome-based biodiversity payments for improving on private lands can be successful (McDonald et al. 2017). This incentive realignment means rewarding private landowners for environmental benefits, such as biodiversity and ecosystem services provided on their land, but also including negative incentives for actions against conservation targets and interfering with services, such as taxation for persecution of protected carnivores or constricting waterways for communities downstream (Jack et al. 2008, Hanley 2015). Property rights can be arranged so as to regulate access to the commons, whereby rules and customs are developed from within communities by all those affected at local levels, and the establishment of multiple layers of nested communities coming together at larger scales to govern the complete system (Ostrom 1990). Market failures can be solved. For example, the creation of positive incentives can grant ecological benefits that can even out against profits from individual gains. Externalities affecting services enjoyed by others in or outside the community can be penalized.

Biodiversity inhabiting stakeholders' lands may not necessarily threaten their livelihoods, but the mere perception that a threat exists marks wildlife as detrimental to human wellbeing, generating conflicts all the same whether or not losses of crops or livestock actually occur (Dickman 2010). Therefore, while ecological approaches can determine whether arguments have empirical basis and offer experimental evidence of mitigation strategies, a combination of approaches from the social sciences (such as strategies emanating from the economic or sociological spectrums) can manage the conciliation of opposing interests in situations where conflicts cannot be resolved by successful mitigation strategies, or even when no biological basis is found. Admittedly, failures in conservation actions are often due to overlooking the historical and cultural levels in social conflicts that underlie conservation success (Madden 2004).

To summarize, we find multiple causes of problems for stakeholders whose short-term solutions clearly oppose conservation aims, leading to conflicts (Table 1). However, root causes are difficult to discern, since they underlie problems that when taken at face value may be overlooked. These can often be tightly linked to the hidden impacts of human-wildlife conflicts (Barua et al. 2013). Proximate causes of conflicts may be the immediate problems behind them, but root causes are distal causes that must be understood to explain a conflict and managed to prevent further conflicts from breaking out. For these reasons, as a complementary tool to ecological approaches, we submit to the land-sharing enterprise the use of Conservation Conflict Transformation (*sensu* Madden and McQuinn 2014), specifically, the Levels of Conflict model (Canadian Institute for Conflict Resolution 2000). Because managing tangible ecological variables to untangle problems that generate conflicts may not always resolve competing interests, the existence of root causes to those problems and how they may be approached must be considered in all attempted land-sharing strategies.

Table 1. Typification of conservation conflicts. Root causes, such as social identity needs and rights violations, may form distal drivers for resurging problems that may or may not have a biological basis, whose short-term solutions for stakeholders directly conflict with conservation aims. These are mere stereotypes of problems to exemplify the complexity of each case.

Drivers	**Problem**	**Biological basis**	**Solution**	**Conflicting interests**
Social identity needs	Livestock predation	Carnivore prey switching for net gain	Persecution	Livestock rancher vs carnivore conservation
Unfulfilled food security	Crop raiding	Herbivore optimal foraging	Persecution	Subsistence farming vs herbivore conservation
Perception of rights violation	Poaching	None	Armed conflicts	Economic necessities vs park functioning
Increase in global food and commodity consumption	Land use change	Habitat and protected area allocation	Land sparing/sharing	Land development vs habitat conservation

Reconciliation of farming and wild nature by conflict transformation

Conflict transformation perceives disputes and problems as opportunities to enact change in social systems and seeks to manage conflicts in such a way as to create problem solving dynamics (Lederach 2003). Conflict transformation creates these dynamics by focusing on relations in a systemic context, working to reconcile negative relations by developing processes that establish conditions where all sides can understand each other, essentially moving from an antagonistic mentality to a collaborative “one team” mentality (Madden and McQuinn 2014).

The Levels of Conflict model allows assessing the complexity of a conflict in distinct settings by describing conflicts in three levels along with their matching processes of transformation which are used to address present and future conflicts (Fig. 2). Disputes are observable problems that may reach a *settlement*. Strategies based on ecological theory are capable of settling disputes. When disputes remain unsettled and enough frustrations and emotional reactions build up, an underlying conflict emerges, granting complexity to new disputes that need *resolution*. Lastly, when prejudices take root and assumptions are rooted deep in a group’s identity, long-lasting processes of *reconciliation* may be needed. This seems to be the norm, as most conservation conflicts exist in parallel with social and usually deeper interactions between groups of people, instead of between people and wildlife. The deep-rooted issue may not be related at all to wildlife and instead only pertain to threatening a group’s identity. The same can be said for future shared lands. Newly formed productive landscapes integrating wildlife conservation might also benefit from a Conflict Transformation approach. Conflicts arising in a land-sharing context may be quickly settled, carefully resolved, or might even be a symbolic representation of a deeper conflict that will require conservation professionals to align with social scientists to help reconcile interests that conflict with the occurrence of wildlife on productive lands (Dickman 2010).

Madden and McQuinn (2014) identify the limitations facing current approaches to conflict management, coinciding with our observations from the land-sharing literature. Since conservation emerges from biology, professionals can be biased towards researching wild nature and not humans, resulting in a failure to account for the historical drivers of social conflict in a landscape and therefore do not address social-psychological needs during the formulation of solutions (Madden and McQuinn 2014). In essence, only by considering all dimensions involved in the birth a conflict will it be possible to design strategies that counterattack problems at all levels involved, from addressing identity needs at deep-rooted levels to managing more mechanistic and biological factors to aid in settling disputes.

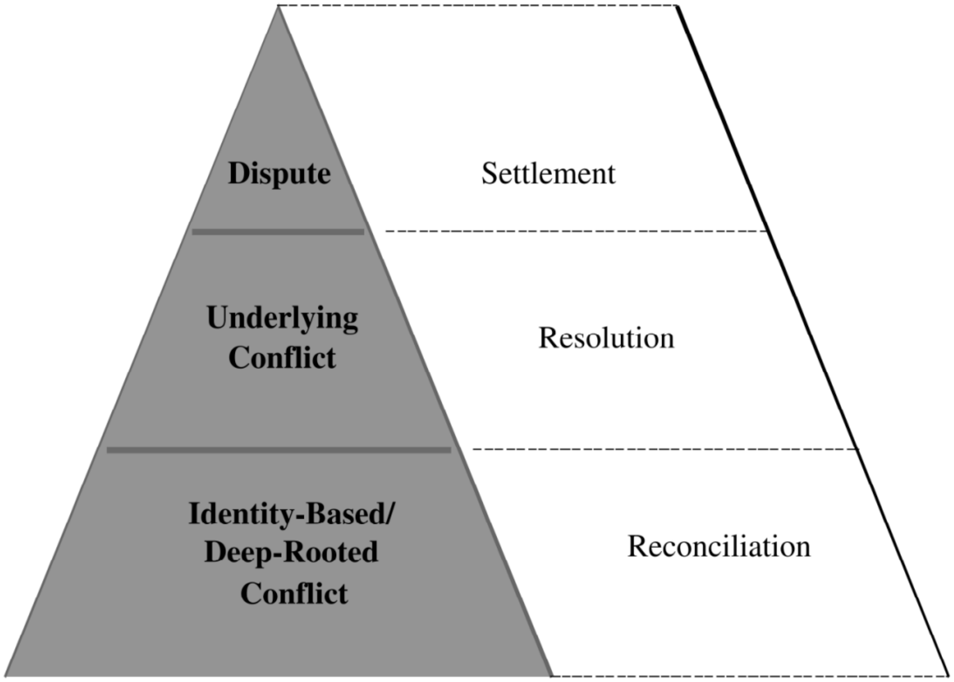

Figure 2. Levels of conflict model. Conservation conflicts are classified according to complexity and intensity occurring at three levels, with conflicts of higher concern owing to a deeper and more established section of the pyramid. Matching processes used to address conflicts are next to each level. Source: adapted by Madden and McQuinn (2014) from The Canadian Institute for Conflict Resolution (2000).

Multidisciplinary approaches will be key to reconciling farming with nature. It is up to a combination of ecology, economy and sociology to settle the myriad disputes that will surface by integrating multiple uses of land with wildlife conservation before underlying conflicts can form. Extending land-sharing to already occupied landscapes for productive purposes will likely necessitate resolving underlying conflicts and reconciling deep-rooted and identity-based conflicts. Having established an agroecological landscape, and once land-sharing can be said to have been attained through processes of reconciliation, one must remain vigilant to avoid further conflicts from taking root. In fact, conflicts are fundamental to society and cannot be viewed as a single event (Lederach 2003), therefore deep-rooted conflicts should be considered an ever-looming threat that must be continually be kept at bay. Disputes about biodiversity should be settled quickly and attention should be paid to frustrations that may accumulate by repeated engagements with wildlife to avoid underlying conflicts caused by affected emotions. Once emotions are affected, the socio-ecological system is once again vulnerable to prejudices and assumptions taking hold. Sharing land with nature will require establishing a dynamic system capable of adapting to new disputes constantly and eschewing the creation of "sides" without fail by making sure that all involved understand the whole system, where production and biodiversity work towards the same goal of sustainability.

Conclusions

To be ecologically and economically sustainable, land-sharing needs more than conflict resolution, it needs reconciliation. Beyond biological and managerial aspects impinging upon livestock predation, which might resolve conflicts, addressing deep rooted beliefs about wild animals that may even form identity needs is required to achieve reconciliation between humans and wildlife, fostering a landscape of coexistence between wildlife and humans, minimizing losses and agreeing on acceptable thresholds of loss on both fronts (Oriol-Cotterill et al. 2015). Despite conflict reconciliation and the resulting coexistence being tantamount to land-sharing, so far human-wildlife conflicts have not yet found their way into the land-sharing/sparing framework, and until they do, land-sharing strategies face the danger of becoming secret wars: wildlife and humans co-occurring, but not coexisting. A contested land is a land not shared, a scenario where all, biodiversity and humans, lose.

Supporting Information

A list of the studies subjected to review is provided as Table S1 and are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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Table S1. References reviewed.

No	AUTHORS	TITLE	JOURNAL	YEAR	CONSERVATION CONFLICT PRESENT	CONFLICTS AS THE AIM	CONFLICT RESOLUTION
1	Desquilbet, M; Dorin, B; Couvet, D	Land Sharing vs Land Sparing to Conserve Biodiversity: How Agricultural Markets Make the Difference	ENVIRONMENTAL MODELING & ASSESSMENT	2017	0	0	0
2	Donaldson, L; Wilson, RJ; Maclean, IMD	Old concepts, new challenges: adapting landscape-scale conservation to the twenty-first century	BIODIVERSITY AND CONSERVATION	2017	1	0	0
3	Fischer, J; Abson, DJ; Bergsten, A; Collier, NF; Dorresteijn, I; Hanspach, J; Hylander, K; Schultner, J; Senbeta, F	Reframing the Food-Biodiversity Challenge	TRENDS IN ECOLOGY & EVOLUTION	2017	1	0	0
4	Koning, AA; Moore, J; Suttidate, N; Hannigan, R; McIntyre, PB	Aquatic Ecosystem Impacts of Land Sharing Versus Sparing: Nutrient Loading to Southeast Asian Rivers	ECOSYSTEMS	2017	0	0	0
5	Law, EA; Bryan, BA; Meijaard, E; Mallawaarachchi, T; Struebig, MJ; Watts, ME; Wilson, KA	Mixed policies give more options in multifunctional tropical forest landscapes	JOURNAL OF APPLIED ECOLOGY	2017	0	0	0
6	Lerner, A; Zuluaga, AF; Chara, J; Etter, A; Searchinger, T	Sustainable Cattle Ranching in Practice: Moving from Theory to Planning in Colombia's Livestock Sector	ENVIRONMENTAL MANAGEMENT	2017	1	0	0
7	Mertz, O; Mertens, CF	Land Sparing and Land Sharing Policies in Developing Countries - Drivers and Linkages to Scientific Debates	WORLD DEVELOPMENT	2017	1	0	0
8	Mukul, SA; Saha, N	Conservation Benefits of Tropical Multifunctional Land-Uses in and Around a Forest Protected Area of Bangladesh	LAND	2017	0	0	0
9	Quinn, JE; Awada, T; Trindade, F; Fulginiti, L; Perrin, R	Combining habitat loss and agricultural intensification improves our understanding of drivers of change in avian abundance in a North American cropland anthrome	ECOLOGY AND EVOLUTION	2017	0	0	0
10	Rescia, AJ; Sanz-Canada, J; Del Bosque-Gonzalez, I	A new mechanism based on landscape diversity for funding farmer subsidies	AGRONOMY FOR SUSTAINABLE DEVELOPMENT	2017	0	0	0
11	Salles, JM; Teillard, F; Tichit, M; Zanella, M	Land sparing versus land sharing: an economist's perspective	REGIONAL ENVIRONMENTAL CHANGE	2017	0	0	0
12	Villasenor, NR; Tulloch, AIT; Driscoll, DA; Gibbons, P; Lindenmayer, DB	Compact development minimizes the impacts of urban growth on native mammals	JOURNAL OF APPLIED ECOLOGY	2017	0	0	0
13	Wittman, H; Chappell, MJ; Abson, DJ; Kerr, R; Blesh, J; Hanspach, J; Perfecto, I; Fischer, J	A social-ecological perspective on harmonizing food security and biodiversity conservation	REGIONAL ENVIRONMENTAL CHANGE	2017	0	0	0
14	Carpio, AJ; Oteros, J; Tortosa, FS; Guerrero-Casado, J	Land use and biodiversity patterns of the herpetofauna: The role of olive groves	ACTA OECOLOGICA-INTERNATIONAL JOURNAL OF ECOLOGY	2016	0	0	0
15	Caryl, FM; Lumsden, LF; van der Ree, R; Wintle, BA	Functional responses of insectivorous bats to increasing housing density support "land-sparing' rather than "land-sharing' urban growth strategies	JOURNAL OF APPLIED ECOLOGY	2016	0	0	0
16	Cierjacks, A; Pommeranz, M; Schulz, K; Almeida-Cortez, J	Is crop yield related to weed species diversity and biomass in coconut and banana fields of northeastern Brazil?	AGRICULTURE ECOSYSTEMS & ENVIRONMENT	2016	0	0	0
17	Cong, RG; Ekroos, J; Smith, HG; Brady, MV	Optimizing intermediate ecosystem services in agriculture using rules based on landscape composition and configuration indices	ECOLOGICAL ECONOMICS	2016	0	0	0
18	de Sartre, XA; Oszwald, J; Veiga, I; Castro, M; de Assis, WS; Michelloti, F; Rocha, C; Souza, H; Sebille, P; Doledec, S; Lavelle, P	Sustainable development policies and the spread of land-sharing practices - A statistical assessment in a frontier region of the Brazilian Amazon	JOURNAL OF RURAL STUDIES	2016	1	0	0
19	Dotta, G; Phalan, B; Silva, TW; Green, R; Balmford, A	Assessing strategies to reconcile agriculture and bird conservation in the temperate grasslands of South America	CONSERVATION BIOLOGY	2016	0	0	0
20	Field, RH; Hill, RK; Carroll, MJ; Morris, AJ	Making explicit agricultural ecosystem service trade-offs: a case study of an English lowland arable farm	INTERNATIONAL JOURNAL OF AGRICULTURAL SUSTAINABILITY	2016	0	0	0
21	Hardman, CJ; Harrison, DPG; Shaw, PJ; Nevard, TD; Hughes, B; Potts, SG; Norris, K	Supporting local diversity of habitats and species on farmland: a comparison of three wildlife-friendly schemes	JOURNAL OF APPLIED ECOLOGY	2016	0	0	0
22	Hardman, CJ; Norris, K; Nevard, TD; Hughes, B; Potts, SG	Delivery of floral resources and pollination services on farmland under three different wildlife-friendly schemes	AGRICULTURE ECOSYSTEMS & ENVIRONMENT	2016	0	0	0

23	Jeliazkov, A; Mimet, A; Charge, R; Jiguet, F; Devictor, V; Chiron, F	Impacts of agricultural intensification on bird communities: New insights from a multi-level and multi-facet approach of biodiversity	AGRICULTURE ECOSYSTEMS & ENVIRONMENT	2016	0	0	0
24	Katayama, N	Bird diversity and abundance in organic and conventional apple orchards in northern Japan	SCIENTIFIC REPORTS	2016	0	0	0
25	Lamb, A; Balmford, A; Green, RE; Phalan, B	To what extent could edge effects and habitat fragmentation diminish the potential benefits of land sparing?	BIOLOGICAL CONSERVATION	2016	0	0	0
26	Lamb, A; Green, R; Bateman, I; Broadmeadow, M; Bruce, T; Burney, J; Carey, P; Chadwick, D; Crane, E; Field, R; Goulding, K; Griffiths, H; Hastings, A; Kasoar, T; Kindred, D; Phalan, B; Pickett, J; Smith, P; Wall, E; Ermgassen, EKHJZ; Balmford, A	The potential for land sparing to offset greenhouse gas emissions from agriculture	NATURE CLIMATE CHANGE	2016	0	0	0
27	Lerouge, F; Sannen, K; Gulinck, H; Vranken, L	Revisiting production and ecosystem services on the farm scale for evaluating land use alternatives	ENVIRONMENTAL SCIENCE & POLICY	2016	0	0	0
28	Marr, EJ; Howley, P; Burns, C	Sparing or sharing? Differing approaches to managing agricultural and environmental spaces in England and Ontario	JOURNAL OF RURAL STUDIES	2016	1	0	0
29	Marull, J; Font, C; Tello, E; Fullana, N; Domene, E; Pons, M; Galan, E	Towards an energy-landscape integrated analysis? Exploring the links between socio-metabolic disturbance and landscape ecology performance (Mallorca, Spain, 1956-2011)	LANDSCAPE ECOLOGY	2016	0	0	0
30	Michael, DR; Wood, JT; O'Loughlin, T; Lindenmayer, DB	Influence of land sharing and land sparing strategies on patterns of vegetation and terrestrial vertebrate richness and occurrence in Australian endangered eucalypt woodlands	AGRICULTURE ECOSYSTEMS & ENVIRONMENT	2016	0	0	0
31	Milligan, MC; Johnson, MD; Garfinkel, M; Smith, CJ; Njoroge, P	Quantifying pest control services by birds and ants in Kenyan coffee farms	BIOLOGICAL CONSERVATION	2016	0	0	0
32	Montoya-Molina, S; Giraldo-Echeverri, C; Montoya-Lerma, J; Chara, J; Escobar, F; Calle, Z	Land sharing vs. land sparing in the dry Caribbean lowlands: A dung beetles' perspective	APPLIED SOIL ECOLOGY	2016	0	0	0
33	Ortega, M; Pascual, S; Rescia, AJ	Spatial structure of olive groves and scrublands affects Bactrocera oleae abundance: a multi-scale analysis	BASIC AND APPLIED ECOLOGY	2016	0	0	0
34	Pedroli, B; Correia, TP; Primdahl, J	Challenges for a shared European countryside of uncertain future. Towards a modern community-based landscape perspective	LANDSCAPE RESEARCH	2016	0	0	0
35	Ponisio, LC; M'Gonigle, LK; Kremen, C	On-farm habitat restoration counters biotic homogenization in intensively managed agriculture	GLOBAL CHANGE BIOLOGY	2016	0	0	0
36	Rotem, G; Ziv, Y	Crop diversity and rotation may increase dispersal opportunities of reptiles in a heterogeneous agroecosystem	AGRICULTURE ECOSYSTEMS & ENVIRONMENT	2016	0	0	0
37	Sato, CE; Wood, JT; Stein, JA; Crane, M; Okada, S; Michael, DR; Kay, GM; Florance, D; Seddon, J; Gibbons, P; Lindenmayer, DB	Natural tree regeneration in agricultural landscapes: The implications of intensification	AGRICULTURE ECOSYSTEMS & ENVIRONMENT	2016	0	0	0
38	Schulte, LA; MacDonald, AL; Niemi, JB; Helmers, MJ	Prairie strips as a mechanism to promote land sharing by birds in industrial agricultural landscapes	AGRICULTURE ECOSYSTEMS & ENVIRONMENT	2016	0	0	0
39	Vongvisouk, T; Broegaard, RB; Mertz, O; Thongmanivong, S	Rush for cash crops and forest protection: Neither land sparing nor land sharing	LAND USE POLICY	2016	0	0	0
40	Yamaura, Y; Shoji, Y; Mitsuda, Y; Utsugi, H; Tsuge, T; Kuriyama, K; Nakamura, F	How many broadleaved trees are enough in conifer plantations? The economy of land sharing, land sparing and quantitative targets	JOURNAL OF APPLIED ECOLOGY	2016	0	0	0
41	Balmford, A; Green, R; Phalan, B	Land for Food & Land for Nature?	DAEDALUS	2015	0	0	0
42	Barral, MP; Benayas, JMR; Meli, P; Maceira, NO	Quantifying the impacts of ecological restoration on biodiversity and ecosystem services in agroecosystems: A global meta-analysis	AGRICULTURE ECOSYSTEMS & ENVIRONMENT	2015	0	0	0
43	Botham, MS; Fernandez-Ploquin, EC; Brereton, T; Harrower, CA; Roy, DB; Heard, MS	Lepidoptera communities across an agricultural gradient: how important are habitat area and habitat diversity in supporting high diversity?	Journal of Insect Conservation	2015	0	0	0
44	Bouyer, Y; Gervasi, V; Poncin, P; Beudels-Jamar, RC; Odden, J; Linnell, JDC	Tolerance to anthropogenic disturbance by a large carnivore: the case of Eurasian lynx in south-eastern Norway	ANIMAL CONSERVATION	2015	1	0	0
45	Butsic, V; Kuemmerle, T	Using optimization methods to align food production and biodiversity conservation beyond land sharing and land sparing	ECOLOGICAL APPLICATIONS	2015	0	0	0
46	Ceddia, MG; Gunter, U; Corriveau-Bourque, A	Land tenure and agricultural expansion in Latin America: The role of Indigenous Peoples' and local communities' forest rights	GLOBAL ENVIRONMENTAL CHANGE-HUMAN AND POLICY DIMENSIONS	2015	0	0	0
47	Chaplin-Kramer, R; Sharp, RP; Mandle, L; Sim, S; Johnson, J; Butnar, I; Canals, LMI; Eichelberger, BA; Ramler, I; Mueller, C; McLachlan, N; Yousefi, A; King, H; Kareiva, PM	Spatial patterns of agricultural expansion determine impacts on biodiversity and carbon storage	PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES OF THE UNITED STATES OF	2015	0	0	0

			AMERICA					
48	Charpentier, A	Insights from life history theory for an explicit treatment of trade-offs in conservation biology	CONSERVATION BIOLOGY	2015	0	0	0
49	Didham, RK; Barker, GM; Bartlam, S; Deakin, EL; Denmead, LH; Fisk, LM; Peters, JMR; Tylianakis, JM; Wright, HR; Schipper, LA	Agricultural Intensification Exacerbates Spillover Effects on Soil Biogeochemistry in Adjacent Forest Remnants	PLOS ONE	2015	0	0	0
50	Edwards, DP; Gilroy, JJ; Thomas, GH; Uribe, CAM; Haugaasen, T	Land-Sparing Agriculture Best Protects Avian Phylogenetic Diversity	CURRENT BIOLOGY	2015	0	0	0
51	Garfinkel, M; Johnson, M	Pest-removal services provided by birds on small organic farms in northern California	AGRICULTURE ECOSYSTEMS & ENVIRONMENT	2015	0	0	0
52	Giam, X; Hadiaty, RK; Tan, HH; Parenti, LR; Wowor, D; Sauri, S; Chong, KY; Yeo, DCJ; Wilcove, DS	Mitigating the impact of oil-palm monoculture on freshwater fishes in Southeast Asia	CONSERVATION BIOLOGY	2015	0	0	0
53	Habel, JC; Teucher, M; Hornetz, B; Jaetzold, R; Kimatu, JN; Kasili, S; Mairura, Z; Mulwa, RK; Eggermont, H; Weisser, WW; Lens, L	Real-world complexity of food security and biodiversity conservation	BIODIVERSITY AND CONSERVATION	2015	0	0	0
54	Hill, R; Miller, C; Newell, B; Dunlop, M; Gordon, IJ	Why biodiversity declines as protected areas increase: the effect of the power of governance regimes on sustainable landscapes	SUSTAINABILITY SCIENCE	2015	0	0	0
55	Kamp, J; Urazaliev, R; Balmford, A; Donald, PF; Green, RE; Lamb, AJ; Phalan, B	Agricultural development and the conservation of avian biodiversity on the Eurasian steppes: a comparison of land-sparing and land-sharing approaches	JOURNAL OF APPLIED ECOLOGY	2015	0	0	0
56	Katayama, N; Osawa, T; Amano, T; Kusumoto, Y	Are both agricultural intensification and farmland abandonment threats to biodiversity? A test with bird communities in paddy-dominated landscapes	AGRICULTURE ECOSYSTEMS & ENVIRONMENT	2015	0	0	0
57	Kehoe, L; Kuemmerle, T; Meyer, C; Levers, C; Vaclavik, T; Kreft, H	Global patterns of agricultural land-use intensity and vertebrate diversity	DIVERSITY AND DISTRIBUTIONS	2015	1	0	0
58	Kremen, C	Reframing the land-sparing/land-sharing debate for biodiversity conservation	YEAR IN ECOLOGY AND CONSERVATION BIOLOGY	2015	0	0	0
59	Law, EA; Meijaard, E; Bryan, BA; Mallawaarachchi, T; Koh, LP; Wilson, KA	Better land-use allocation outperforms land sparing and land sharing approaches to conservation in Central Kalimantan, Indonesia	BIOLOGICAL CONSERVATION	2015	0	0	0
60	Law, EA; Wilson, KA	Providing Context for the Land-Sharing and Land-Sparing Debate	CONSERVATION LETTERS	2015	0	0	0
61	Lindenmayer, D; Messier, C; Paquette, A; Hobbs, RJ	Managing tree plantations as novel socioecological systems: Australian and North American perspectives	CANADIAN JOURNAL OF FOREST RESEARCH	2015	0	0	0
62	Macchi, L; Grau, HR; Phalan, B	Agricultural production and bird conservation in complex landscapes of the dry Chaco	JOURNAL OF LAND USE SCIENCE	2015	0	0	0
63	Marull, J; Tello, E; Fullana, N; Murray, I; Jover, G; Font, C; Coll, F; Domene, E; Leoni, V; Decolli, T	Long-term bio-cultural heritage: exploring the intermediate disturbance hypothesis in agro-ecological landscapes (Mallorca, c. 1850-2012)	BIODIVERSITY AND CONSERVATION	2015	0	0	0
64	Mastrangelo, ME; Laterra, P	From biophysical to social-ecological trade-offs: integrating biodiversity conservation and agricultural production in the Argentine Dry Chaco	ECOLOGY AND SOCIETY	2015	0	0	0
65	Merckx, T; Pereira, HM	Reshaping agri-environmental subsidies: From marginal farming to large-scale rewilding	BASIC AND APPLIED ECOLOGY	2015	0	0	0
66	Paul, C; Knoke, T	Between land sharing and land sparing - what role remains for forest management and conservation?	INTERNATIONAL FORESTRY REVIEW	2015	1	0	0
67	Puech, C; Poggi, S; Baudry, J; Aviron, S	Do farming practices affect natural enemies at the landscape scale?	LANDSCAPE ECOLOGY	2015	0	0	0
68	Pywell, RF; Heard, MS; Woodcock, BA; Hinsley, S; Ridding, L; Nowakowski, M; Bullock, JM	Wildlife-friendly farming increases crop yield: evidence for ecological intensification	PROCEEDINGS OF THE ROYAL SOCIETY B-BIOLOGICAL SCIENCES	2015	0	0	0
69	Shackelford, GE; Steward, PR; German, RN; Sait, SM; Benton, TG	Conservation planning in agricultural landscapes: hotspots of conflict between agriculture and nature	DIVERSITY AND DISTRIBUTIONS	2015	1	1	0
70	Soga, M; Yamaura, Y; Aikoh, T; Shoji, Y; Kubo, T; Gaston, KJ	Reducing the extinction of experience: Association between urban form and recreational use of public greenspace	LANDSCAPE AND URBAN PLANNING	2015	0	0	0
71	Stephens, PA	Land sparing, land sharing, and the fate of Africa's lions	PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES OF THE UNITED STATES OF AMERICA	2015	1	0	0
72	Stott, I; Soga, M; Inger, R; Gaston, KJ	Land sparing is crucial for urban ecosystem services	FRONTIERS IN ECOLOGY AND THE ENVIRONMENT	2015	0	0	0

73	Teuscher, M; Vorlaufer, M; Wollni, M; Brose, U; Mulyani, Y; Clough, Y	Trade-offs between bird diversity and abundance, yields and revenue in smallholder oil palm plantations in Sumatra, Indonesia	BIOLOGICAL CONSERVATION	2015	0	0	0
74	Yoshii, C; Yamaura, Y; Soga, M; Shibuya, M; Nakamura, F	Comparable benefits of land sparing and sharing indicated by bird responses to stand-level plantation intensity in Hokkaido, northern Japan	JOURNAL OF FOREST RESEARCH	2015	0	0	0
75	Yue, S; Brodie, JF; Zipkin, EF; Bernard, H	Oil palm plantations fail to support mammal diversity	ECOLOGICAL APPLICATIONS	2015	0	0	0
76	Ahmadi, M; Lopez-Bao, JV; Kaboli, M	Spatial Heterogeneity in Human Activities Favors the Persistence of Wolves in Agroecosystems	PLOS ONE	2014	1	0	0
77	Andersson, E; Lindborg, R	Species Richness and Assemblages in Landscapes of Different Farming Intensity - Time to Revise Conservation Strategies?	PLOS ONE	2014	0	0	0
78	Baudron, F; Giller, KE	Agriculture and nature: Trouble and strife?	BIOLOGICAL CONSERVATION	2014	1	0	0
79	Brandle, JR; Schoeneberger, MM	WORKING TREES: SUPPORTING AGRICULTURE AND HEALTHY LANDSCAPES	JOURNAL OF TROPICAL FOREST SCIENCE	2014	0	0	0
80	Cattarino, L; McAlpine, CA; Rhodes, JR	Land-use drivers of forest fragmentation vary with spatial scale	GLOBAL ECOLOGY AND BIOGEOGRAPHY	2014	0	0	0
81	Cerda, R; Deheuvels, O; Calvache, D; Niehaus, L; Saenz, Y; Kent, J; Vilchez, S; Villota, A; Martinez, C; Somarriba, E	Contribution of cocoa agroforestry systems to family income and domestic consumption: looking toward intensification	AGROFORESTRY SYSTEMS	2014	0	0	0
82	Christensen, AA; Svenningsen, SR; Lommer, MS; Brandt, J	New multifunctional hunting landscapes in Denmark	GEOGRAFISK TIDSSKRIFT-DANISH JOURNAL OF GEOGRAPHY	2014	0	0	0
83	Christiansen, P; Steen, KA; Jorgensen, RN; Karstoft, H	Automated Detection and Recognition of Wildlife Using Thermal Cameras	SENSORS	2014	0	0	0
84	Cohn, AS; Mosnier, A; Havlik, P; Valin, H; Herrero, M; Schmid, E; O'Hare, M; Obersteiner, M	Cattle ranching intensification in Brazil can reduce global greenhouse gas emissions by sparing land from deforestation	PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES OF THE UNITED STATES OF AMERICA	2014	0	0	0
85	Crespin, SJ; Garcia-Villalta, JE	Integration of Land-Sharing and Land-Sparing Conservation Strategies Through Regional Networking: The Mesoamerican Biological Corridor as a Lifeline for Carnivores in El Salvador	AMBIO	2014	0	0	0
86	Desiree, JI; Pita, AV; Floor, VDH; Andre, PCF	Biodiversity impacts of bioenergy crop production: a state-of-the-art review	GLOBAL CHANGE BIOLOGY BIOENERGY	2014	0	0	0
87	Douglas, DJT; Nalwanga, D; Katebaka, R; Atkinson, PW; Pomeroy, DE; Nkuutu, D; Vickery, JA	The importance of native trees for forest bird conservation in tropical farmland	ANIMAL CONSERVATION	2014	0	0	0
88	Dutta, S; Jhala, Y	Planning agriculture based on landuse responses of threatened semiarid grassland species in India	BIOLOGICAL CONSERVATION	2014	1	0	0
89	Edwards, DP; Gilroy, JJ; Woodcock, P; Edwards, FA; Larsen, TH; Andrews, DJR; Derhe, MA; Docherty, TDS; Hsu, WW; Mitchell, SL; Ota, T; Williams, LJ; Laurance, WF; Hamer, KC; Wilcove, DS	Land-sharing versus land-sparing logging: reconciling timber extraction with biodiversity conservation	GLOBAL CHANGE BIOLOGY	2014	0	0	0
90	Fischer, J; Abson, DJ; Butsic, V; Chappell, MJ; Ekroos, J; Hanspach, J; Kuemmerle, T; Smith, HG; von Wehrden, H	Land Sparing Versus Land Sharing: Moving Forward	CONSERVATION LETTERS	2014	0	0	0
91	Franks, JR	Sustainable intensification: A UK perspective	FOOD POLICY	2014	0	0	0
92	Frigeri, E; Cassano, CR; Pardini, R	Domestic dog invasion in an agroforestry mosaic in southern Bahia, Brazil	TROPICAL CONSERVATION SCIENCE	2014	0	0	0
93	Gilroy, JJ; Edwards, FA; Uribe, CAM; Haugaasen, T; Edwards, DP	Surrounding habitats mediate the trade-off between land-sharing and land-sparing agriculture in the tropics	JOURNAL OF APPLIED ECOLOGY	2014	0	0	0
94	Gilroy, JJ; Woodcock, P; Edwards, FA; Wheeler, C; Uribe, CAM; Haugaasen, T; Edwards, DP	Optimizing carbon storage and biodiversity protection in tropical agricultural landscapes	GLOBAL CHANGE BIOLOGY	2014	0	0	0
95	Goswami, VR; Sridhara, S; Medhi, K; Williams, AC; Chellam, R; Nichols, JD; Oli, MK	Community-managed forests and wildlife-friendly agriculture play a subsidiary but not substitutive role to protected areas for the endangered Asian elephant	BIOLOGICAL CONSERVATION	2014	1	0	0
96	Hart, R; Brady, M; Olsson, O	Joint Production of Food and Wildlife: Uniform Measures or Nature Oases?	ENVIRONMENTAL & RESOURCE ECONOMICS	2014	0	0	0
97	Hernandez-Ruedas, MA; Arroyo-Rodriguez, V; Meave, JA; Martinez-Ramos, M; Ibarra-Manriquez, G; Martinez, E; Jamangape, G; Melo, FPL; Santos, BA	Conserving Tropical Tree Diversity and Forest Structure: The Value of Small Rainforest Patches in Moderately-Managed Landscapes	PLOS ONE	2014	0	0	0

98	Hertel, TW; Ramankutty, N; Baldos, ULC	Global market integration increases likelihood that a future African Green Revolution could increase crop land use and CO2 emissions	PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES OF THE UNITED STATES OF AMERICA	2014	0	0	0
99	Laurance, WF; Sayer, J; Cassman, KG	Agricultural expansion and its impacts on tropical nature	TRENDS IN ECOLOGY & EVOLUTION	2014	1	0	0
100	Lee, JSH; Garcia-Ulloa, J; Ghazoul, J; Obidzinski, K; Koh, LP	Modelling environmental and socio-economic trade-offs associated with land-sparing and land-sharing approaches to oil palm expansion	JOURNAL OF APPLIED ECOLOGY	2014	0	0	0
101	Lenders, HJR; Janssen, IAW	The Grass Snake and the Basilisk: From Pre-Christian Protective House God to the Antichrist	ENVIRONMENT AND HISTORY	2014	0	0	0
102	Mastrangelo, ME; Weyland, F; Villarino, SH; Barral, MP; Nahuelhual, L; Laterra, P	Concepts and methods for landscape multifunctionality and a unifying framework based on ecosystem services	LANDSCAPE ECOLOGY	2014	0	0	0
103	Mendenhall, CD; Frishkoff, LO; Santos-Barrera, G; Pacheco, J; Mesfun, E; Quijano, FM; Ehrlich, PR; Ceballos, G; Daily, GC; Pringle, RM	Countryside biogeography of Neotropical reptiles and amphibians	ECOLOGY	2014	0	0	0
104	Palomo, I; Martin-Lopez, B; Zorrilla-Miras, P; Del Amo, DG; Montes, C	Deliberative mapping of ecosystem services within and around Donana National Park (SW Spain) in relation to land use change	REGIONAL ENVIRONMENTAL CHANGE	2014	0	0	0
105	Phalan, B; Green, R; Balmford, A	Closing yield gaps: perils and possibilities for biodiversity conservation	PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B-BIOLOGICAL SCIENCES	2014	0	0	0
106	Railsback, SF; Johnson, MD	Effects of land use on bird populations and pest control services on coffee farms	PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES OF THE UNITED STATES OF AMERICA	2014	0	0	0
107	Shaw, P; Njoroge, P; Otieno, V; Mlamba, E	The range, abundance and habitat of Hinde's Babbler Turdoides hindei: fine-scale changes in abundance during 2000-2011 reflect temporal variation in scrub cover	BIRD CONSERVATION INTERNATIONAL	2014	0	0	0
108	Soga, M; Yamaura, Y; Koike, S; Gaston, KJ	Land sharing vs. land sparing: does the compact city reconcile urban development and biodiversity conservation?	JOURNAL OF APPLIED ECOLOGY	2014	0	0	0
109	Tisovec, KC; Cassano, CR; Boubli, JP; Pardini, R	Mixed-species Groups of Marmosets and Tamarins Across a Gradient of Agroforestry Intensification	BIOTROPICA	2014	0	0	0
110	Troupin, D; Carmel, Y	Can agro-ecosystems efficiently complement protected area networks?	BIOLOGICAL CONSERVATION	2014	1	0	0
111	Vaast, P; Somarriba, E	Trade-offs between crop intensification and ecosystem services: the role of agroforestry in cocoa cultivation	AGROFORESTRY SYSTEMS	2014	0	0	0
112	von Wehrden, H; Abson, DJ; Beckmann, M; Cord, AF; Klotz, S; Seppelt, R	Realigning the land-sharing/land-sparing debate to match conservation needs: considering diversity scales and land-use history	LANDSCAPE ECOLOGY	2014	0	0	0
113	Barthel, S; Crumley, CL; Svedin, U	Biocultural Refugia: Combating the Erosion of Diversity in Landscapes of Food Production	ECOLOGY AND SOCIETY	2013	0	0	0
114	Blanco, V; Waltert, M	Does the tropical agricultural matrix bear potential for primate conservation? A baseline study from Western Uganda	JOURNAL FOR NATURE CONSERVATION	2013	0	0	0
115	Ceddia, MG; Sedlacek, S; Bardsley, NO; Gomez-y-Paloma, S	Sustainable agricultural intensification or Jevons paradox? The role of public governance in tropical South America	GLOBAL ENVIRONMENTAL CHANGE-HUMAN AND POLICY DIMENSIONS	2013	0	0	0
116	Chandler, RB; King, DI; Raudales, R; Trubey, R; Chandler, C; Chavez, VJA	A Small-Scale Land-Sparing Approach to Conserving Biological Diversity in Tropical Agricultural Landscapes	CONSERVATION BIOLOGY	2013	0	0	0
117	Fagan, ME; DeFries, RS; Sesnie, SE; Arroyo, JP; Walker, W; Soto, C; Chazdon, RL; Sanchun, A	Land cover dynamics following a deforestation ban in northern Costa Rica	ENVIRONMENTAL RESEARCH LETTERS	2013	0	0	0
118	Gabriel, D; Sait, SM; Kunin, WE; Benton, TG	Food production vs. biodiversity: comparing organic and conventional agriculture	JOURNAL OF APPLIED ECOLOGY	2013	0	0	0
119	Grau, R; Kuemmerle, T; Macchi, L	Beyond 'land sparing versus land sharing': environmental heterogeneity, globalization and the balance between agricultural production and nature conservation	CURRENT OPINION IN ENVIRONMENTAL SUSTAINABILITY	2013	1	0	0
120	Habel, JC; Weisser, WW; Eggermont, H; Lens, L	Food security versus biodiversity protection: an example of land-sharing from East Africa	BIODIVERSITY AND CONSERVATION	2013	0	0	0
121	Hulme, MF; Vickery, JA; Green, RE; Phalan, B; Chamberlain, DE; Pomeroy, DE; Nalwanga, D; Mushabe, D; Katebaka, R; Bolwig, S; Atkinson, PW	Conserving the Birds of Uganda's Banana-Coffee Arc: Land Sparing and Land Sharing Compared	PLOS ONE	2013	0	0	0

122	Lindenmayer, DB; Cunningham, SA	Six principles for managing forests as ecologically sustainable ecosystems	LANDSCAPE ECOLOGY	2013	0	0	0
123	Loeuille, N; Barot, S; Georgelin, E; Kylafis, G; Lavigne, C	Eco-Evolutionary Dynamics of Agricultural Networks: Implications for Sustainable Management	ADVANCES IN ECOLOGICAL RESEARCH, VOL 49: ECOLOGICAL NETWORKS IN AN AGRICULTURAL WORLD	2013	0	0	0
124	Macchi, L; Grau, HR; Zelaya, PV; Marinaro, S	Trade-offs between land use intensity and avian biodiversity in the dry Chaco of Argentina: A tale of two gradients	AGRICULTURE ECOSYSTEMS & ENVIRONMENT	2013	1	0	0
125	Maskell, LC; Crowe, A; Dunbar, MJ; Emmett, B; Henrys, P; Keith, AM; Norton, LR; Scholefield, P; Clark, DB; Simpson, IC; Smart, SM	Exploring the ecological constraints to multiple ecosystem service delivery and biodiversity	JOURNAL OF APPLIED ECOLOGY	2013	0	0	0
126	Mendenhall, CD; Archer, HM; Brenes, FO; Sekercioglu, CH; Sehgal, RNM	Balancing biodiversity with agriculture: Land sharing mitigates avian malaria prevalence	CONSERVATION LETTERS	2013	0	0	0
127	Minang, PA; van Noordwijk, M	Design challenges for achieving reduced emissions from deforestation and forest degradation through conservation: Leveraging multiple paradigms at the tropical forest margins	LAND USE POLICY	2013	0	0	0
128	Phelps, J; Carrasco, LR; Webb, EL; Koh, LP; Pascual, U	Agricultural intensification escalates future conservation costs	PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES OF THE UNITED STATES OF AMERICA	2013	1	0	0
129	Ramankutty, N; Rhemtulla, J	Land sparing or land sharing: context dependent	FRONTIERS IN ECOLOGY AND THE ENVIRONMENT	2013	0	0	0
130	Scariot, A	Land sparing or land sharing: the missing link	FRONTIERS IN ECOLOGY AND THE ENVIRONMENT	2013	0	0	0
131	Van Asselen, S; Verburg, PH	Land cover change or land-use intensification: simulating land system change with a global-scale land change model	GLOBAL CHANGE BIOLOGY	2013	0	0	0
132	Adams, WM	Feeding the next billion: hunger and conservation	ORYX	2012	0	0	0
133	Anderson-Teixeira, KJ; Duval, BD; Long, SP; DeLucia, EH	Biofuels on the landscape: Is "land sharing" preferable to "land sparing"?	ECOLOGICAL APPLICATIONS	2012	0	0	0
134	Balmford, A; Green, R; Phalan, B	What conservationists need to know about farming	PROCEEDINGS OF THE ROYAL SOCIETY B-BIOLOGICAL SCIENCES	2012	0	0	0
135	Benayas, JMR; Bullock, JM	Restoration of Biodiversity and Ecosystem Services on Agricultural Land	ECOSYSTEMS	2012	1	0	0
136	Butsic, V; Radeloff, VC; Kuemmerle, T; Pidgeon, AM	Analytical Solutions to Trade-Offs between Size of Protected Areas and Land-Use Intensity	CONSERVATION BIOLOGY	2012	0	0	0
137	Edwards, DP; Laurance, SG	Green labelling, sustainability and the expansion of tropical agriculture: Critical issues for certification schemes	BIOLOGICAL CONSERVATION	2012	1	0	0
138	Egan, JF; Mortensen, DA	A comparison of land-sharing and land-sparing strategies for plant richness conservation in agricultural landscapes	ECOLOGICAL APPLICATIONS	2012	0	0	0
139	Eloy, L; Meral, P; Ludewigs, T; Pinheiro, GT; Singer, B	Payments for ecosystem services in Amazonia. The challenge of land use heterogeneity in agricultural frontiers near Cruzeiro do Sul (Acre, Brazil)	JOURNAL OF ENVIRONMENTAL PLANNING AND MANAGEMENT	2012	0	0	0
140	Erb, KH	How a socio-ecological metabolism approach can help to advance our understanding of changes in land-use intensity	ECOLOGICAL ECONOMICS	2012	0	0	0
141	Holland, JM; Smith, BM; Birkett, TC; Southway, S	Farmland bird invertebrate food provision in arable crops	ANNALS OF APPLIED BIOLOGY	2012	0	0	0
142	Kremen, C; Miles, A	Ecosystem Services in Biologically Diversified versus Conventional Farming Systems: Benefits, Externalities, and Trade-Offs	ECOLOGY AND SOCIETY	2012	0	0	0
143	Lentini, PE; Gibbons, P; Fischer, J; Law, B; Hanspach, J; Martin, TG	Bats in a Farming Landscape Benefit from Linear Remnants and Unimproved Pastures	PLOS ONE	2012	0	0	0
144	Lindenmayer, DB; Franklin, JF; Lohmus, A; Baker, SC; Bauhus, J; Beese, W; Brodie, A; Kiehl, B; Kouki, J; Pastur, GM; Messier, C; Neyland, M; Palik, B; Sverdrup-Thygeson, A; Volney, J; Wayne, A; Gustafsson, L	A major shift to the retention approach for forestry can help resolve some global forest sustainability issues	CONSERVATION LETTERS	2012	0	0	0

145	Lusiana, B; van Noordwijk, M; Cadisch, G	Land sparing or sharing? Exploring livestock fodder options in combination with land use zoning and consequences for livelihoods and net carbon stocks using the FALLOW model	AGRICULTURE ECOSYSTEMS & ENVIRONMENT	2012	0	0	0
146	Mahood, SP; Lees, AC; Peres, CA	Amazonian countryside habitats provide limited avian conservation value	BIODIVERSITY AND CONSERVATION	2012	0	0	0
147	Mastrangelo, ME; Gavin, MC	Trade-Offs between Cattle Production and Bird Conservation in an Agricultural Frontier of the Gran Chaco of Argentina	CONSERVATION BIOLOGY	2012	0	0	0
148	Navarro, LM; Pereira, HM	Rewilding Abandoned Landscapes in Europe	ECOSYSTEMS	2012	1	0	0
149	Pautasso, M; Doring, TF; Garbelotto, M; Pellis, L; Jeger, MJ	Impacts of climate change on plant diseases-opinions and trends	EUROPEAN JOURNAL OF PLANT PATHOLOGY	2012	0	0	0
150	Phalan, B; Balmford, A; Green, RE	Agriculture as a key element for conservation: reasons for caution	CONSERVATION LETTERS	2012	0	0	0
151	Pirard, R; Belna, K	Agriculture and Deforestation: Is REDD+ Rooted In Evidence?	FOREST POLICY AND ECONOMICS	2012	1	0	0
152	Pywell, RF; Heard, MS; Bradbury, RB; Hinsley, S; Nowakowski, M; Walker, KJ; Bullock, JM	Wildlife-friendly farming benefits rare birds, bees and plants	BIOLOGY LETTERS	2012	0	0	0
153	Quinn, JE; Brandle, JR; Johnson, RJ	The effects of land sparing and wildlife-friendly practices on grassland bird abundance within organic farmlands	AGRICULTURE ECOSYSTEMS & ENVIRONMENT	2012	0	0	0
154	Tscharntke, T; Clough, Y; Wanger, TC; Jackson, L; Motzke, I; Perfecto, I; Vandermeer, J; Whitbread, A	Global food security, biodiversity conservation and the future of agricultural intensification	BIOLOGICAL CONSERVATION	2012	0	0	0
155	Waldron, A; Justicia, R; Smith, L; Sanchez, M	Conservation through Chocolate: a win-win for biodiversity and farmers in Ecuador's lowland tropics	CONSERVATION LETTERS	2012	1	0	0
156	Wright, HL; Lake, IR; Dolman, PM	Low-impact agriculture requires urgent attention not greater caution: response to Phalan and colleagues	CONSERVATION LETTERS	2012	0	0	0
157	Wright, HL; Lake, IR; Dolman, PM	Agriculture-a key element for conservation in the developing world	CONSERVATION LETTERS	2012	0	0	0
158	Yamaura, Y; Oka, H; Taki, H; Ozaki, K; Tanaka, H	Sustainable management of planted landscapes: lessons from Japan	BIODIVERSITY AND CONSERVATION	2012	0	0	0
159	Acevedo, MF	Interdisciplinary progress in food production, food security and environment research	ENVIRONMENTAL CONSERVATION	2011	1	0	0
160	Baudron, F; Corbeels, M; Andersson, JA; Sibanda, M; Giller, KE	Delineating the drivers of waning wildlife habitat: The predominance of cotton farming on the fringe of protected areas in the Mid-Zambezi Valley, Zimbabwe	BIOLOGICAL CONSERVATION	2011	1	0	0
161	Clough, Y; Barkmann, J; Juhrbandt, J; Kessler, M; Wanger, TC; Anshary, A; Buchori, D; Cicuzza, D; Darras, K; Putra, DD; Erasmi, S; Pitopang, R; Schmidt, C; Schulze, CH; Seidel, D; Steffan-Dewenter, I; Stenchly, K; Vidal, S; Weist, M; Wielgoss, AC; Tscharntke, T	Combining high biodiversity with high yields in tropical agroforests	PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES OF THE UNITED STATES OF AMERICA	2011	0	0	0
162	Gockowski, J; Sonwa, D	Cocoa Intensification Scenarios and Their Predicted Impact on CO2 Emissions, Biodiversity Conservation, and Rural Livelihoods in the Guinea Rain Forest of West Africa	ENVIRONMENTAL MANAGEMENT	2011	0	0	0
163	Godfray, HCJ	Food and Biodiversity	SCIENCE	2011	0	0	0
164	Helsen, K; Van Meerbeek, K; Honnay, O; Hermy, M	Conservation credit for plant species diversity of small nature reserves in an agricultural matrix	PLANT ECOLOGY AND EVOLUTION	2011	1	0	0
165	Kamp, J; Urazaliev, R; Donald, PF; Holzel, N	Post-Soviet agricultural change predicts future declines after recent recovery in Eurasian steppe bird populations	BIOLOGICAL CONSERVATION	2011	0	0	0
166	Lambin, EF; Meyfroidt, P	Global land use change, economic globalization, and the looming land scarcity	PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES OF THE UNITED STATES OF AMERICA	2011	0	0	0
167	Mendenhall, CD; Sekercioglu, CH; Brenes, FO; Ehrlich, PR; Daily, GC	Predictive model for sustaining biodiversity in tropical countryside	PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES OF THE UNITED STATES OF AMERICA	2011	1	0	0
168	Peral, AT; Garcia-Barrios, L; Casalduero, AG	AGRICULTURE AND CONSERVATION IN LATIN AMERICA IN THE 21ST CENTURY: SHALL WE CELEBRATE THE 'FOREST TRANSITION' OR ACTIVELY BUILD THE 'NATURE MATRIX'	INTERCIENCIA	2011	0	0	0

169	Perlut, NG; Strong, AM; Alexander, TJ	A Model for Integrating Wildlife Science and Agri-Environmental Policy in the Conservation of Declining Species	JOURNAL OF WILDLIFE MANAGEMENT	2011	0	0	0
170	Phalan, B; Balmford, A; Green, RE; Scharlemann, JPW	Minimising the harm to biodiversity of producing more food globally	FOOD POLICY	2011	1	0	0
171	Phalan, B; Onial, M; Balmford, A; Green, RE	Reconciling Food Production and Biodiversity Conservation: Land Sharing and Land Sparing Compared	SCIENCE	2011	0	0	0
172	Ramirez, PA; Simonetti, JA	Conservation opportunities in commercial plantations: The case of mammals	JOURNAL FOR NATURE CONSERVATION	2011	0	0	0
173	Schroth, G; Faria, D; Araujo, M; Bede, L; Van Bael, SA; Cassano, CR; Oliveira, LC; Delabie, JHC	Conservation in tropical landscape mosaics: the case of the cacao landscape of southern Bahia, Brazil	BIODIVERSITY AND CONSERVATION	2011	0	0	0
174	Sheldon, FH; Styring, AR	BIRD DIVERSITY DIFFERS BETWEEN INDUSTRIAL TREE PLANTATIONS ON BORNEO: IMPLICATIONS FOR CONSERVATION PLANNING	RAFFLES BULLETIN OF ZOOLOGY	2011	0	0	0
175	Sunderland, TCH	Food security: why is biodiversity important?	INTERNATIONAL FORESTRY REVIEW	2011	0	0	0
176	Whittingham, MJ	The future of agri-environment schemes: biodiversity gains and ecosystem service delivery?	JOURNAL OF APPLIED ECOLOGY	2011	0	0	0
177	Anand, MO; Krishnaswamy, J; Kumar, A; Bali, A	Sustaining biodiversity conservation in human-modified landscapes in the Western Ghats: Remnant forests matter	BIOLOGICAL CONSERVATION	2010	0	0	0
178	Chiron, F; Filippi-Codaccioni, O; Jiguet, F; Devictor, V	Effects of non-cropped landscape diversity on spatial dynamics of farmland birds in intensive farming systems	BIOLOGICAL CONSERVATION	2010	0	0	0
179	Edwards, DP; Hodgson, JA; Hamer, KC; Mitchell, SL; Ahmad, AH; Cornell, SJ; Wilcove, DS	Wildlife-friendly oil palm plantations fail to protect biodiversity effectively	CONSERVATION LETTERS	2010	0	0	0
180	Ghazoul, J; Koh, LP; Butler, RA	A REDD Light for Wildlife-Friendly Farming	CONSERVATION BIOLOGY	2010	0	0	0
181	Hennessy, DA; Lapan, H	BUYING ECOLOGICAL SERVICES: FRAGMENTED RESERVES, CORE AND PERIPHERY NATIONAL PARK STRUCTURE, AND THE AGRICULTURAL EXTENSIFICATION DEBATE	NATURAL RESOURCE MODELING	2010	0	0	0
182	Hodgson, JA; Kunin, WE; Thomas, CD; Benton, TG; Gabriel, D	Comparing organic farming and land sparing: optimizing yield and butterfly populations at a landscape scale	ECOLOGY LETTERS	2010	0	0	0
183	Perfecto, I; Vandermeer, J	The agroecological matrix as alternative to the land-sparing/agriculture intensification model	PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES OF THE UNITED STATES OF AMERICA	2010	0	0	0
184	Wade, ASI; Asase, A; Hadley, P; Mason, J; Ofori-Frimpong, K; Preece, D; Spring, N; Norris, K	Management strategies for maximizing carbon storage and tree species diversity in cocoa-growing landscapes	AGRICULTURE ECOSYSTEMS & ENVIRONMENT	2010	0	0	0
185	Chappell, MJ; Vandermeer, J; Badgley, C; Perfecto, I	Wildlife-friendly farming vs land sparing	FRONTIERS IN ECOLOGY AND THE ENVIRONMENT	2009	0	0	0
186	Delibes-Mateos, M; Ferreras, P; Villafuerte, R	European rabbit population trends and associated factors: a review of the situation in the Iberian Peninsula	MAMMAL REVIEW	2009	1	0	0
187	Duncan, DH; Dorrough, JW	Historical and current land use shape landscape restoration options in the Australian wheat and sheep farming zone	LANDSCAPE AND URBAN PLANNING	2009	0	0	0
188	Ewers, RM; Scharlemann, JPW; Balmford, A; Green, RE	Do increases in agricultural yield spare land for nature?	GLOBAL CHANGE BIOLOGY	2009	0	0	0
189	Gabriel, D; Carver, SJ; Durham, H; Kunin, WE; Palmer, RC; Sait, SM; Stagl, S; Benton, TG	The spatial aggregation of organic farming in England and its underlying environmental correlates	JOURNAL OF APPLIED ECOLOGY	2009	0	0	0
190	Koh, LP; Levang, P; Ghazoul, J	Designer landscapes for sustainable biofuels	TRENDS IN ECOLOGY & EVOLUTION	2009	0	0	0
191	Phalan, B; Fitzherbert, EB; Rafflegeau, S; Struebig, MJ; Verwilghen, A	Conservation in Oil-Palm Landscapes	CONSERVATION BIOLOGY	2009	0	0	0
192	Rudel, TK; Schneider, L; Uriarte, M; Turner, BL; DeFries, R; Lawrence, D; Geoghegan, J; Hecht, S; Ickowitz, A; Lambin, EF; Birkenholtz, T; Baptista, S; Grau, R	Agricultural intensification and changes in cultivated areas, 1970-2005	PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES OF THE UNITED STATES OF AMERICA	2009	0	0	0
193	Ceotto, E	Grasslands for bioenergy production. A review	AGRONOMY FOR SUSTAINABLE DEVELOPMENT	2008	0	0	0

194	Fischer, J; Brosi, B; Daily, GC; Ehrlich, PR; Goldman, R; Goldstein, J; Lindenmayer, DB; Manning, AD; Mooney, HA; Pejchar, L; Ranganathan, J; Tallis, H	Should agricultural policies encourage land sparing or wildlife-friendly farming?	FRONTIERS IN ECOLOGY AND THE ENVIRONMENT	2008	0	0	0
195	Fitzherbert, EB; Struebig, MJ; Morel, A; Danielsen, F; Bruhl, CA; Donald, PF; Phalan, B	How will oil palm expansion affect biodiversity?	TRENDS IN ECOLOGY & EVOLUTION	2008	1	0	0
196	Grau, HR; Gasparri, NI; Aide, TM	Balancing food production and nature conservation in the Neotropical dry forests of northern Argentina	GLOBAL CHANGE BIOLOGY	2008	1	0	0
197	Norris, K	Agriculture and biodiversity conservation: opportunity knocks	CONSERVATION LETTERS	2008	0	0	0
198	Perfecto, I; Vandermeer, J	Biodiversity conservation in tropical agroecosystems - A new conservation paradigm	YEAR IN ECOLOGY AND CONSERVATION BIOLOGY 2008	2008	0	0	0
199	Dorrough, J; Moll, J; Crosthwaite, J	Can intensification of temperate Australian livestock production systems save land for native biodiversity?	AGRICULTURE ECOSYSTEMS & ENVIRONMENT	2007	1	0	0
200	Makowski, D; Dore, T; Gasquez, J; Munier-Jolain, N	Modelling land use strategies to optimise crop production and protection of ecologically important weed species	WEED RESEARCH	2007	0	0	0
201	Steffan-Dewenter, I; Kessler, M; Barkmann, J; Bos, MM; Buchori, D; Erasmi, S; Faust, H; Gerold, G; Glenk, K; Gradstein, SR; Guhardja, E; Harteveld, M; Hertel, D; Hohn, P; Kappas, M; Kohler, S; Leuschner, C; Maertens, M; Marggraf, R; Migge-Kleian, S; Mogea, J; Pitopang, R; Schaefer, M; Schwarze, S; Sporn, SG; Steingrebe, A; Tjitrosoedirdjo, SS; Tjitrosoemito, S; Twele, A; Weber, R; Woltmann, L; Zeller, M; Tscharntke, T	Tradeoffs between income, biodiversity, and ecosystem functioning during tropical rainforest conversion and agroforestry intensification	PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES OF THE UNITED STATES OF AMERICA	2007	0	0	0
202	Vandermeer, J; Perfecto, I	The agricultural matrix and a future paradigm for conservation	CONSERVATION BIOLOGY	2007	0	0	0
203	Wallis De Vries, MF; Parkinson, AE; Dulphy, JP; Sayer, M; Diana, E	Effects of livestock breed and grazing intensity on biodiversity and production in grazing systems. 4. Effects on animal diversity	GRASS AND FORAGE SCIENCE	2007	0	0	0
204	Aratrakorn, S; Thunhikorn, S; Donald, PF	Changes in bird communities following conversion of lowland forest to oil palm and rubber plantations in southern Thailand	BIRD CONSERVATION INTERNATIONAL	2006	0	0	0
205	Manning, AD; Fischer, J; Lindenmayer, DB	Scattered trees are keystone structures - Implications for conservation	BIOLOGICAL CONSERVATION	2006	0	0	0
206	Matson, PA; Vitousek, PM	Agricultural intensification: Will land spared from farming be land spared for nature?	CONSERVATION BIOLOGY	2006	0	0	0
207	Morton, DC; DeFries, RS; Shimabukuro, YE; Anderson, LO; Arai, E; Espirito-Santo, FD; Freitas, R; Morisette, J	Cropland expansion changes deforestation dynamics in the southern Brazilian Amazon	PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES OF THE UNITED STATES OF AMERICA	2006	0	0	0
208	Balmford, A; Green, RE; Scharlemann, JPW	Sparing land for nature: exploring the potential impact of changes in agricultural yield on the area needed for crop production	GLOBAL CHANGE BIOLOGY	2005	0	0	0
209	Green, RE; Cornell, SJ; Scharlemann, JPW; Balmford, A	Farming and the fate of wild nature	SCIENCE	2005	0	0	0
210	Mattison, EHA; Norris, K	Bridging the gaps between agricultural policy, land-use and biodiversity	TRENDS IN ECOLOGY & EVOLUTION	2005	1	0	0

Chapter 2

Global patterns of livestock predation show that vegetation cover has more potential than wild prey availability as a management tool to reach human-carnivore coexistence in shared lands

Abstract

Food production and nature compete for space and various management strategies have been conceived in search of dynamics that allow both to coexist, most prominently land-sharing. To achieve a state of coexistence between livestock ranchers and wildlife we considered managing the availability of wild prey to minimize rates of livestock predation. To this end we formulated two sets of hypotheses around two explanations for livestock predation based on the abundance of wild prey, 1) either by itself or 2) relative to the abundance of domestic prey. We used a literature-based approach to data collation to accrue a global dataset, and tested predictions by model averaging generalized linear models derived from our hypotheses. Among our two explanations, we found that only absolute density of wild prey explained carnivore predation rate on livestock, however it increases the amount of livestock lost by predation. We found domestic prey density and vegetation type to be covariates of wild prey density, with higher abundances of domestic prey predictably increasing the rate of predation and closed vegetation also increasing loss of livestock. We find that model averaged estimates indicate that increasing one individual of wild and domestic prey also increases the number of livestock killed by 9.7% and 7.6%, respectively. Therefore, instead of managing prey availability of both wild and domestic prey, we suggest managing livestock vulnerability by spatially segregating livestock from denser vegetation but maintaining sufficiently large pockets of natural habitat for wildlife.

Introduction

Conservation conflicts have only recently been integrated into the land-sharing narrative and their resolution advanced as necessary for farming and nature to coexist (Crespin & Simonetti 2018). The land-sharing approach, which stems from the framework established by Green et al. (2005) and depicts dichotomous strategies based on traditional sparing of nature from production of goods (land-sparing) or the integration of food production and biodiversity conservation on the same land (land-sharing), has previously overlooked the coexistence between humans and wildlife needed for its successful implementation. To address the nexus between food production and biodiversity conservation, newer frameworks suggest shifting from focusing only on production to viewing landscapes as social-ecological systems whose dynamics can be managed to enable food security and conservation goals (Fischer et al. 2017). However, no matter the conceptual framework, any strategy implemented with the purpose of allowing the co-occurrence of food production and wild nature cannot be successful until conflicts are resolved, and coexistence achieved.

Chief among conservation conflicts are those pertaining to human-carnivore interactions, which emerge when native species prey on domestic animals intended as food and material for humans (Redpath et al. 2013). Sharing land is necessary for the conservation of wildlife, and particularly for large-bodied species such as carnivores, which require extensive areas for habitat (Baker et al. 2008), particularly in this century where an increasingly crowded planet threatens the exclusion of nonhuman species (Crist et al. 2017). Empirical evidence points to examples such as snow leopards in Mongolia, where 40% of protected areas in the leopard's distribution cannot abide the home range of adult leopards (Johansson et al. 2016). Countries with extensively transformed landscapes and small protected areas may have no other choice than to look toward integration strategies, such as the Republic of El Salvador, whose protected areas cannot sustain viable populations for 87% of its extant carnivore species (Crespin & Garcia-Villalta 2014). Such predators roaming outside protected areas might prey upon livestock, turning predation of livestock the forefront of biological interactions preventing coexistence, and consequently any strategy akin to land-sharing.

Carnivores conflict with humans when switching from wild to domestic prey. This shift emerges because predators choose the most profitable prey when considering the energy expended while seeking out and handling prey (MacArthur & Pianka 1966). When natural prey is scarce due to population fluctuations or anthropogenic impacts, a livestock kill becomes more profitable for predators as the alternative available prey (Sacks & Neale 2002, Polisar et al., 2003; Bauer & de Iongh, 2005; Azevedo & Murray 2007, Sacks & Neale 2007, Kumaraguru et al. 2011, Mondal et al. 2011, Amador-Alcalá et al. 2013, Kabir et al. 2014, Khorozyan et al. 2015). Big cats might synchronize predation of livestock to temporal patterns of wild prey availability (Loveridge et al. 2010) while canids have been found to have opposing short- and long-term responses to fluctuations of prey availability, with higher abundances of wild prey inciting prey switching from livestock to wild prey in the short-term (Meriggi & Lovari 1996) but increasing livestock predation rate in the long-term by the increase in canid populations in response to more wild prey (Wagner 1988). In general, a higher availability of wild prey decreases the predation of domestic animals by different carnivores in the short term through prey switching by shortening time searching for prey. Therefore, focusing on the most dire and visible conservation conflicts, we propose dealing with human-carnivore conflicts by addressing the age-old hypothesis that a sufficient amount of available alternative prey might decrease the rate of livestock predation.

Modulating prey availability is possible by managing the resources available to them in a given landscape, be they related to habitat structure or food. Consequently, manipulating the amount of prey resource present in a landscape could be a feasible solution for management to address livestock predation by carnivores. To determine if the availability of wild prey can enact prey switching from livestock as an overall global tendency in carnivores, the first explanation for livestock predation that we explore is the absolute density of wild prey (explanation 1, Table 1).

Supposing that an increase in the abundance of livestock populations renders prey switching an active response by carnivores (Holling 1959), then a wild-to-domestic prey ratio might be more useful than the absolute number of wild prey. In fact, the functional response might not be unveiled until one considers how the effect of fluctuations in the relative density of wild prey influences the rate of predation on domestic prey. In light of prey switching acting as a decision-making mechanism that depends on the availability of both wild and domestic prey, the second explanation we assess is that rates of livestock predation are a function of the density of wild prey relative to the density of co-occurring livestock (explanation 2, Table 1).

Table 1. Hypotheses of predator response that form the basis of a priori models for carnivore kills of domestic prey.

Explanation	Covariate	Hypothesis
1 Absolute wild prey density	a. None	More wild prey lower kills
	b. Domestic prey density	More wild prey and less domestic prey lower kills
	c. Wild and domestic prey density interaction	More wild prey lower kills depending on the density of domestic prey
	d. Vegetation	More wild prey and less vegetation cover lower kills
	e. Domestic prey size	More wild prey and larger domestic prey size lower kills
	f. Wild prey size	More wild prey and larger wild prey size lower kills
	g. Predator size	More wild prey and larger predator size lower kills
2 Relative wild prey density	a. None	More wild prey in relation to domestic prey lower kills
	b. Vegetation	More wild prey in relation to domestic prey and vegetation cover lower kills
	c. Domestic prey size	More wild prey in relation to domestic prey and larger domestic prey size lower kills
	d. Wild prey size	More wild prey in relation to domestic prey and larger wild prey size lower kills
	e. Predator size	More wild prey in relation to domestic prey and larger predator size lower kills

In general, we test if increased availability of wild prey reduces livestock predation, either by absolute availability or its relative availability regarding livestock (hypothesis 1a, 2a, Table 1). If true, then understanding and managing the factors that determine the density of natural prey can help prevent the predation of livestock and facilitate the coexistence of native carnivores on farmland. However, the conditions under which absolute or relative densities of wild prey can explain livestock predation are unclear. Conditions that might affect the relation between natural prey availability and livestock predation are many, but from an ecological perspective they most notably include domestic prey density, the amount of vegetation, and the size of predator and prey, both wild and domestic. A higher density of domestic prey may make encountering livestock frequent enough to entice carnivores (hypothesis 1b, Table 1) and interact with the density of wild prey (hypothesis 1c, Table 1) to create density thresholds of prey selection below which carnivores continue selecting wild prey and beyond which they switch to livestock (Khorozyan et al. 2015). Vegetation cover may increase predators' capacity to remain unseen, increase ambush opportunities and facilitate kills (Elliott et al. 1977), although it also allows prey to increase their chances of remaining hidden, as predation risk increases with distance to cover (Hughes & Ward 1993) (hypothesis 1d, 2b, Table 1). Larger predator size enables the hunting of bigger prey (MacArthur 1972) but may also require greater amounts of smaller livestock kills for sustenance (hypothesis 1g, 2e, Table 1). Prey size should also factor in, as overall smaller livestock may be easier to kill yet larger wild prey may capture carnivores' attention by yielding more resource per kill (hypothesis 1e,1f, 2c, 2d, Table 1). These factors could have a direct effect on livestock predation by modulating the success of predators or the vulnerability of livestock to attack but might also have a distal effect by modulating the availability of natural prey as a resource.

Here, we ask if it is possible for shared landscapes to offset carnivore predation of livestock by employing wild prey as an alternative resource to livestock (Table 1). We propose hypotheses (see Table 1) based on carnivore predation patterns regarding prey switching and offer two plausible explanations mediating carnivore kills of livestock: first, the absolute density of wild prey (prediction 1, figure 1a), and second, the relative density of wild prey (prediction 2, figure 1b), both modulated by covariates such as domestic prey density, vegetation cover, predator size and prey size of both domestic and wild animals. To search for a general pattern, we use cases from the literature with sufficient data to allow testing of our hypotheses (see Table 1), codify them into regression equation models and select the most parsimonious ones. If managing biodiversity variables that simultaneously aid conservation efforts can modulate and minimize loss of livestock by predation, then coexistence may yet be an attainable goal, turning land-sharing into a realizable strategy. We tested these hypotheses based on a review of available information regarding livestock predation by wild carnivores worldwide.

Fig 1a.Predictions based on absolute wild prey density (explanation 1, more wild prey lowers kills):

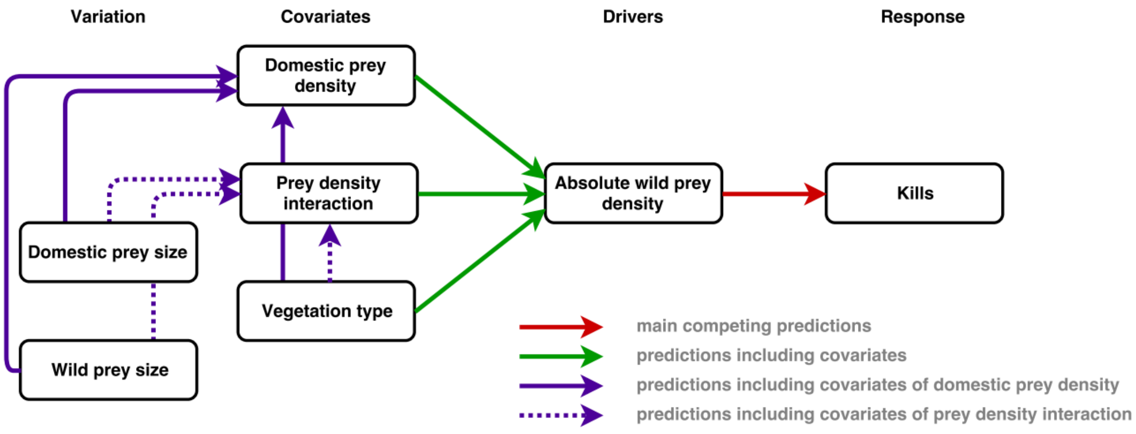

Fig 1b. Predictions based on relative wild prey density (explanation 2, more wild prey in relation to domestic prey lowers kills):

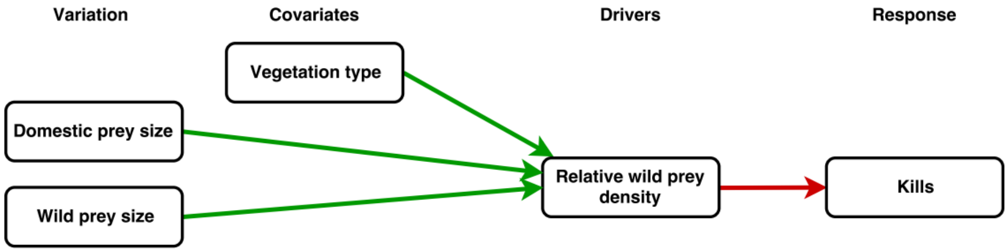

Figure 1. Specific predictions for carnivore kills of domestic prey based on the hypotheses presented in table 1. These predictions were then used to develop a set of a priori candidate models. We also include specific predictions about how extrinsic (vegetation) and intrinsic (predator and prey size) variation might be associated with drivers of carnivore kills of domestic prey. The two original hypothesis predictors function as drivers of predation, and covariates include alternative hypothesis composed by plausible effects. Arrows indicate predictions of the main competing explanations (red), covariates (green), and extrinsic or intrinsic variation accompanying domestic prey density (purple) or prey density interaction (dotted purple).

Methods

Data collation

To assess a global pattern of carnivore predation on livestock we performed a literature review by searching case studies and extracting those with quantitative data suitable for statistical analysis of the necessary factors for hypothesis testing. We employed several Boolean search strings on the ISI Web of Knowledge by permuting the terms “domestic”, “farm”, “husbandry” or “livestock” with “alternative prey”, “natural prey”, “predation”, “prey abundance”, “prey availability” or “wild prey”, including the asterisk operator as a placeholder for possible variations on all these terms (*e.g.* livestock* AND predat*). We then compiled a full list of the found literature up to April 2016 and filtered by those whose titles indicated relation to ecology, agriculture, livestock management or wildlife management.

Our primary requisite for the inclusion of a case study was the extraction of all the explanatory factors needed for hypothesis testing. If an article was missing one of the necessary factors we set as a benchmark, it was discarded from the dataset. Namely, we extracted the number of livestock kills, density of domestic animals and wildlife, and the type of vegetation present. We interpreted vegetation type based on openness of structure according to the descriptions given in each study area per article, and is a categorical variable of openness, ranging from closed canopy (forests), mixed intermediate between closed and open canopy (mixed), and open canopy (shrubland), with a single category of sites that include clearly segregated both open and closed areas (shrubland-woodland). If not indicated, we estimated the relative density of wildlife in relation to the domestic and wild prey total. To account for temporal and spatial variation and standardize the sampling effort between studies, we also included the duration of the study (years) and the assessed surface area (km^2). In addition, we collected data on the median size of the domestic animals, mammalian wild prey, and predators for each case, extracting the information from the PanTHERIA database (Jones et al. 2009). Each article can contain more than one case study.

Model set construction

We use the number of kills made by a carnivore per year and area (km^2) for a given case study as the response variable to represent a rate of livestock lost to predation. All other variables act as predictors for rate of livestock predation.

We offer absolute and relative densities of wild prey as two major explanations for predation of livestock (Table 1). However, to avoid multicollinearity, we performed preliminary Spearman's rank order correlations between all predictors and chose a threshold of 0.6 (rho) as criteria for identifying collinearity (as per Dormann et al. 2013). In fact, predator size is correlated with absolute density of wild prey, which is a key explanation of our hypothesis (See Supplementary Table S1 for multicollinearity tolerance levels). Therefore, we eliminated predator size as a predictor from this point forward.

We then expanded both explanations into prediction pathways (see Fig. 1), each representing the relation between explanatory variables and the covariates that comprise our hypotheses. We predict that either absolute or relative wild prey density function as drivers of variation for livestock kills by carnivores, either by themselves or modulated through covariates. Covariates comprise domestic prey density, the interaction between domestic and wild prey densities, and vegetation type (we chose the forest as the controlling treatment, the most closed structure). Third-tier distal sources of variation to number of livestock killed by carnivores may also be explained by the size of domestic prey, wild prey and predators following the hypotheses presented in Table 1. To test our hypothesis, we codified our predictions into a set of *a priori* mathematical candidate models (Table 2) and assessed them by Generalized Linear Models (GLMs) on a negative binomial distribution with a log link function. We performed likelihood ratio tests on each model with the x^2 metric based on residual deviance to assess goodness-of-fit.

Table 2. Candidate model derived from the a priori hypotheses set based on predictions of explanations for carnivore kills of domestic prey.

Model	Drivers	Covariates	Variation
wd	Absolute wild prey density	None	None
wd+dd	Absolute wild prey density	Domestic prey density	None
wd+dd+veg	Absolute wild prey density	Domestic prey density	Vegetation
wd+dd+dsize	Absolute wild prey density	Domestic prey density	Domestic prey size
wd+dd+wsize	Absolute wild prey density	Domestic prey density	Wild prey size
wd*dd	Absolute wild prey density	Wild and domestic prey density interaction	None
(wd*dd)+veg	Absolute wild prey density	Wild and domestic prey density interaction	Vegetation
(wd*dd)+dsize	Absolute wild prey density	Wild and domestic prey density interaction	Domestic prey size
(wd*dd)+wsize	Absolute wild prey density	Wild and domestic prey density interaction	Wild prey size
wd+veg	Absolute wild prey density	Vegetation	None
rwd	Relative wild prey density	None	None
rwd+veg	Relative wild prey density	Vegetation	None
rwd+dsize	Relative wild prey density	None	Domestic prey size
rwd+wsize	Relative wild prey density	None	Wild prey size

wd = absolute wild prey density, rwd = relative wild prey density, dd = domestic prey density, veg = vegetation type, wsize = wild prey size, dsize = domestic prey size.

Model selection and averaging

To select the most parsimonious model we applied the corrected Akaike information criterion for small samples (AICc). We estimated Akaike model weights to determine the relative likelihood of a model and interpreted as conditional probabilities of relative support for most accurate description of the observations (Burnham & Anderson 2002).

Since Akaike weight is distributed among the candidate models, selecting only the model with highest support results in losing information from other models. Therefore, we calculated model-averaged coefficients for each predictor among the candidate models weighted by AICc along with unconditional standard errors and associated confidence intervals (Burnham & Anderson 2002). Lastly, to determine how the mean number of livestock kills changes in response to a change in predictors, we computed the exponential of the estimate (estimates are logarithmically transformed by link function). We performed all analyses in R and used the MuMIn package for model averaging.

Results

Dataset overview

We retrieved 3818 publications. From these, 511 concerned ecology, livestock or wildlife management, of which only 11 articles contained all the required data for statistical inclusion. In total, we collated 21 case studies which we employed as individual observations of livestock predation by carnivores (see Supplementary Material S2). Cases include the predation of a wide variety of livestock types and sizes, including ovine, caprine, bovine, equine, and camelids. Predators comprise mostly pantherinae or big cats (tiger, lion, jaguar, leopard and snow leopard), some felinae (cheetah, puma, lynx, caracal and serval), and other carnivores of varying sizes (jackal, coyote, brown hyaena, African wild dog and honey badger). Wild prey consists of an even wider range of animals, including but not limited to lagomorphs, rodents and species belonging to Bovidae, Cervidae, Suidae (see Supplementary Material S2 for full list).

Models of variation in livestock predation

Two models virtually account for all the Akaike weight, corresponding to number of livestock killed, that is: absolute density of wild prey acts as a predictor of carnivore predation on livestock (Table 3). Furthermore, both models include domestic prey density and vegetation type as explanatory variables, which we included as covariates of wild prey density. The best model according to AICc that explains predation on livestock includes absolute densities of wild and domestic prey and vegetation type (w_i = 0.73, goodness of fit = 0.63), while the second-best model includes again all three predictors as well as the interaction between wild and domestic prey (w_i = 0.27, goodness of fit = 0.76). The model containing absolute densities of wild and domestic prey plus vegetation type is 2.7 times more likely to be correct than the second-ranked model which differs in only that it includes the interaction between absolute prey densities (evidence ratio = 0.73/0.27), indicating that a model with predictive power over livestock kills may not require interaction between prey densities.

Table 3. Candidate model set based on predictions derived from the a priori hypotheses of explanations for carnivore kills of domestic prey. Generalized linear models with negative binomial distribution ordered according to AICc, with associated degrees of freedom (df), number of parameters in the model (k), AICc, ∆AICc and Akaike model weights, and p-value corresponding to deviance goodness of fit.

Model	*k*	logLik	AICc	∆AICc	weight	Chi-squared	df	p-value
wd + dd + veg	6	-101.01	220.01	0	0.729	12.68	15	0.63
(wd × dd) + veg	7	-99.69	222.00	1.99	0.270	10.05	14	0.76
wd + veg	5	-109.50	233.00	12.99	0.001	29.67	16	0.02
wd + dd	3	-121.67	250.76	30.74	0	52.01	18	0.00
wd + dd + dsize	4	-120.63	251.76	31.75	0	51.93	17	0.00
wd × dd	4	-120.79	252.09	32.08	0	52.26	17	0.00
wd + dd + wsize	4	-121.30	253.09	33.08	0	53.26	17	0.00
(wd × dd) + dsize	5	-119.78	253.56	33.54	0	50.22	16	0.00
(wd × dd) + wsize	5	-120.27	254.55	34.53	0	51.21	16	0.00
rwd + veg	5	-124.26	262.51	42.50	0	59.18	16	0.00
rwd + wsize	3	-133.18	273.77	53.75	0	77.04	18	0.00
rwd	2	-138.57	281.81	61.80	0	87.81	19	0.00
rwd + dsize	3	-137.91	283.24	63.22	0	86.49	18	0.00
wd	2	-146.74	298.15	78.14	0	114.15	19	0.00

wd = absolute wild prey density, rwd = relative wild prey density, dd = domestic prey density, veg = vegetation type, wsize = wild prey size, dsize = domestic prey size.

Model averaged livestock predation predictors

Model-averaging coefficients of predictors reveal that the absolute density of wild prey, domestic prey density, their interaction, and vegetation types, are the only predictors whose 95% Confidence Intervals do not overlap with zero and hence can be inferred to have an effect (Table 4). An increase of one individual of wild and domestic prey increases the number of livestock killed by 9.7% and 7.6%, respectively. However, the interaction between wild and domestic prey densities decreases the coefficient (slope) of the other by -0.002. When comparing the effects of the tested vegetation types to forest, shrubland-woodlands increase livestock kills by thirty times relative to forests, shrublands by 2.7 times as much, and mixed vegetation contains almost 57 times as many livestock depredated as in forests.

Table 4. Summary results of the working hypotheses after model averaging: effects of each parameter on number of livestock kills by predators. Parameters indicate predictor variables, estimate the predictor coefficients, SE the unconditional standard errors, and CI the confidence intervals at 95% (upper and lower limits, respectively).

Parameter	Estimate	SE	95% CI
(Intercept)	-7.811	0.510	(-8.810, -6.811)
Wild prey density	0.093	0.025	(0.044, 0.142)
Domestic prey density	0.073	0.024	(0.027, 0.119)
Mixed vegetation	4.041	0.455	(3.150, 4.933)
Shrubland vegetation	0.990	0.483	(0.044, 1.937)
Shrubland-woodland vegetation	3.407	0.650	(2.133, 4.682)
Domestic-wild prey density interaction	-0.002	0.001	(-0.004, -0.000)
Domestic prey size	0.000	0.000	(-0.000, 0.000)
Wild prey size	0.000	0.000	(-0.000, 0.000)
Relative wild prey density	-2.253	1.310	(-4.821, 0.315)

Caveats

We insist on two caveats. First, the increase of livestock kills in different vegetation types relative to forests seems large; however, we caution that we counted with only seven cases for forests and mixed vegetation, five for shrublands, and only two for shrubland-woodlands. The surface area of these studies is large and did not allow standardized discretization of vegetation types. Second, due to the variable nature of the data and low number of observations accumulated, we conclude that predicting with a composite model of the model averaged estimates would not be suitable. Thus, we intend our findings to help explain, but not predict, the number of livestock killed by predators.

Discussion

Testing wild prey availability as an explanation for livestock predation

We tested two explanations for predation of livestock, an impediment to human-carnivore coexistence on productive landscapes. Based on our models, we find that between absolute and relative densities of wild prey the weight of the evidence lies on absolute density (Fig 1a) as a plausible explanation for loss of livestock to predation, indicating that it acts as a driver for loss of livestock by predation rather than relative density of wild prey (Fig 1b). It seems that the ratio of wild prey density in relation to domestic prey may not be an important factor to consider when managing the loss of livestock by predation. Instead, we might need to focus on the absolute number of wild prey individuals as a viable means to manage livestock loss.

There is a downside to using density of wild prey as a management tool: contrary to our expectations, density of wild prey increases the number of livestock killed. There are several plausible explanations for this. Interestingly, although most cases involved felids (86%), this emerging pattern most resembles dynamics observed in canids, whereby increases in wild prey densities are followed by higher predation rates on livestock (Wagner 1988). Such dynamics have been observed in felids to a lesser extent. For example, the predation rate of livestock by snow leopard increases with higher abundances of wild prey due to greater support for cat populations (Suryawanshi et al. 2013). However, if carnivores in general are prey switchers, then lag time for predator-prey population dynamics would explain why an increasing wild prey ensemble might synchronize with higher carnivore predation rates on livestock, since a decrease in wild prey populations might trigger a switch to livestock but switching back to wild prey might not be immediate. Alternative prey patterns may be convoluted or not easily explained: shifting dynamics might have indirect effects with consequences beyond single species, seeping into ensemble or community level impacts. This can be seen when higher stocks of wild prey increase tiger numbers, competitively displacing leopards which then intensifies their predation on livestock in their new hunting grounds (Harihar et al. 2011). In other words, a possible explanation for a positive relationship between density of wild prey and livestock predation might be a simple numbers game, since areas closer to wild nature generally support higher densities of wild prey and therefore also predators, than areas with less natural cover and fauna, resulting in more opportunities for predators and livestock to co-occur and interact. Although we did not envision predator density data as a hypothesis, we surmise that wild prey and predator densities might be positively correlated.

Sources of variation for livestock predation

Among the two top-ranked models we also find other predictors that act as covariates for density of wild prey, namely domestic prey density, the interaction between wild and domestic prey densities, and vegetation type. In fact, upon performing model averaging, these covariates along with absolute density of wild prey are the only predictors that we can conclude to have an effect on livestock predation (Table 4).

Among covariates, density of domestic prey increases the loss of livestock, as predicted by prey switching, conforming to theory. Higher abundances of livestock increase the likelihood of encountering domestic prey to frequent enough levels capable of surpassing encounter rates with wild prey, and thus also increasing rates of livestock predation. The interaction between wild and domestic prey densities also has an effect, albeit a negative one. This interaction can be interpreted as a decrease in the effect (slopes of regression lines) of either wild or domestic prey density when the other increases. This interaction means that both prey densities maintain a positive effect on livestock predation (as seen by their additive effects), but the effect of either density lessens as the other increases. This factor presently expresses prey switching, yet its actual effect on the slopes of either density is paltry compared to the magnitude of the coefficients (see Table 4) and managing the abundances of either type of prey to compensate for the other is not feasible. Regardless of the strength of the interaction term between prey densities, the fact that domestic prey density not only increases the rate of predation but so does wild prey density, ultimately defeats the purpose of considering prey switching as a means of managing carnivore selection of livestock.

Regarding vegetation type, cover can increase a predator’s efficiency and affect the vulnerability of livestock to attack. Forest, the reference class, has the lowest rates of livestock predation, probably due to the fact that most livestock types reported in the studies are foraging ruminants (supplementary material S2), which are preferably kept in areas where increased amounts of grassy foliage are available to them, most likely outside of forested areas. Both types of vegetation cover that included open and closed cover increase rate of livestock predation many-fold, situations where predators that prefer cover can either mingle in sympatry with domestic ruminants or exist in peripatry by maintaining stealth in adjacent cover until heading out on hunting ventures. Lastly, open areas also increase livestock predation in relation to closed areas, yet the increase is much smaller compared to vegetation types containing both open and closed canopies. Such a disparity between exclusively open areas and those with both open and closed canopies might be due to felines’ penchant for maintaining cover, the predominant carnivore taxa in the studies assessed and present in 95% of total cases included in the analysis. Availability of cover seems to jump from covariate status to the prime driver capable of explaining loss of livestock to carnivores, supporting previous studies (see Michalski et al. 2006).

Prospectus for management

In general, the density of wild prey has an effect on the number of livestock killed by carnivores independent of the density of co-occurring livestock (absolute wild prey density). However, increases in both wild prey and domestic prey densities have a positive effect on loss of livestock, suggesting segregation of wildlife and livestock (land-sparing) as feasible solution to livestock predation, but at first glance disabling both abundances from being considered management tools for farming and nature to coexist (land-sharing), at least not as a catchall solution. All in all, the onus on achieving coexistence in integrated lands for livestock production and conservation still lies in alternative methods. Notably cover, assessed here through openness of vegetation type, emerges as a strong contender to function as a management tool for carnivores overall.

Managing vegetation cover presents important tradeoffs. First, is the increased predation rate in closed vegetation types and second is the space occupied by vegetation cover instead of would-be pasture for livestock to consume. Both premises appear sufficient to dissuade stakeholders from allowing more natural vegetation on their plots of land. However, simply eliminating remnants of natural vegetation is contrary to the stipulations of land-sharing, therefore awareness of surrounding vegetation with the potential of sourcing cover to predators is crucial to lessen the risk of predation when managing where livestock graze. A balance between the amount of natural vegetation and pasture might exist in which the remaining vegetation is enough to function as habitat for wild prey to be consumed by predators while leaving sufficient pasture for the production of livestock, all the while maintaining livestock segregated from denser vegetation cover. Wild prey populations would be immersed in vegetation while carnivores roam between these patches of wild prey. Livestock outside of vegetation would be at lower risk of attack by disallowing cover for carnivores. In essence, with this we propose local-scale land-sparing seen as landscape-scale land-sharing (but see Phalan et al. 2011).

However, we must stress that this analysis uses data from the literature that includes varied species sets of carnivores, wild prey and domestic ruminants; all the effects garnered in this assessment must be considered no more than a general tendency. Studies at specific single localities might elucidate what factors affect livestock predation more so than research with general findings that are too broad ever could. The case studies we used as observations range in area from 20 to 4000 km^2, and although we factored area in as a method of standardization, the larger study sites inevitably include more variability than smaller ones, a phenomenon that may obscure results. Whether prey switching between wild and domestic prey can still be a useful management tool for coexistence at the local level remains to be seen. The species of carnivore and wild prey involved, along with type of livestock reared, may determine whether a carnivore decides to pursue livestock or not.

Furthermore, we call attention to the fact that only 11 articles contained sufficient data to test our predictions. These articles contain data that allowed analyses for livestock such as bovine and ovine domestic ruminants (up to April 2016). This is too few a number considering a quick search for these terms (regarding “ovine” and “bovine”) on the Web of Science delivers over 250k results. Therefore, we would like to request that when available, data such as season, study site information (area, types of vegetation, presence or abundance of predators and natural prey), and duration of the study, be delivered to the reader as succinctly as possible, to allow an easier extraction for future quantitative reviews and meta-analyses. When working with livestock and wildlife, we suggest always including a supplementary table with all data used during an article's data processing as well as secondary and tertiary information (*e.g.* supplementary material S2). This information will foster research regarding potential management tools to mitigate and avoid predation on livestock.

Corollary

Reaching coexistence, the immediate need for agroecological ventures to be considered a proper integration of food production and conservation, requires maintaining an extended sympatry between livestock and carnivores while reducing predation upon domestic animals. In general, we submit that the availability of wild prey has an effect on livestock predation, just not one that adheres to classic optimal foraging theory. Wild prey availability cannot function as a management option to integrate coexistence into the food-biodiversity nexus as a catchall. Instead, land-sharing endeavors involving animal husbandry and seeking human-carnivore coexistence will need to recognize the importance of maintaining enough vegetation for wild prey while keeping livestock segregated so as to not allow carnivores cover to attack livestock.

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Table S1. Correlation matrix. Spearman's rho for for all predictors. Threshold of rho = 0.6 was used to avoid collinearity. Only significant correlations are shown ($p<0.05$).

	wd	rwd	dd	dsize	wsize	psize
wd	1	0.519476				0.605062
rwd		1	-0.59844		0.457474	
dd			1			
dsize				1		0.466306
wsize					1	
psize						1

wd = absolute wild prey density, rwd = relative wild prey density, dd = domestic prey density, veg = vegetation type, wsize = wild prey size, dsize = domestic prey size.

Table S2. Case studies employed as individual observations of livestock predation by carnivores.

Case	Author	Journal	Title	Year
1	Johansson, Orjan; McCarthy, Tom; Samelius, Gustaf; Andren, Henrik; Tumursukh, Lkhagvasumberel; Mishra, Charudutt	Snow leopard predation in a livestock dominated landscape in Mongolia	Biological Conservation	2015
2	Johansson, Orjan; McCarthy, Tom; Samelius, Gustaf; Andren, Henrik; Tumursukh, Lkhagvasumberel; Mishra, Charudutt	Snow leopard predation in a livestock dominated landscape in Mongolia	Biological Conservation	2015
3	Johansson, Orjan; McCarthy, Tom; Samelius, Gustaf; Andren, Henrik; Tumursukh, Lkhagvasumberel; Mishra, Charudutt	Snow leopard predation in a livestock dominated landscape in Mongolia	Biological Conservation	2015
4	Tumenta, Pricelia N.; Visser, Hermen D.; van Rijssel, Jacco; Muller, Lana; de Iongh, Hans H.; Funston, Paul J.; de Haes, Helias A. Udo	Lion predation on livestock and native wildlife in Waza National Park, northern Cameroon	mammalia	2013
5	Thorn, Michelle; Green, Matthew; Scott, Dawn; Marnewick, Kelly	Characteristics and determinants of human-carnivore conflict in South African farmland	biodiversity and conservation	2013
6	Banerjee, Kausik; Jhala, Yadvendradev V.; Chauhan, Kartikeya S.; Dave, Chittranjan V.	Living with Lions: The Economics of Coexistence in the Gir Forests, India	PLoS ONE	2013
7	Wegge, Per; Shrestha, Rinjan; Flagstad, Oystein	Snow leopard Panthera uncia predation on livestock and wild prey in a mountain valley in northern Nepal: implications for conservation management	wildlife biology	2012
8	Wegge, Per; Shrestha, Rinjan; Flagstad, Oystein	Snow leopard Panthera uncia predation on livestock and wild prey in a mountain valley in northern Nepal: implications for conservation management	wildlife biology	2012
9	Wegge, Per; Shrestha, Rinjan; Flagstad, Oystein	Snow leopard Panthera uncia predation on livestock and wild prey in a mountain valley in northern Nepal: implications for conservation management	wildlife biology	2012
10	Wegge, Per; Shrestha, Rinjan; Flagstad, Oystein	Snow leopard Panthera uncia predation on livestock and wild prey in a mountain valley in northern Nepal: implications for conservation management	wildlife biology	2012
11	Thorn, Michelle; Green, Matthew; Dalerum, Fredrik; Bateman, Philip W.; Scott, Dawn M.	What drives human-carnivore conflict in the North West Province of South Africa?	Biological Conservation	2012
12	Sundararaj, Vijayan; McLaren, Brian E.; Morris, Douglas W.; Goyal, S. P.	Can rare positive interactions become common when large carnivores consume livestock?	ecology	2012
13	Sundararaj, Vijayan; McLaren, Brian E.; Morris, Douglas W.; Goyal, S. P.	Can rare positive interactions become common when large carnivores consume livestock?	ecology	2012
14	Polisar, J; Maxit, I; Scognamillo, D; Farrell, L; Sunquist, ME; Eisenberg, JF	Jaguars, pumas, their prey base, and cattle ranching: ecological interpretations of a management problem	Biological Conservation	2003
15	Polisar, J; Maxit, I; Scognamillo, D; Farrell, L; Sunquist, ME; Eisenberg, JF	Jaguars, pumas, their prey base, and cattle ranching: ecological interpretations of a management problem	Biological Conservation	2003
16	Sacks, BN; Neale, JCC	Foraging strategy of a generalist predator toward a special prey: Coyote predation on sheep	Ecological Applications	2002
17	Stahl, P; Vandel, JM; Herrenschmidt, V; Migot, P	Predation on livestock by an expanding reintroduced lynx population: long-term trend and spatial variability	Journal of Applied Ecology	2001
18	Sekhar, NU	Crop and livestock depredation caused by wild animals in protected areas: the case of Sariska Tiger Reserve, Rajasthan, India	Environmental Conservation	1998
19	Sekhar, NU	Crop and livestock depredation caused by wild animals in protected areas: the case of Sariska Tiger Reserve, Rajasthan, India	Environmental Conservation	1998
20	Sekhar, NU	Crop and livestock depredation caused by wild animals in protected areas: the case of Sariska Tiger Reserve, Rajasthan, India	Environmental Conservation	1998
21	Sekhar, NU	Crop and livestock depredation caused by wild animals in protected areas: the case of Sariska Tiger Reserve, Rajasthan, India	Environmental Conservation	1998

Table S2. Continued

Case	kills	wd	rwd	dd	veg	dsize	wsize	psize
1	50	0.432353	0.022453	18.82353	shrubland	43242.18	91773	32500
2	10	0.258824	0.785714	0.070588	shrubland	403598.5	91773	32500
3	5	0.258824	0.285714	0.647059	shrubland	492714.5	91773	32500
4	35	1.888824	0.132615	12.35412	shrubland-woodland	47386.47	109250	158623.9
5	347	12.26761	0.769768	3.669142	shrubland-woodland	47386.47	179778.8	16999.98
6	180	39.6	0.485294	42	forest	586579.2	130997	158623.9
7	38	8.448	0.618992	5.2	mixed	47386.47	52335	32500
8	20	8.448	0.739496	2.976	mixed	39097.89	52335	32500
9	16	8.448	0.579265	6.136	mixed	618642.4	52335	32500
10	3	8.448	0.853678	1.448	mixed	403598.5	52335	32500
11	2853	9.646486	0.2925	23.33295	mixed	225492.5	85058	42977.93
12	192	58.7	0.709794	24	shrubland	618642.4	69500	158623.9
13	94	49.1	0.816972	11	shrubland	618642.4	69500	158623.9
14	10	9.901324	0.300553	23.04237	forest	511120.5	25333	83943.09
15	29	9.901324	0.300553	23.04237	forest	511120.5	25333	53954.05
16	185	14.6	0.208719	55.35055	mixed	39097.89	1207	11989.1
17	137	1.471333	0.142989	8.8185	mixed	39097.89	22502	19300
18	14	18.25	0.855302	3.0875	forest	47386.47	130997	107157.3
19	6	18.25	0.956123	0.8375	forest	47386.47	130997	107157.3
20	3	18.25	0.926984	1.4375	forest	47386.47	130997	107157.3
21	2	18.25	0.927632	1.42375	forest	47386.47	130997	107157.3

Table S2. Continued

Case	Time (years)	Area (km2)	Predator type	Domestic prey type	wild prey type
1	5	1700	snow leopard	ovine, caprine	ibex, argali
2	5	1700	snow leopard	equine	ibex, argali
3	5	1700	snow leopard	camelids	ibex, argali
4	2	1700	lion	ovine, caprine, bovine	kob, topi, roan antelope, red fronted gazelle, warthog, giraffe
5	1	4174	jackal, caracal, leopard, cheetah, african wild dog, brown hyaena, serval, honey badger	ovine, caprine, bovine	eland, kudu, warthog, blue wildebeest, bushbuck, waterbuck, zebra, red hartebeest, blesbok, impala
6	2.416667	1913	lion	bovine, camelids	chital deer, sambar, nilgai, wild boar
7	2	125	snow leopard	caprine	bharal
8	2	125	snow leopard	ovine	bharal
9	2	125	snow leopard	bovine	bharal
10	2	125	snow leopard	equine	bharal
11	2	4134	caracal, jackal, leopard, cheetah, brown hyaena	ovine, caprine, bovine, equine	springbok, ostrich, impala, blesbok, steenbok, common duiker, mountain reedbuck, roan, sable antelope, kudu, gemsbok, blue wildebeest, nyala, warthog, bushbuck, zebra
12	1	450	lion	bovine	chital deer
13	1	450	lion	bovine	chital deer
14	4.416667	632.27	jaguar	bovine, equine	white-tailed deer, collared peccary, white-lipped peccary, agouti, cottontail rabbit, nine-banded armadillo, giant anteater, capybara
15	5.666667	632.27	puma	bovine, equine	white-tailed deer, collared peccary, white-lipped peccary, agouti, cottontail rabbit, nine-banded armadillo, giant anteater, capybara
16	2.416667	21.68	coyote	ovine	black-tailed deer, lagomorph, small rodent
17	11	6000	lynx	ovine	roe deer
18	3	800	tiger, leopard	ovine, caprine, bovine	sambar, chital deer, nilgai, wild boar
19	3	800	tiger, leopard	ovine, caprine, bovine	sambar, chital deer, nilgai, wild boar
20	3	800	tiger, leopard	ovine, caprine, bovine	sambar, chital deer, nilgai, wild boar
21	3	800	tiger, leopard	ovine, caprine, bovine	sambar, chital deer, nilgai, wild boar

Chapter 3

Reaching human-carnivore coexistence by changing wild prey availability: a case study of fox predation on ovine livestock in Isla Riesco, Chilean Patagonia

Abstract

Land sharing is an emergent strategy that aims to provide the conditions necessary for the compatibility between food production and conservation yet is unfeasible when livestock production conflicts with carnivore conservation. We tested whether wild prey availability is capable of modulating predation rate on livestock by testing four explanations regarding density and biomass of wild prey, both in absolute and relative terms with regards to livestock. As a model system, we considered the human-fox conflicts surrounding ovine production in the Chilean Patagonia. We assessed the effect of rodent and arthropod availability on the variation of Culpeo fox predation rate on ovine livestock in separate pasture fields, and included covariates such as predator occurrence, vegetation cover, availability of domestic prey and the occurrence of an alternative wild prey in the exotic European hare. We found that the most parsimonious hypotheses that explain variation of ovine kills among pastures include hare occurrence and the relative terms of wild prey density and biomass. However, multimodel inference indicates that only the occurrence of the exotic hare affects ovine kills, specifically by decreasing kill rate when hare occurrence increases. These results suggest that manipulating the availability of wild prey can affect predation rate on livestock by inciting prey switching in carnivores. However, the size of wild prey may be a determining factor in prey switching, since only the occurrence of hare had an effect, which is proportionally closer in size to ovine than rodents or arthropods. We do not endorse the use of the exotic hare in Patagonia, but we suggest looking towards larger native prey. Manipulating native prey similar in size to livestock in productive landscapes in

such a way as to reach population levels that decrease carnivore attacks and loss of livestock can aid land sharing be a tenable goal by ensuring human-carnivore coexistence and might constitute a realizable target for future conservation treaties.

Introduction

Sharing land between farming and wild nature cannot be achieved without ensuring human-wildlife coexistence (Crespin & Simonetti 2018). Land-sharing is an emerging strategy meant to provide the conditions required for the compatibility between biological diversity and the production of goods and services for human society on the same land. Sharing land is internationally required as indicated in the Aichi Biodiversity Target 7 (Convention on Biological Diversity 2010), yet its application in livestock productive landscapes is currently unfeasible due to continuing conflicts between animal farming and wildlife, particularly when the conservation of mammalian carnivores clashes with the production of livestock. Predation of livestock by carnivores is one of the most prominent biodiversity impacts, hurting farmers' livelihoods and in many cases leading to carnivore persecution, resulting in human-carnivore conflicts (Baker et al 2008). Reconciling carnivore conservation and livestock production requires eliminating and preventing such conflicts (Young et al. 2010).

Carnivores have large home ranges and require extensive areas to reach viable populations, increasing the odds of carnivore-livestock cooccurrence (Woodroffe & Ginsberg 1998). An expanding human population also encroaches upon carnivore habitat and results in the loss of wild prey (Ripple et al 2014). It has been touted that unless availability of livestock exceeds that of wild prey, carnivores prefer wild prey (Sacks & Neale 2007, Loveridge et al 2010, Khorozyan et al. 2015, Khorozyan et al 2017), essentially that classical frequency dependent predation or prey switching account for carnivore predation of livestock on human-dominated lands (Crespin & Simonetti Chapter

2). Prey depletion coupled with increased probability of carnivore-livestock cooccurrence where carnivores increasingly prey upon livestock, generates situations resulting in stakeholders suffering damages to their livelihoods. However, the global pattern of carnivore predation of domestic animals on human-dominated lands shows that increased prey availability, both wild and domestic, increases loss of livestock (Crespin & Simonetti Chapter 2), bringing into question the directionality of the relation. Also, assessing studies from around the globe considers a wide breadth of variation between sets of carnivores, wild prey, domestic animals and vegetation. Consequently, the conditions under which scenarios of prey switching emerge between wild and domestic prey remain unclear at the local level.

Predators choose the most profitable prey when considering the energy expended while seeking and handling prey (MacArthur & Pianka 1966). Therefore, if wild prey is scarce, a livestock kill is more profitable. The biomass of wild prey should be sufficient to support local populations of predators, but if biomass of domestic prey far exceeds that of wild prey, then predators will continue to prey on livestock due to lower search times and larger amounts of resource (Polisar et al. 2003). In both cases, the effect of wild prey availability via density or biomass is relative to domestic prey. If availability of wild prey explains livestock predation, then understanding and managing the factors that determine the density or biomass of wild prey can prevent livestock predation and allow for the presence of native carnivores on farmlands. Since predators have historically relied on wild prey, one might expect that a higher availability of wild prey might factor into decreasing the rate of livestock predation; therefore, landscapes with a higher wild-to-domestic prey ratio should reflect lower rates of attacks on livestock. However, an alternative scenario is also feasible. Predation upon livestock might increase as availability of wild prey rises. Areas of high density or biomass of wild prey might instead attract carnivores. If livestock is raised in such areas, their cooccurrence might increase the likelihood of attacks upon livestock. These two scenarios denote prey switching, a particular expression of functional response, because changes in the relative frequency with which wild prey is encountered relative to domestic prey will also change predator foraging behavior (Holling 1959).

These premises along with the emerging global pattern indicating an effect on behalf of wild prey density on carnivore predation of livestock (Crespin & Simonetti Chapter 2) allow us to offer four explanations for carnivore kills of domestic prey based on both absolute and relative values of wild prey density and biomass (Table 1). Availability of wild prey can be assessed quantitatively by density, however sites with higher absolute density of wild prey can still have lower relative density when domestic prey is more abundant. Therefore, our first and second explanations expand from absolute and relative density of wild prey. Also, since a wild prey individual may differ in size to domestic prey, density may not be the most appropriate proxy of availability, hence our decision to also include absolute and relative biomass of wild prey as third and fourth explanations, respectively.

Table 1: Hypotheses of predator response that form the basis of a priori models for carnivore kills of domestic prey.

Explanation	Covariate	Hypothesis
1 Absolute wild prey density	a. None	More wild prey lower kills
	b. Domestic prey density	More wild prey and less domestic prey lower kills
	c. Wild and domestic prey density interaction	More wild prey lower kills depending on the density of domestic prey
	d. Understory cover	More wild prey and less vegetation cover lower kills
	e. Fox occurrence	More wild prey and lower fox occurrence lower kills
	f. Hare occurrence	More wild prey and higher hare occurrence lower kills
	g. Dog occurrence	More wild prey and higher dog occurrence lower kills
2 Relative wild prey density	a. None	More wild prey in relation to domestic prey lower kills
	b. Understory cover	More wild prey in relation to domestic prey and vegetation cover lower kills
	c. Fox occurrence	More wild prey in relation to domestic prey and lower fox occurrence lower kills
	d. Hare occurrence	More wild prey in relation to domestic prey and higher hare occurrence lower kills
	e. Dog occurrence	More wild prey in relation to domestic prey and higher dog occurrence lower kills
3 Wild prey mass	a. None	More wild prey mass lowers kills
	b. Domestic prey mass	More wild prey mass and less domestic prey mass lower kills
	c. Wild and domestic prey mass interaction	More wild prey mass lowers kills depending on the mass of domestic prey
	d. Understory cover	More wild prey mass and less vegetation cover lower kills
	e. Fox occurrence	More wild prey mass and lower fox occurrence lower kills
	f. Hare occurrence	More wild prey mass and higher hare occurrence lower kills
	g. Dog occurrence	More wild prey mass and higher dog occurrence lower kills
4 Relative wild prey mass	a. None	More wild prey mass in relation to domestic prey mass lowers kills
	b. Understory cover	More wild prey mass in relation to domestic prey mass and less vegetation cover lower kills
	c. Fox occurrence	More wild prey mass in relation to domestic prey mass and lower fox occurrence lower kills
	d. Hare occurrence	More wild prey mass in relation to domestic prey mass and higher hare occurrence lower kills
	e. Dog occurrence	More wild prey mass in relation to domestic prey mass and higher dog occurrence lower kills

Prey availability might not be the sole predictor of livestock predation, and several other factors might act as covariates and affect the relation between wild prey availability and livestock predation. First, the availability of domestic prey can directly affect the predictive prowess of wild prey when taking prey switching into account. Domestic prey availability is implicitly included in explanations regarding relative availability but should also be assessed by itself as a predictor on its own, potentially modulating the effect of absolute availability of wild prey. The frequency of carnivore occurrence might also affect how wild prey explains livestock predation by increasing probability of carnivore-livestock encounter. The same can be said for areas which employ guardian dogs, as the frequency with which guardian dogs patrol an area by deterring predator attacks might deter carnivores or increase the probability of encounters between dog and carnivore. Finally, cover offered by vegetation might increase opportunities for stealth and ambush, for sneaking past dogs and approaching unaware livestock. These factors might have a direct effect on livestock predation by modulating the vulnerability of livestock to attack, but also exert a distal effect by modulating the availability of wild prey (Fig. 1).

Here, we empirically assess the functional response of predators to changes in wild prey density and biomass, an expression of prey switching. Switching from domestic to wild prey will be assessed as changes in the number of livestock killed. We attempt to explain how a livestock production system consisting of shared land can transition from a state of co-occurrence to coexistence by managing the biological basis for human-carnivore conflicts, predation of livestock, specifically through prey switching. As our model, we use a landscape based on ovine production in the Chilean Patagonia suffering from predation, mainly by the Culpeo fox (*Lycalopex culpaeus*) whose main threats include persecution to reduce predation on livestock (Lucherini 2016) and assess availability of wild prey as predictor of ovine kills among field pastures.

Fig 1a.Predictions based on absolute wild prey density (explanation 1, more wild prey lowers kills):

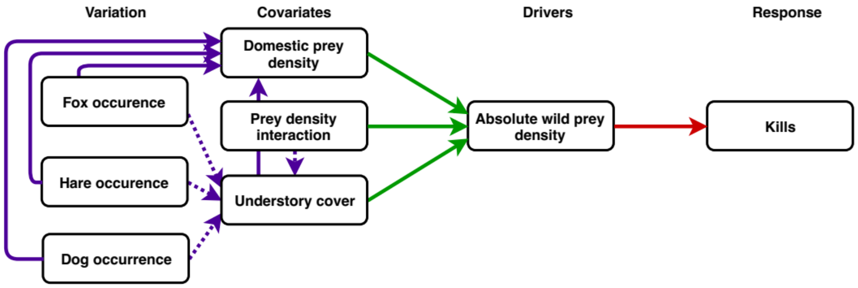

Fig 1b. Predictions based on relative wild prey density (explanation 2, more wild prey in relation to domestic prey lower kills):

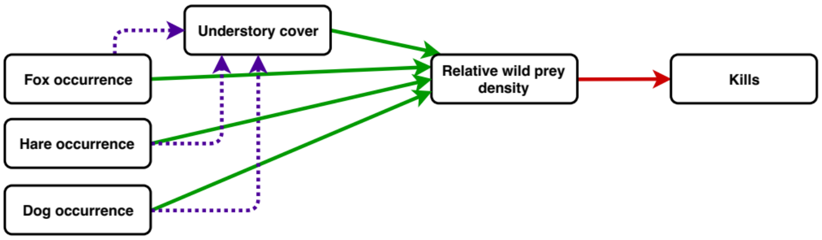

Fig 1c. Predictions based on absolute wild prey mass (explanation 3, more wild prey mass lowers kills):

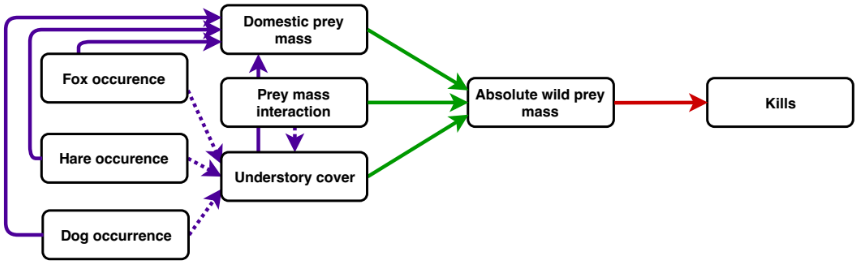

Fig 1d. Predictions based on relative wild prey mass (explanation 4, more wild prey mass in relation to domestic prey lowers kills):

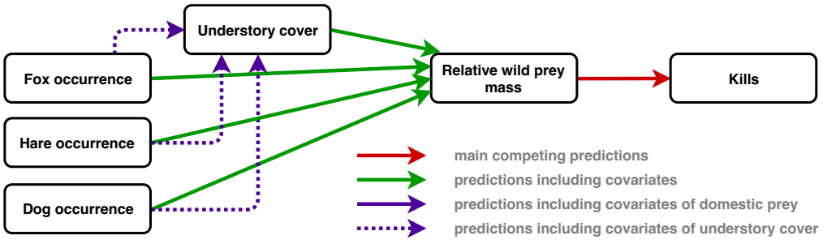

Figure 1. Predictions for carnivore kills of domestic prey based on four explanations that might act as drivers and the proceeding hypotheses for covariates presented in table 1. These specific predictions were used to develop a set of a priori candidate models. We also include specific predictions on possible covariates (domestic prey density and biomass, fox, hare and dog occurrence, understory cover) that may be associated with drivers of carnivore kills of domestic prey. The four original explanations function as drivers of predation, and covariates include alternative hypotheses of plausible effects. Arrows indicate predictions of the main competing explanations (red), covariates (green), and third-degree sources of variation accompanying domestic prey density (purple) or understory cover (dotted purple).

Methods

Study site and natural history

We studied predation rates on domestic sheep (*Ovis aries*) by culpeo and chilla foxes (*Lycalopex culpaeus* and *L. griseus*) in distinct livestock raising field pastures. We worked on Anita Beatriz sheep ranch on Isla Riesco, part of the Rio Verde commune of the Magallanes and Chilean Antarctic Region, Chilean Patagonia (Fig. 2A). The tail-end of the 1800s saw the introduction of sheep husbandry to Magallanes, which has since flourished and given rise to a combined livestock raising industry worth ~1% of total GDP by 2009 (ODEPA 2009) and currently stocks 1,571,056 ovine heads (INE 2017). Among Chilean Regions, Magallanes holds the highest stock of sheep at 77% of all ovine heads, however it also has the highest rate of loss (67% of total ovine losses in Chile occur in Magallanes), of which 42% are caused by predation (INE 2017). In fact, 54% of ovine heads lost to predators in Magallanes are attributed to foxes (INE 2017). Isla Riesco is the fourth largest island in Chile, home to a dozen ranches whose principal production is centered around sheep raising in the lower western reaches of the island, while the steeper eastern inland consists of the Alacalufes protected area. Vegetation is a mix of wooded areas and shrub-steppes. Anita Beatriz ranch (52°51'S, 71° 33'W) is particularly wooded in some fields, consisting mainly of patches of deciduous beeches (*Nothofagus antarctica* and *N. pumilio*), while other fields are shrub laden with barberry (*Berberis microphylla*).

Fox natural prey in Patagonia includes a diverse array of rodents, birds, reptiles and arthropods (Novaro et al. 2000, Palacios et al. 2012). Based on biomass, most of the culpeo and chilla fox's diet is distributed among native mammals (52% and 25%, respectively) and arthropods (17% and 54%, respectively), while birds and reptiles are consumed less (5% each for culpeo, 5% and 2% for chilla) (Palacios et al. 2012). Potential rodents preyed upon by culpeo foxes on Riesco Island might include *Oligoryzomys longicaudatus*, *Abrothrix longipilis*, *A.*

lanosus, *A. xanthorhinus*, *Euneomys chinchilloides*, and *Loxodontomys micropus* (Markham 1970, 1971; Patterson et al. 2007). The introduced European hare (*Lepus europaeus*) also occurs on Riesco Island and are often found in fox diets (Palacios et al. 2012). Temporal patterns of activity for fox and rodent determine temporal overlap, since both culpeo and chilla foxes are active and hunt at night along with their rodent prey present in the study area (Iriarte 2007). Puma (*Puma concolor*) is also present on the island, yet scarce at the study site. Only one specimen was recorded throughout 3 months of camera-trapping (March-May 2014), a young male which may have been undergoing a dispersal process. Locals told us that puma tend to stay towards the highlands, the eastern forested areas of the island. Therefore, the major human-carnivore conflict on the island centers around fox predation of sheep.

Anita Beatriz ranch measures 7.6 km^2 in surface area and is divided into 10 fields with a rotational holistic management system for the maintenance of sufficient feed resource for domestic sheep (Mann & Sherren 2018). Sheep are diurnal and remain inactive at night but out in the open at Anita Beatriz Ranch, allowing temporal and spatial overlap with foxes and rodents (see Squires 1975 for a review of activity patterns of sheep). Despite employing multiple guardian dogs, the ranch suffers from frequent fox attacks on the approximately 1200 ovine heads that are on average present year-round, as the pilot study we conducted in 2014 showed the appearance of two freshly killed lamb carcasses in the span of two days during camera setup, corroborating the perceived loss by the owner.

Experimental design

We based our assessment of the availability of wild prey and sheep predation on a natural experiment, on several fields within Anita Beatriz ranch. Each sampling of an individual field comprises an observation. Differences between fields amount to spatial variation, however, the abundance of native species changes seasonally, therefore a repeated sampling in a different season embraces the whole range of temporal variation in the ratio of natural prey to livestock. Also, synchronized ewe fertilization in Magallanes concentrates lambing during summer, further increasing possible temporal variation of observations throughout the year. Anita Beatriz ranch is divided into 10 fields. However, we specifically sampled fields Ana, Jorge, Mayeya, Carneros, Gaucho, Gaucho-chico, Ema and Guachicles during summer, fall, winter and spring of 2016, measuring variables in ~3 fields per season (Fig 2B., see TableS1 for details) for a total of 11 observations.

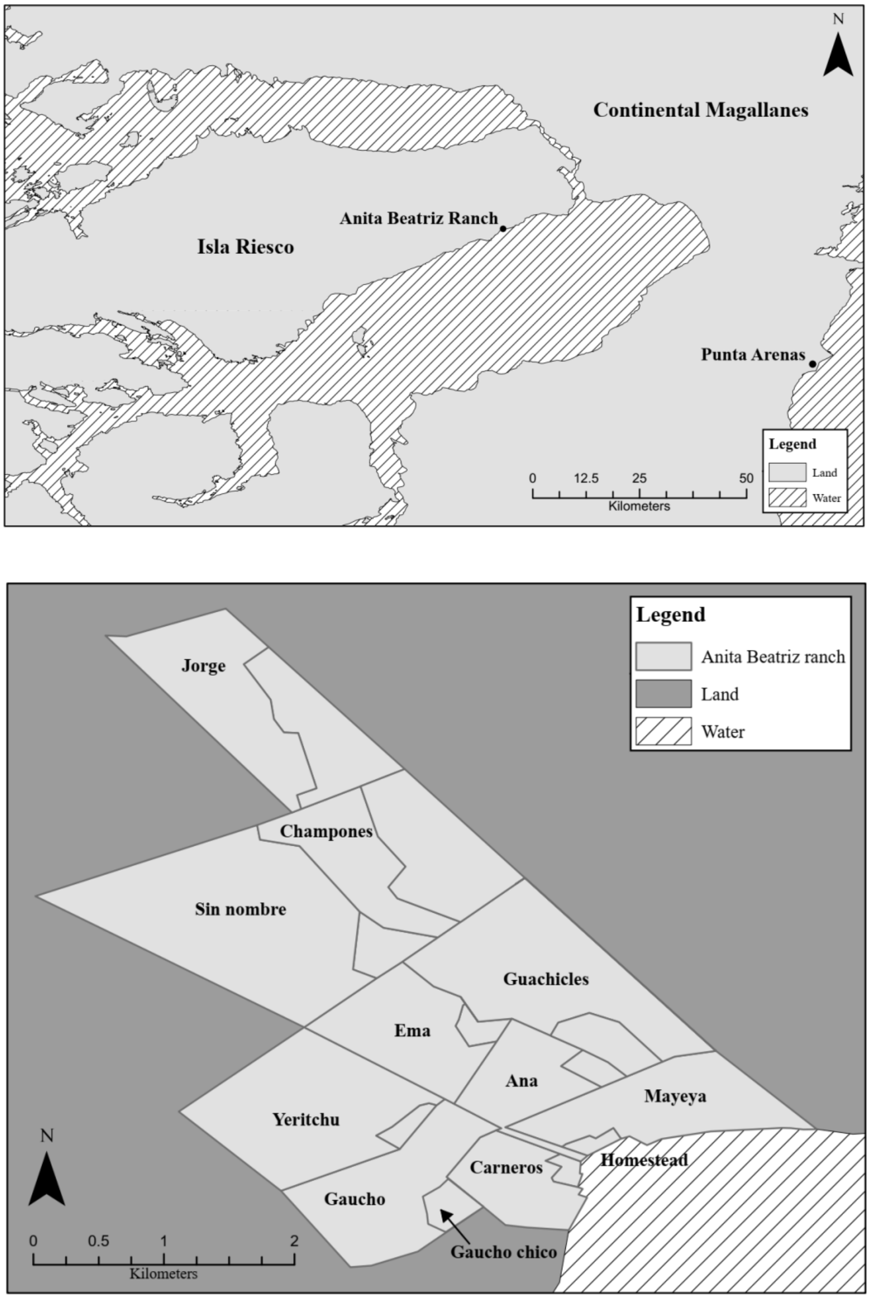

Figure 2. Study area. We studied sheep predation by foxes in ovine rearing fields on Anita Beatriz Ranch, located on Isla Riesco, Magallanes and Chilean Antarctic Region, the Chilean Patagonia (Top). We assessed kill rate and possible ecological predictors at each local site (Bottom).

Predictors of variation

We assessed whether availability of wild prey reduces fox predation on sheep among fields with varying amounts of wild and domestic prey. Our four main explanations regarding prey availability involve both absolute and relative density and biomass of wild prey. Each explanation is also associated with various covariates which potentially predict how predation may vary among fields spatially and temporally (see Table 1). We measured the response variable and all predictors at each observation site. We measured the rate of livestock predation, our response variable, as livestock killed per day during the sampling periods. Because consumption of birds and reptiles is low relative to mammals and arthropods, we estimated natural prey availability as the abundance of rodent and arthropod species only. We estimated absolute availability of wild prey as the number of individuals per hectare and biomass as kg per hectare of rodents and arthropods. We calculated relative availability of wild prey as the amount of wild prey relative to sheep in both density (individuals per hectare) and biomass (kg per hectare). Regarding domestic prey availability, we estimated absolute and relative densities and biomass (individuals and kg per hectare, respectively). Hare might be an important prey for foxes, therefore we included it as another proxy of wild prey availability and estimated hare availability as frequency of occurrence. Regarding fox and guardian dog occurrences, we estimated them from camera trap sightings per day (number of sightings per 24h). For vegetation, we used percentage (%) of understory cover.

To measure these variables and collate the necessary data, we conducted a series of observations in each field. To measure the rate of livestock predation, we scoured each sampled field daily to determine new ovine deaths from the night before. We verified the predator involved by examining the carcass and inspecting the surroundings for predation and feeding patterns, following the protocols proposed by Guarda et al. (2010) and officially sanctioned by the Chilean Agricultural and Livestock Service. Our response variable is then number of kills, an absolute number that is later averaged by the duration of the sampling period in days.

To calculate density of wild prey, we first estimated abundance of rodents and arthropods separately. We estimated rodent abundance by live-trapping and direct enumeration. We installed a grid of Sherman live traps (5 by 10) separated by 10m in each field and baited each trap with dry flaked oats. We placed wool inside each trap to offer refuge from the cold weather conditions. Each rodent we caught at dawn was identified, weighed and individually marked by fur clipping for the duration of the sampling period. We used the minimum number known to be alive as proxy of absolute abundance of rodents (Simonetti 1986). For arthropods, we used pitfall traps without funnel or roof in 5x5 grids with 10m distances between traps, filling each one with 300 ml of water and 5 drops of detergent to break surface tension (after Cheli & Corley 2010). We collected the trap contents every five days and considered the whole grid as one observation. Examination of fox feces during the pilot study showed the consumption arthropods of 3 cm in length, therefore we only included arthropod species of 2 cm in length and above as potential fox diet and total number caught as proxy of absolute abundance of arthropods. We used the sum of rodent and arthropod absolute abundance as wild prey abundance and then standardized by surface area to obtain the absolute density of wild prey for each field. To calculate the density of domestic prey, we obtained the number of ovine head per field from the owner’s logs and standardized by a field’s surface area in hectares.

To calculate biomass of wild prey, we began by estimating biomass for rodents and arthropods separately. Having previously weighed rodents, we used the median weight for each species and multiplied by the absolute density for an estimate of rodent biomass. For arthropods, we used Ganihar’s (1997) models for biomass estimation of terrestrial arthropods from body length, specifically the power function model on coleopteran species and the exponential function model for lepidopteran larvae. We measured the length of caught specimens and used the median weight along with the model coefficients presented by Ganihar (1997) to calculate arthropod biomass. We added rodent and arthropod biomass to obtain absolute biomass of wild prey. To calculate the biomass for domestic prey, we used the value of weight for *Ovis aries* presented in the PanTHERIA database (Jones et al. 2009), which also uses median values, and multiplied that amount by the absolute density of sheep in each field. Biomass estimates are in kilograms per hectare. We calculated relative density and biomass of wild prey as relative to the total amount of prey, wild and domestic, in percentages.

To estimate occurrences for hares, foxes and guardian dogs, we used camera-trapping in a 3x3 grid separated by 300 meters and around the Sherman and pitfall trap grid locations. We sampled without lures and used infrared-triggered cameras (Bushnell Trophy Cam 119537, Bushnell Outdoor Products) for the duration of each sampling period (see TableS1). We mounted cameras on trees and stumps ca. 40-80 cm above ground pending on the height of the grass and set the camera to capture three photos per trigger. Photos were reviewed and inspected after each sampling, registering hare, fox or guardian dog occurrence, and excluding photos within 20 min of each other to avoid registering the same event. We then standardized trap sightings per the number of days the cameras were activated. Finally, to measure understory cover as proxy of vegetation cover, we used the line intercept method. We used five parallel transects measuring 50 meters in length separated by 10 meters and calculated the percentage of cover.

Model set construction

We use absolute ovine kill number by foxes offset by time (number of days sampled) and area (hectares the field measured) as the response variable to represent rate of fox predation upon sheep. All other variables act as predictors for rate of sheep predation. We offer four major explanations for number of sheep killed stemming from prey availability, both the absolute and relative variables of density and biomass of wild prey (Table 1). We then expanded all four explanations into 40 prediction pathways by incorporating covariables into the hypotheses (Fig 1.). Prediction pathways are specifically structured: all are variations of a prediction based on one of the four major explanations. They are structured as follows: 4 predictions only pertain to the major competing explanations, 14 include one of the covariate variables, 8 include domestic prey and another source of variation, and 14 include understory cover and other sources of variation.

To avoid multicollinearity, we ran preliminary Spearman’s rank order correlations between predictors on a 0.6 (rho) threshold. A correlation matrix shows breach of tolerance levels between two major explanatory variables (relative density and biomass of wild prey) and guardian dog occurrence (see Table S2 for multicollinearity tolerance levels). Predictor variables corresponding to major explanations do not interact in our hypotheses, however because dog occurrence crosses prediction pathways with all four major explanatory variables (see Fig 1.), we eliminated guardian dog occurrence as a predictor from this point forward. This leaves only 32 valid prediction pathways whose predictors are not heavily correlated.

According to our prediction pathways, the explanations derived from prey availability (absolute and relative density or biomass of wild prey) might function as drivers of fox predation on sheep, issuing a functional response in foxes, alone or accompanied by a covariate. Covariates follow our preestablished predictions, which for absolute wild prey density and biomass include: domestic prey density, the interaction between wild and domestic prey densities, and understory cover as covariates, along with fox and hare occurrences as distal sources of variation. Conversely, changes in relative wild prey density and biomass implicitly include domestic prey, therefore direct covariates are understory cover along with fox and hare occurrences, with the last two also accounting for distal sources of variation. To test our predictions, we codified them into a set of a priori mathematical candidate models (Table 2) corresponding to the 32 valid prediction pathways which we then used to fit Generalized Linear Models (GLMs) on a negative binomial distribution with a log link function. We assessed model goodness-of-fit with the likelihood ratio test based on the x^2 metric using residual deviance.

Multimodel inference

We used the corrected Akaike information criterion for small samples (AICc) to select the best model by parsimony. We then estimated Akaike model weights, the weight of evidence in favor of a model being the most accurate description of the observed data (Burnham & Anderson 2002). However, selecting only the model with highest relative support results in losing information from other models because Akaike weight is distributed among all *a priori* candidate models. Therefore, instead of inferring from a single model, we used the entire set of candidate models weighted by AICc to calculate model-averaged coefficients for each predictor including unconditional standard errors and corresponding confidence intervals (Burnham & Anderson 2002). Finally, to determine how many sheep are killed in response to changes in predictor variables, we computed the exponential of the model-averaged coefficients, which are logarithmically transformed by the GLM link function during modelling. We used R to perform all analyses and the MuMIn package specifically for model averaging.

Table 2. Candidate model set based on predictions derived from the a priori hypotheses.

Model	Drivers	Covariates	Variation
wd	absolute wild prey density	none	none
wd+dd	absolute wild prey density	domestic prey density	none
wd+dd+ucov	absolute wild prey density	domestic prey density	understory cover
wd+dd+fox	absolute wild prey density	domestic prey density	fox
wd+dd+hare	absolute wild prey density	domestic prey density	hare
wd*dd	absolute wild prey density	wild and domestic prey density interaction	none
wd+ucov	absolute wild prey density	understory cover	none
(wd*dd)+ucov	absolute wild prey density	understory cover	wild and domestic prey density interaction
wd+ucov+fox	absolute wild prey density	understory cover	fox
wd+ucov+hare	absolute wild prey density	understory cover	hare
rwd	relative wild prey density	none	none
rwd+ucov	relative wild prey density	understory cover	none
rwd+ucov+fox	relative wild prey density	understory cover	fox
rwd+ucov+hare	relative wild prey density	understory cover	hare
rwd+fox	relative wild prey density	fox	none
rwd+hare	relative wild prey density	hare	none
wm	absolute wild prey mass	none	none
wm+dm	absolute wild prey mass	domestic prey mass	none
wm+dm+ucov	absolute wild prey mass	domestic prey mass	understory cover
wm+dm+fox	absolute wild prey mass	domestic prey mass	fox
wm+dm+hare	absolute wild prey mass	domestic prey mass	hare
wm*dm	absolute wild prey mass	wild and domestic prey mass interaction	none
wm+ucov	absolute wild prey mass	understory cover	none
(wm*dm)+ucov	absolute wild prey mass	understory cover	wild and domestic prey mass interaction
wm+ucov+fox	absolute wild prey mass	understory cover	fox
wm+ucov+hare	absolute wild prey mass	understory cover	hare
rwm	relative wild prey mass	none	none
rwm+ucov	relative wild prey mass	understory cover	none
rwm+ucov+fox	relative wild prey mass	understory cover	fox
rwm+ucov+hare	relative wild prey mass	understory cover	hare
rwm+fox	relative wild prey mass	fox	none
rwm+hare	relative wild prey mass	hare	none

wd = absolute wild prey density, rwd = relative wild prey density, dd = domestic prey density, ucov = understory cover, wm = wild prey mass, dm = domestic prey mass, rwm = relative wild prey mass, fox = fox/24hr, hare = hare/24hr, dog = dog/24hr, wd*dd= wild and domestic prey density interaction, wm*dm = wild and domestic prey mass interaction.

Results

Community overview

We recorded several predator and prey species over ca. 1294 camera-days. We registered both culpeo (*L. culpaeus*) and chilla foxes (*L. griseus*), totaling 215 occurrences. Distinguishing between fox species was particularly difficult due to most images capturing only partial bodies, hence our decision to name the predator variable “fox occurrence”. We also recorded 20 raptor occurrences (*Caracara plancus* and *Phalcoboenus chimango*), of which 80% interestingly occurred during the lambing season, and five records of domestic cat. We had previously registered one Puma (*P. concolor*) during our pilot study in 2014, but not during our proper sampling period in 2016. Among prey species, we registered 230 hare (*L. europaeus*) occurrences by camera trapping and live-captured three rodent species 366 times, registering a minimum number known to be alive of 183 individuals, specifically *Abrothrix lanosus* (n=97), *A. longipilis* (n=15) and *Oligoryzomis magellanicus* (n= 71). We also collected 4173 arthropods from 396 taxa, although we only found 111 individuals from 7 taxa over our minimum of 2cm length as potential fox prey. Specifically, we found six coleopterans (*Ceroglossus suturalis* n=6, *Chauliognathus spp* n=4, *Listroderes sp1* n=19, *Listroderes sp2* n=3, *Neopraocis reflexicollis* n=37, *Sericoides sp* n=18) and several lepidopteran larvae (n=24). Lastly, camera trapping also revealed 142 guardian dog occurrences.

Models of variation in sheep killed by foxes

The best model that explains predation on livestock includes relative biomass of wild prey along with hare occurrence (*w*=0.35), while the second-best model contains relative density of wild prey and again hare occurrence (w=0.29). Together, these two models account for 64% of the weight of evidence, both including the occurrence of hare and a predictor of relative availability of wild prey. The third best model includes relative wild prey biomass (w=0.1). Subsequent models contain Akaike weights lower than 10%. Because the best model is only 1.23 times more likely to be better than the second-best model (evidence ratio = 0.35/0.29) and the weight of evidence is not skewed towards any one model over 90% (Table 3), accepting only one model as correct is likely to ignore the evidence supported by the other models. Therefore, employing model averaged estimated coefficients of explanations will allow for the best prediction of ovine kills.

Table 3. Top ten candidate model set based on predictions derived from the a priori hypotheses. Generalized linear models with negative binomial distribution ordered according to AICc, with associated degrees of freedom (df), number of parameters in the model (k), AICc, ∆AICc and Akaike model weights.

Model	*k*	logLik	AICc	∆AICc	weight	Chi-squared	df	p-value
rwm + hare	4	-23.28	61.23	0	0.351	11.33	8	0.18
rwd + hare	4	-23.49	61.65	0.42	0.285	11.56	8	0.17
rwm	3	-27.15	63.73	2.51	0.100	11.24	9	0.26
rwd	3	-27.61	64.65	3.43	0.063	11.55	9	0.24
wm	3	-28.01	65.45	4.23	0.042	11.71	9	0.23
wd	3	-28.05	65.52	4.30	0.041	11.60	9	0.24
wd + dd + hare	5	-22.78	67.57	6.34	0.015	11.41	7	0.12
wm + dm + hare	5	-22.79	67.59	6.36	0.015	11.34	7	0.12
rwm + ucov + hare	5	-23.14	68.27	7.05	0.010	11.14	7	0.13
rwm + fox	4	-27.06	68.80	7.57	0.008	11.10	8	0.20

wd = absolute wild prey density, rwd = relative wild prey density, dd = domestic prey density, ucov = understory cover, wm = wild prey mass, dm = domestic prey mass, rwm = relative wild prey mass, fox = fox/24hr, hare = hare/24hr, dog = dog/24hr, wd*dd= wild and domestic prey density interaction, wm*dm = wild and domestic prey mass interaction.

Model averaged livestock predation predictors and composite model

Among model-averaged coefficients of predictors with 95% Confidence Intervals that do not overlap with zero, only hare occurrence explains the number of sheep killed (Table 4). We found that increasing the occurrence of hare by one unit would result in a reduction of ovine deaths due to fox kills by exp(-10.758) times. Thus, a composite model should only consist of hare occurrence as the predicting factor.

Table 4. Summary results of the working hypotheses after model averaging: effects of each parameter on number of livestock kills by predators. Parameters indicate predictor variables, estimate the predictor coefficients, SE the unconditional standard errors, and CI the confidence intervals at 95% (upper and lower limits, respectively).

Parameter	Estimate	SE	95% CI
(Intercept)	16.232	66.628	(-114.356, 146.820)
Relative wild prey mass	-2.684	3.238	(-9.030, 3.662)
Hare occurrence	-10.278	3.576	(-17.286, -3.270)
Relative wild prey density	-0.558	1.013	(-2.543, 1.426)
Wild prey mass	-0.005	0.016	(-0.036, 0.026)
Wild prey density	0.000	0.000	(-0.000, 0.000)
Domestic density	0.062	0.066	(-0.068, 0.193)
Domestic mass	0.002	0.002	(-0.002, 0.005)
Understory cover	0.009	0.041	(-0.072, 0.089)
Fox ocurrence	-0.432	4.318	(-8.896, 8.032)
Wild and domestic prey density interaction	0.000	0.000	(-0.000, 0.000)
Wild and domestic prey mass interaction	0.000	0.000	(-0.000, 0.000)

Discussion

Availability of wild prey as explanation for livestock predation

We empirically tested four explanations for livestock predation regarding prey availability, both through prey density and biomass and in absolute and relative (to domestic prey) terms. We found evidence that availability of wild prey explains ovine kills only when taking into account changes in the wild-to-domestic prey ratio, with domestic prey predation increasing as the ratio skews more towards domestic animals for both relative prey density and biomass. Additionally, the frequency of hare occurrence, another proxy of wild prey availability, also holds a negative relation with livestock predation. However, only hare occurrence offers consistent support from the evidence as predictor for ovine predation: neither relative density nor biomass of wild prey can be said to have an effect on ovine kills when taking all the evidence into account. We surmise this is because we used rodents and arthropods as the potential wild prey in all four of our predictor variables postulated as explanations, and these prey items may simply not suitably cover fox diet breadth in such a way as to offer sufficiently large enough net energy gain for Culpeo foxes, despite being the most frequently occurring prey in fox diet at an aggregate 69% (Palacios et al. 2012). However, the size of the introduced European hare is at least closer to sheep than rodents and arthropods, and hence liable to contend with ovine through apostatic selection by predators, potentially leading to prey switching for foxes. Due to how we collected data for our experiment our variable for hare occurrence is not relative to ovine occurrence, and consequently this evidence does not help to determine possible minimum thresholds of wild prey as some have been able to (see Khorozyan et al. 2015). However, hare occurrence having an effect but not density or biomass of rodents and arthropods, implies that not only is availability of wild prey an important factor, but also reinforces the idea that type of prey has a large role in explaining predation on livestock.

Prospectus for management

Our finding lends credence to the hypothesis that prey manipulation might change predation rates of livestock as a functional response to increased availability of wild prey if the right wild prey is present. We find that rate of predation declines with increased wild prey availability, yet a global pattern denotes the opposite (Crespin & Simonetti Chapter 2). Thus, we can surmise that the pattern might vary widely between localities or according to the identity of the species involved. Having established hare occurrence as a predictor of ovine kills, one might plan to enact management regimes whereby hare population density is managed for coexistence in this system. The large slope of the effect of hare occurrence on ovine kills tells us that the mere presence of large enough wild prey such as hare can incite prey switching from domestic to wild prey. We sought to find plausible correlations for hare frequency of occurrence and found that it has a strong negative correlation with understory cover (Spearman’s rho = -0.61, $p < 0.05$). Understory cover is easier to manipulate directly and offers a practical avenue to approach if hare availability is the sole predictor for sheep predation in our model system.

In practice however, having hare as the sole wild prey which livestock production systems in the Chilean Patagonia can manage to induce prey switching in foxes from ovine to alternate food sources is a problem: European hare is an exotic species in Chile. As an invasive species, the usage of hare would run counter to the land-sharing approach which seeks coexistence with native biodiversity. Also, ample evidence suggests that introduced lagomorphs graze on native bush and tree seedlings (Jaksic & Fuentes 1980, Fuentes *et al*. 1983, Simonetti and Fuentes 1983), impeding the renewal of vegetation. Furthermore, evidence of hare preference for gramineous species (Kufner et al 2008) might indicate possible competition between hare and ovine livestock. Hence, we do not endorse increasing hare density in our model system or otherwise. Solutions to this conundrum are not easy to come by, since managing native prey large enough to compete with ovine or even cattle as resource in the eyes of potential predatory carnivores might not be feasible where the general consensus among livestock stakeholders is that wild ungulates also compete with livestock for pasture, ending in diminishing returns when livestock fail to thrive. We find that the use of wild prey as a management tool for livestock loss to predation in the Chilean Patagonia is paradoxical in nature, because large native prey is antagonized and considered to compete with livestock while hare is an exotic animal.

Caveats

We address three caveats. First, the number of observations we obtained could skew the gamut of observable data and affect regression slopes. If such is the case, this might be amended by an increased sampling effort. Second, as is intended, this study is focused at the local-scale. Reasoning inductively to other systems might not prove to be a fruitful decision, since unique agroecological systems present constant spatial and temporal turnover at the community level, not to mention distinct socio-ecological interactions, inhibiting opportunities for extrapolation (Crespin & Simonetti 2018, see Crespin & Simonetti Chapter 2). We emphasize that conflict resolution methods need management at the local level. Finally, focusing on the model system, despite finding that hare occurrence has a negative effect on livestock predation, our observations fit on a temporal scale of weeks, therefore it is possible that medium- or long-term effects of increased wild prey availability might act differently by allowing predator populations to increase. Further research into time scaled effects of prey availability on livestock predation by carnivores might elucidate why the global pattern, composed of studies years-long, finds that increased wild prey also increases predation rate (Crespin & Simonetti Chapter 2), contrary to our findings at the local level.

Concluding Remarks

The evidence accrued during this study reinforces the idea that wild prey availability can predict predation on livestock. Our primary predictors were based on rodent and arthropod densities and biomass but were not supported by the evidence, instead we found that ovine predation rate decreases when hare occurrence increases. Since the European hare is proportionally closer in size to ovine livestock than to rodents and arthropods, we conclude that the size of the available wild prey is determinant in the carnivore decision-making process of whether prey switching occurs or not. Conforming to classical optimal foraging theory (MacArthur & Pianka 1966), we surmise that for smaller wild prey to exert an effect on livestock predation rates, their frequency of encounter (*i.e.* search time modulated by availability) and ease of capture (*i.e.* handling time modulated by prey escape strategy) would need to compensate the gap in nourishment acquired by choosing to consume prey as abundant, easy to capture, and the size of livestock. Therefore, future research on strategies dependent on prey switching should look towards managing the availability of native prey large enough to compete with livestock in the eyes of carnivores. Manipulating native wild prey for carnivores in productive landscapes in such a way as to reach population levels that decrease attacks and loss of livestock can help land sharing be a realizable goal by ensuring coexistence and might constitute a reachable target for future conservation treaties.

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Table S1. Observations for each individual field.

No.	site	month	kills	wd	rwd	dd	wm	rwm	dm	fox	hare	dog	ucov	Time (days)	Area (ha)
1	Ana	January	13	1266.7	98.38	20.85	16.19	0.02	815.12	0.06	0.04	0.13	32.05	31	28
2	Jorge1	January	1	5066.7	99.65	17.64	87.90	0.11	689.61	0.14	0.50	0.07	17.25	31	98
3	Jorge2	January	0	3066.7	99.62	11.61	58.51	0.11	453.74	0.03	0.42	0.01	17.25	31	98
4	Mayeya1	May	0	4400.0	99.80	8.69	105.60	0.24	339.95	0.02	0	0.04	46.20	12	59
5	Carneros	May	7	4000.0	99.90	3.95	96.00	0.38	154.24	0.02	0.07	0.13	21.73	12	39
6	Gaucho	May	0	6200.0	99.94	3.96	148.80	0.49	154.66	0.04	0.17	0	65.00	12	55
7	Mayeya2	August	1	2200.0	99.55	10.02	52.80	0.12	391.64	0.28	0.13	0.73	33.64	13	59
8	Gaucho-chico	August	3	3800.0	99.29	27.32	91.20	0.08	1068.14	0.06	0.03	0.15	60.88	13	7
9	Carneros2	October	0	16266.7	100.00	0.15	61.95	0.91	5.97	0.16	0.51	0	19.28	20	39
10	Ema	October	3	1600.0	99.91	1.40	16.21	0.23	54.74	0.38	0.13	0.01	26.80	20	50
11	Guachicles	October	22	16466.7	99.92	13.11	59.57	0.10	512.62	0.47	0.06	0.20	59.16	20	90

Variables	Abbrev.
named field used for observation	site
month of observation	month
number of ovine killed	kills
absolute wild prey density (per hectare)	wd
relative wild prey density (per hectare)	rwd
absolute domestic prey density (per hectare)	dd
absolute wild prey biomass (per hectare)	wm
relative wild prey biomass (per hectare)	rwm
absolute domestic prey biomass (per hectare)	dm
fox occurrences per day	fox
hare occurrences per day	hare
dog occurrences per day	dog
understory cover in %	ucov
number of days	Time
number of hectares	Area

Table S2. Correlation matrix. Spearman's rho for for all predictors. Threshold of rho = 0.6 was used to avoid collinearity. Only significant correlations are shown (p<0.05).

	wd	rwd	dd	wm	dm	rwm	Fox	hare	dog	ucov
wd	1									
rwd	0.72	1								
dd		-0.75	1							
wm	0.62			1						
dm		-0.75	1		1					
rwm		0.75	-0.91		-0.91	1				
fox							1			
hare								1		
dog		-0.61	0.64		0.64	-0.67			1	
ucov										1

wd = absolute wild prey density, rwd = relative wild prey density, dd = domestic prey density, wm = absolute wild prey mass, dm = domestic prey mass, rwm = relative wild prey mass, fox = fox occurrences, hare = hare occurrences, dog = guardian dog occurrences, ucov = understory cover percentage.

General Discussion

Traversing the food-biodiversity nexus: transitioning towards coexistence by manipulating social-ecological system parameters

Agroecological landscapes have the potential to simultaneously meet food security and biodiversity conservation goals. This potential cannot be achieved without ensuring human-biodiversity coexistence (Crespin & Simonetti 2018). Such coexistence entails the elimination and prevention of conflicts stemming from the interactions between human activities and nature (Young et al. 2010), which exist at multiple levels of complexity and intensity (Madden & McQuinn 2014). The most immediate but no less important conservation conflicts are those that emerge directly from a biological basis and are predicated on quantitative tradeoffs between conservation interests and food productivity. When these opposing interests that impact either society or biodiversity are based on clear socio-ecological components, the system can be managed by understanding underlying dynamics and processes, enabling the identification and manipulation of parameters that lead to coexistence.

Land solely for nature is increasingly rare and projected to be insufficient for conserving the world's species (Svancara et al. 2005). In light of this, already transformed land can either be restored to a state resembling landscapes before transformation or reframed into dual purpose landscapes, allowing for both nature and human activities to integrate, such as in agroecological landscapes. The latter is the land-sharing approach, originally depicted as low intensity farming that enables wildlife to occupy the same land and devised from a mathematical model describing tradeoffs between food production and wildlife abundances (Green et al. 2005). Now, a framework has been introduced to analyze and navigate this food-biodiversity nexus, the "social-ecological systems model of the food security-biodiversity nexus" (Fischer et al. 2017). The food-biodiversity nexus describes a simple model based on two axes of biodiversity and food security, where four quadrants illustrating alternative system states emerge depending on the tradeoff between food security and biodiversity in a landscape: degraded lands, intensive agricultural landscapes, fortress conservation and agroecological landscapes (Fig 1.). Among the available system states, only the agroecological landscape optimizes both food security and biodiversity on the same land, *i.e.* the land-sharing approach. Land-sharing requires abdicating complete human domination of a landscape and establishing a degree of syntopy between wildlife and domesticated plants or animals meant to be reared as food for human society. This scenario is primed for the emergence of conflicts.

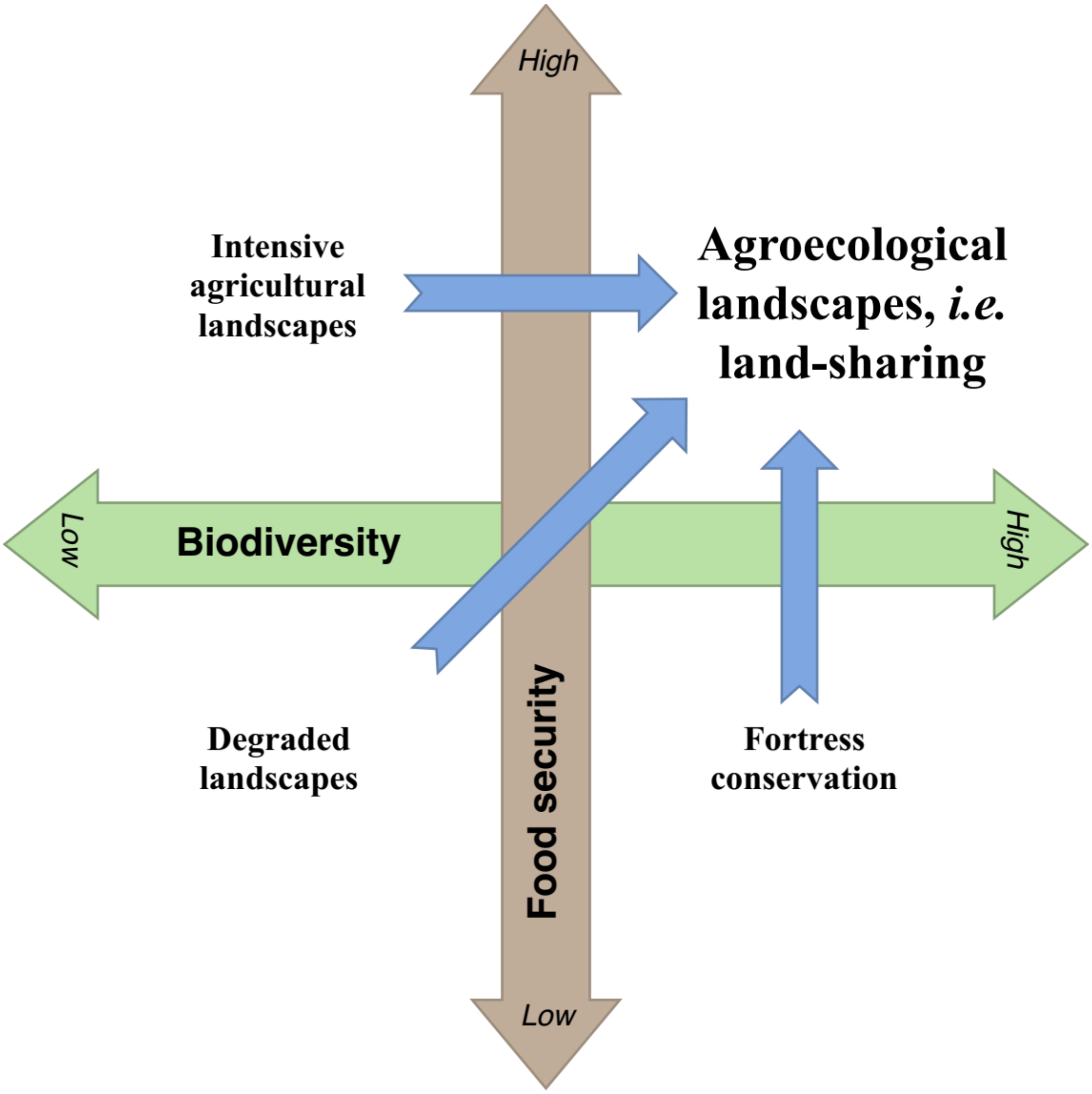

Figure 1. The social-ecological systems model of the food-biodiversity nexus presents four quadrants depicting alternative system states emerging as tradeoffs between food security and biodiversity in a landscape, wherein only agroecological landscapes optimize both food security and biodiversity by sharing land. This model is a jumping-off point for conceptual viewing of landscapes as systems and allows abstract identification of possible parameters to nudge a system towards land-sharing. Adapted from Fischer et al. (2017).

Coexistence is required to fully transition towards land-sharing (Crespin & Simonetti 2018), and therefore must also be necessary to navigate the nexus from any alternative system state to an agroecological context. We propose navigating the nexus by searching for parameters that minimize the impacts felt by opposing interests in a social-ecological system. Specifically, we view these *coexistence parameters* as the tangible and perceived variables that dictate coexistence in a system and thus are subject to management. Our aim is to demonstrate how these coexistence parameters can be identified and used to navigate the nexus towards land-sharing.

Conceptual identification of coexistence parameters

Social-ecological systems are interlinked societal and environmental components whose dynamics are shaped by drivers at multiple spatial and temporal scales and which may exist in alternative system states (Fischer et al. 2015). Agroecological landscapes can be understood as social-ecological systems when their major social and ecological components are identified. However, not all the components in a system directly interact in the formation of biodiversity *impacts*, the situations where people negatively impact biodiversity or biodiversity negatively affects human wellbeing (Young et al. 2010). Furthermore, biodiversity impacts may turn into conservation *conflicts* once opposing interests arise when an affected party finds they need to eliminate a biodiversity impact (White et al. 2009). Conflicts, by definition, impede coexistence and if left alone often result in retaliation against the wildlife or the aspect of biodiversity involved. Therefore, to determine which social and ecological factors interact in the development of a conflict we must first understand how the underlying biodiversity impact emerges. Once the formation of biodiversity impacts is sufficiently understood and the factors that directly explain the impact are identified, we may determine which social-ecological factors can be subject to management strategies so as to minimize or eliminate the impact and quell the conflict. Reframing agroecological landscapes as social-ecological systems, we can view the social and ecological factors as system components and focus specifically on those manageable components that explain biodiversity impacts and are hence capable of dampening conflicts. Since managing social-ecological components can in theory eliminate the source of conflicts and shift a system from a state of conflict towards one of coexistence, we can say to have identified the coexistence parameters for that system. The specific social-ecological components that explain biodiversity impacts and consequently the emergence of conflicts define the conditions the system requires for coexistence, hence the reason we consider them to be coexistence parameters.

From socio-ecological drivers to coexistence parameters

To illustrate how coexistence parameters might be identified, first we identify possible ecological drivers of biodiversity impacts and social drivers of tolerance to these impacts. Social and ecological systems on their own exist within levels, such as ecosystems, communities, populations and individuals or society, institutions, groups, and again individuals; therefore, when aspects from the social and ecological realms interact within social-ecological systems, the resulting impacts can be felt at specific levels (Lischka et al. 2018). Defining the hierarchical level at which social-ecological drivers operate to generate biodiversity impacts occur is crucial to identifying possible coexistence parameters.

The most prominent biodiversity impacts result in human-wildlife conflicts, particularly when carnivores kill livestock or herbivores steal crops for consumption, hurting farmers’ livelihoods in the process and in many cases leading to persecution of wildlife (Baker et al 2008). When biodiversity impacts occur at the individual level, operational social-ecological drivers may stem from factors that affect animal behavior and tolerance towards the impact (Lischka et al. 2018). However, impacts might occur at larger scales or higher levels, such as when crop raiding by large elephant herds, primate groups or bird flocks impact whole human communities. Therefore, it follows that if the level at which biodiversity impacts occur broaden, so too must the social and ecological factors which drive them.

Ecological drivers that factor into animal behavior have traditionally been the subject of studies in ecology. Shifts in resource availability affect the probability of attacks on livestock, crops, or people. Decrease in wild prey availability increases the number of sheep killed by foxes (Crespin & Simonetti Chapter 3) and lower prey density during wet seasons increases lion, cheetah and leopard attacks on cattle, goats and sheep (Patterson et al. 2004, Kolowski & Holecamp 2006, Bagchi & Mishra 2006, Mishra 1997). The physical characteristics of the habitat and structures surrounding livestock can also alter livestock vulnerability (Kolowski & Holecamp 2006), since stealthy predators might prefer attacking unaware prey under the presence of cover or when closer to reserves or habitat fragments (Schiess-meier et al. 2007, van Bommel et al. 2007, Michalski et al. 2006). Landscape level thresholds for natural habitat can prevent impacts from taking place, evidenced through a deforestation threshold of 30-40% to avoid human-elephant conflicts (Chartier et al. 2011).

Social aspects that drive tolerance are equally important in determining whether biodiversity impacts become conflicts (Dickman 2010). These can range from universally understood impacts, such as those directly responsible for loss of economic solvency, to deeper rooted identity-based factors involving cultural values (Madden & McQuinn 2014). High economic solvency can offset the loss of livestock or crops, since wealthier landowners may be less impacted by the same amount of livestock or crops lost as smaller landowners. Monetary or physical losses may not even need to be present for conflicts to emerge, since the mere perception of a biodiversity impact can trigger feelings of threat (Dickman 2010) and the perceived risk of losses to wildlife are usually higher than reality (Hill 2004). Cultural or religious values can be broader level social drivers of tolerance (Zinn et al. 2000), further complicating matters.

Landscapes where carnivores and livestock or herbivores and crops cooccur are at risk of generating biodiversity impacts, but determining what factors predict these impacts might allow for modifications to management regimes that lower livestock vulnerability to predation or probability of crops being raided. Once identified, these clear and manageable impact drivers can act within the food-biodiversity nexus as coexistence parameters in food production systems.

We submit that for a landscape pertaining to a particular social-ecological system, if an identifiable factor drives the source of biodiversity impacts or societal tolerance and can be manipulated sufficiently well to allow for the formulation of management strategies, then we can interpret them as coexistence parameters in that particular system for the purpose of transitioning the system towards coexistence and a true agroecological landscape.

Usefulness of the coexistence parameter concept

Here, we opt to view the social and ecological factors which decrease biodiversity impacts or increase tolerance as system parameters, for their potential capacity to move a social-ecological system from states of conflict to alternative desired system states devoid of major losses for both food security and biodiversity, *i.e.* coexistence. However, social-ecological systems are complex, with multiple components stemming from both people and nature, shaped by intrinsic and extrinsic societal and ecological variables (Fischer et al. 2015). These systems are interlinked across scales, they do not exist alone (Ostrom 2009). Hence, it is to be expected that multiple variables may need managing to transition from one system state to another. The same can be said of those social-ecological systems working towards land-sharing scenarios and seeking to transition towards agroecological landscapes, since emergent conflicts may not solely depend on one variable, dampening the opportunities for coexistence when either food security, biodiversity conservation or both are endangered.

Conflicts occur at differing levels of complexity (Lederach 2003, Madden 2004, Madden & McQuinn 2014). Best visualized by the Levels of Conflict model (Canadian Institute for Conflict Resolution 2000), mere disputes can be settled by managing concrete ecological variables and mitigating biodiversity impacts, but unsettled disputes can build up emotions and create underlying conflicts that require resolution, and further deep-rooted prejudices require reconciliation tactics. As such, when conflicts deepen, the variables that affect tolerance may become harder to distinguish or separate between them, increase their interactions and thus the number of variables that need to be addressed, ultimately obstructing the identification of coexistence parameters. Therefore, when managing a socio-ecological system for conflicts, one should expect a multiplicity of parameters defining the system state. Because of this operational complexity, conceptually recognizing parameters that define a desired system state may enable easier assessment of a landscape's state and identification of the required actions needed to transition towards coexistence.

For example, if an underlying conflict is based on perceived damages which do not exist, no matter how much loss to predation is reduced or even eliminated by managing ecological variables, if stakeholder perception remains unchanged, the underlying conflict will not be resolved. In deep-rooted conflicts, prejudice may take hold in belief systems or even form part of a community's identity. Persecution of carnivores that are not large enough to attack livestock and other trophically unrelated groups incapable of the same feat is a common occurrence in many communities and can even have become culturally ingrained (Dickman 2010). Communities dependent on landscapes with fewer sources of food and shelter for livelihood also tend to become antagonistic towards wild animals because they are more vulnerable: they have more to lose than those who enjoy multiple sources of wealth and income (Sjoberg et al. 2004). Defense against wildlife becomes part of the way of life. These cases show deeper levels of conflict that are more complex than quantitative tradeoffs of food production and biodiversity. Their unique socio-ecological context is translated into unique combinations of socio-ecological variables that dictate a state of conflict, and thus also the parameters capable of transitioning the system into the target state of coexistence. Therefore, by determining what variables must be manipulated in order to allow human-wildlife syntopy, no matter whether they must be approached from the social, economic or ecological sciences, identifying possible coexistence parameters might allow the formulation of management strategies tailor-made for each system, with a higher chance of success than one-size-fits-all strategies based on general patterns.

Caveats

Here we emphasize that conflict resolution methods need management at the local level. We mean to illustrate how coexistence parameters can be identified to work in the context of the “food-biodiversity nexus” conceptual framework and thus do not intend to offer the complete repertoire of coexistence parameters that a complex socio-ecological system immersed in underlying conflicts would truly need to rely on for coexistence.

Concluding Remarks

The social-ecological systems model of the food-biodiversity nexus provides distinct system states of which agroecological landscapes represent the land-sharing strategy, a necessary approach to biodiversity conservation in a world devoid of sufficient land for nature. Since sharing land requires reaching human-wildlife coexistence, we sought to exemplify the searching of parameters that when modified can enable coexistence dynamics in these systems. In general, conceptual identification of coexistence parameters for each system with conflicts will reveal unique parameter combinations, so perhaps manipulation of just one ecological or social factor component might not be enough to reduce biodiversity impact or increase tolerance levels, instead requiring tailor-made management of multiple parameters to transition toward coexistence states. As a concept, social-ecological systems provide a means to analyze the food-biodiversity nexus, and we hope our reframing of the various possible variables from distinct disciplines that can be managed for coexistence as parameters helps in this endeavor. Abstract thinking approaches problems in a new light, such that interpreting agroecological landscapes as social-ecological systems at the conceptual level permits variables which dictate impacts or tolerance to be regarded as system parameters of coexistence, allowing for more effective transition strategies. A shared landscape, reaching coexistence with nature while we produce our sustenance, is a win-win scenario where we protect biodiversity while maintaining the necessary components for ecosystem services, so we may call them what they should be: landscapes of coexistence.

“Conservation is a state of harmony between men and land. … Harmony with land is like harmony with a friend; you cannot cherish his right hand and chop off his left. That is to say, you cannot love game and hate predators; you cannot conserve the waters and waste the ranges; you cannot build the forest and mine the farm. The land is one organism.”

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