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The roles of non-production vegetation in agroecosystems: A research framework for filling process knowledge gaps in a social-ecological context

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Abstract

1. An ever-expanding human population, climatic changes and the spread of intensive farming practices are putting increasing pressure on agroecosystems and their inherent biodiversity. Non-production vegetation elements, such as woody patches, riparian margins and restoration plantings, are vital for conserving agroecosystem biodiversity. Furthermore, such elements are key building blocks that are manipulated via land management, thereby influencing the biotic and abiotic processes that underpin functioning agroecosystems.
2. Despite this critical role, there has been a lack of synthesis on which types of vegetation elements drive and/or support ecological processes, and the mechanisms by which this occurs. Using a systematic, quantitative literature review of 342 articles, we asked the following questions: what are the effects of non-production vegetation on agroecosystem processes and how are these processes measured within global agroecosystems?
3. Woody patches, hedgerows and borders, riparian margins, and shelterbelts were the most studied types of non-production vegetation. The majority (61%) of studies showed positive effects of non-production vegetation on ecological processes, where the presence, level or rate of the studied process was increased or enhanced.
4. However, four key research gaps were revealed: (a) most studies (83%) used proxies for, instead of direct measurements of, ecosystem processes related to non-production vegetation; (b) study designs used to investigate non-production vegetation effects on ecosystem processes directly were largely limited to observational comparisons of non-production vegetation types, farm-scale vegetation configurations and different proximities to vegetation in terms of the effect on ecological processes; relatively few studies used manipulative experiments; (c) the relatively few studies directly measuring ecosystem processes were dominated

by four process categories: invertebrate biocontrol, predator and natural enemy spillover, animal movement, and ecosystem cycling and (d) the methods used to directly measure non-production vegetation effects comprised a surprisingly limited set of approaches.

5. To fill key research gaps that will inform the use of non-production vegetation to enhance agroecosystem processes, we present a framework for future research that emphasizes the need to combine an understanding of human decision-making with carefully designed and targeted investigations into the roles of taxa, ecosystem processes, and landscape heterogeneity related to non-production vegetation, at multiple spatial scales within agroecosystems.

KEYWORDS

agriculture, biodiversity, connectivity, decision-making, ecosystem process, landscape, multi-functionality, people

1 | INTRODUCTION

Agricultural lands, comprising almost 40% of the Earth's terrestrial surface, are under increasing pressure. The demand for secure sources of food and other resources, and the uptake of intensive agricultural practices, is increasing and climatic processes, natural disturbance regimes and habitats continue to be disrupted or degraded (e.g. Godfray et al., 2010; Smith et al., 2016; Tilman, Blazer, Hill, & Befort, 2011). Such pressures are drastically altering agroecosystems and their abilities to provide and sustain services at the accelerating rate of human demand (Rockström et al., 2017). A consequence is dramatic losses of biodiversity across agricultural landscapes globally (Newbold et al., 2015). There have been discussions whether the biodiversity crisis in ***agroecosystems*** could be best mitigated via 'land sparing', where larger conservation set asides are spared in one area at the expense of lower biodiversity, higher-yield agricultural areas in other areas, or whether the focus should be on maintaining, retaining and restoring smaller components of the original diversity of taxa, habitats and ecosystem attributes within the production matrix itself ('land sharing'; e.g. Green, Cornell, Scharlemann, & Balmford, 2005; Phalan, 2018). The outcome of these discussions is that perhaps both approaches are essential (Kremen, 2015) and could be combined in different ways depending on the local context (e.g. Grass et al., 2019) to create agroecosystems that exhibit ***multi-functionality*** (Barral, Benayas, Meli, & Maceira, 2015; Manning et al., 2018; see Box 1: Glossary).

There is increasing evidence (e.g. Cardinale et al., 2006; Srivastava & Vellend, 2005; Tilman & Downing, 1994; van der Plas, 2019) that a positive relationship exists between ***biodiversity*** and ***ecosystem function***, although the exact nature and strength of the relationship are process- and context-dependent (Gamfeldt & Roger, 2017; van der Plas, 2019). Thus, biodiversity itself is fundamental to sustaining the biotic and abiotic **ecosystem processes** (i.e. '***functional biodiversity***', sensu Moonen & Barberi, 2008) that underpin ***sustainable and resilient*** agroecosystems (Isbell et al., 2015), and the downstream delivery of ***ecosystem services***

BOX 1 Glossary of key term

- **Agroecosystems** are ecosystems that have been modified from their natural state through time by farming practices, and may also contain other land uses such as settlements, conservation land or other industry. Like natural ecosystems, agroecosystems are composed of organisms (including humans) interacting with each other within an abiotic (chemical and physical) context.
- **Non-production vegetation** elements, which are not directly involved in the farm operation, include trees and woody shrubs, herbaceous vegetation and wetlands. These elements contribute to **landscape heterogeneity**, in that they can vary in their size, shape, arrangement in the agricultural landscape (**landscape configuration**) and in their species composition (**landscape composition**).
- These vegetation elements are primary components of '**functional biodiversity**' on farms, in that they support a range of flora and fauna that contribute to key **ecosystem processes**, such as animal dispersal, pollination, and carbon and nutrient cycling, that determine overall ecosystem function.
- Human-derived benefits may arise from functioning ecosystems in the form of **ecosystem services**, such as clean water, healthy soils, increased crop production and overall well-being. Conversely, functional biodiversity may facilitate processes that lead to **ecosystem disservices**, such as the movement/spread of pests, diseases, or weeds and the knock-on effects for crops, production animals, and/or human health.
- Agricultural landscapes exhibiting **multifunctionality** typically contain high functional biodiversity, have intact ecosystem processes and generate multiple ecosystem services.

(Martin et al., 2019). We consider ecosystem processes to be key mechanisms by which organisms interact with each other and their abiotic environment within agroecosystems, and distinct from ecosystem services, which are human-valued consequences of these processes.

There are two contributions of functional biodiversity that must be considered. First, key taxa can have disproportionate effects within agroecosystems, and their loss from a local species pool can have detrimental impacts on biodiversity and ecological processes (Chapin et al., 1997); the decline in bee populations in some regions provides a poignant example of this, having deleterious consequences for pollination and, ultimately, crop productivity (Vanbergen & the Insect Pollinators Initiative, 2013). This highlights that, while species richness is important, more critical are the functional roles that particular species play in agroecosystems, such as in multi-trophic processes (Soliveres et al., 2016) and in the decomposition of litter and detritus (Gessner et al., 2010).

Second, ***non-production vegetation*** elements provide the surrounding context in which the production components of agroecosystems are embedded. Such non-production vegetation might comprise linear features such as hedgerows, shelterbelts, corridors, and riparian buffers, single trees, patches of vegetation composed of restoration plantings and remnant patches, and other inter-crop components such as underplantings, buffer strips and cover crops. These non-production vegetation elements vary in their size, composition and spatial arrangement in agricultural landscapes, which together largely determine the types of processes and ecosystem services that can be supported (Duarte, Santos, Cornelissen, Ribeiro, & Paglia, 2018). Furthermore, manipulating such elements in agricultural landscapes, via land management decisions, provides a means to influence future ecological outcomes. Indeed, a number of government programmes across the globe, such as agri-environment schemes in the United Kingdom, the United States and Europe, have focused on creating/maintaining non-production vegetation components in agricultural landscapes, with variable outcomes (e.g. Batáry, Dicks, Kleijn, & Sutherland, 2015; Jones et al., 2017; Wood, Holland, Hughes, & Goulson, 2015; Żmihorski, Kotowska, Berg, & Pärt, 2016). While it is clear that multiple processes are required to achieve a resilient ecosystem (Oliver et al., 2015), we lack synthesis in our understanding of the role of non-production vegetation elements in multiple agroecosystem processes. If biodiversity positively affects ecosystem function, it is essential to understand which non-production vegetation elements support different ecosystem processes, and the mechanisms by which this occurs.

In this review, we evaluate the role of non-production vegetation elements within agricultural landscapes, in terms of supporting both abiotic and biotic processes at different spatial scales, and thus their importance in achieving sustainable, resilient agroecosystems. In particular, we ask the following questions: What are the ecological functions and processes associated with non-production vegetation components and how are these processes measured within global agroecosystems? We used a quantitative review methodology (Pickering & Byrne, 2014) to search the relevant literature using specific keywords. We scored papers based on how non-production elements were quantified, and the contributions to biodiversity and ecosystem function(s) demonstrated by these non-production elements. We use these results to make recommendations for future research regarding the roles of non-production vegetation in supporting the function of agroecosystems.

2 | QUANTITATIVE LITERATURE REVIEW

We searched the international literature for relevant articles following a modified systematic review protocol (Pickering & Byrne, 2014). Relevant articles were defined as those that described primary research conducted on farmland that addressed questions regarding any ecological function(s) associated with non-production vegetation. Initially, five distinct search strings, comprised of various keywords (Table S1), were designed to find relevant papers addressing the following broad topics related to non-production vegetation in agroecosystems; faunal diversity and use of vegetation; spatial arrangement of vegetation in the landscape; pests and disease in vegetation; weeds in vegetation; abiotic functional responses to vegetation. Second, the proportion of relevant articles returned by 30 scholarly databases was examined using all five search strings, and nine databases were selected based on the proportion of these relevant returns: BASE, BioOne, Google Scholar, JSTOR, Jurn, ProQuest, Science Direct, Scopus and Web of Science. Third, each search string was entered into each of the nine databases in turn, and all relevant articles were downloaded (where relevance was determined by reading the abstract). If no relevant articles were found for the first 100 returns, we moved on to the next search string. Fourth, for every relevant article found, we also checked all citing articles using the 'Cited by' function in Google Scholar. After the initial two databases were searched, we extracted all keywords from papers and ranked them by the number of occurrences. We updated the search strings to include any commonly used keywords that were missing from the strings (Table S1). The faunal and spatial searches that were carried out first yielded significant overlap relative to our article selection criteria and were ultimately combined into one faunal database. Finally, once all searches were complete, we extracted and cross-referenced all reference lists from the downloaded articles using ParsCit (Councill, Giles, & Kan, 2008) to compile a final list of articles across all searches.

A total of 704 articles were read and 342 were included using the criteria that they were as follows: (a) empirical (not modelling or meta-analysis) studies within agroecosystems and (b) they at least discussed the effects of non-production vegetation on processes, not just biodiversity, within agroecosystems. A range of variables were extracted from every included article (Dataset S1), describing the study design, the stated aims/questions of the study, the taxa studied (e.g. birds, invertebrates, mammals), the non-crop vegetation types (e.g. woody, herbaceous) and their configurations (e.g. forest fragments, hedgerows, corridors), the spatial grain and extent of the study (e.g. field margin, field, farm, catchment, region). We noted whether the inferences made in the paper were regarding ecological processes, biodiversity or both, and what processes were studied, such as biocontrol, pollination, nutrient cycling (Table S2). Finally, we recorded the methods that were used to measure processes directly, including direct observations of animal movements or feeding events, herbivory rate observations, respiration or decomposition rates, or whether the process was inferred via indirect observations or measurements, such as using relative differences in predator relative abundance to infer predation rates between habitat types or using soil physicochemical variables to infer nutrient cycling.

The 342 relevant research articles had a large global distribution (Figure S1) and resulted in 229 described independent studies about fauna, 61 studies about soil and water processes, 32 studies about weeds and 17 about diseases (human diseases, *n* = 5; other animal diseases, *n* = 2; plant diseases, *n* = 10); note that a few articles included more than one independent study. A total of 500 different research questions were asked within the articles regarding the effects of non-production vegetation on agroecosystem processes.

3 | NON-PRODUCTION VEGETATION POSITIVELY AFFECTS AGROECOSYSTEM FUNCTION

Our synthesis shows that the study aims, as stated by reviewed articles, address a wide variety of agroecosystem processes (Figure 1). Across the 342 reviewed articles and 500 independent research questions posed within these articles, the majority of effects of non-production vegetation on ecological processes were positive in that non-crop vegetation increased the presence, level or rate of the studied process (58%; *n* = 290). Of these processes, 10% (*n* = 51) would be classified as '***ecosystem disservices***' because they contribute negatively to human-preferred outcomes in agroecosystems. Of the remaining 90% (*n* = 449) of processes tested, non-crop vegetation caused increases in 61% of the processes (faunal biodiversity, *n* = 146; faunal processes, *n* = 64; soil and water processes, *n* = 53; weed processes, *n* = 4; disease processes, *n* = 5), caused decreases in 4% of the processes, caused variable responses (where the outcome depended on another factor such as vegetation type, taxon/taxa involved, landscape configuration or season) in 14% of the processes and was non-significant or unclear in 21% of processes. Of the 'ecosystem disservice' processes, non-crop vegetation improved (i.e. reduced) the disservice in 35% of all studied processes, and showed a decreased, variable or no effect for 15%, 38% and 12% of the processes studied.

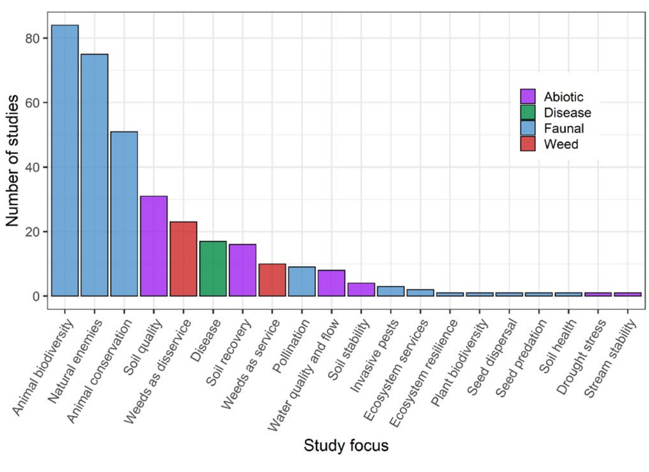


FIGURE 1 The number of total reviewed studies investigating different study aims. Over 90% of the total 342 reviewed studies focused on seven broad study aims with respect to the effects of non-production vegetation: animal biodiversity, natural enemies (i.e. invertebrate biocontrol agents), animal conservation, soil quality, weeds as an ecosystem disservice, disease occurrence and/or spread in agroecosystems (animal, plant and human), and soil recovery, with the remaining <10% of reviewed papers focusing on an additional 13 study aims. Blue bars represent fauna-related processes, purple bars represent soil and water-related (abiotic) processes, red bars represent weed-related processes and the green bar represents disease-related processes

The most commonly studied types of non-production vegetation elements (Table 1) were classed as 'patches', meaning any nonlinear, woody or non-woody, fragment that was either planted or, more frequently, remnant in the agricultural landscape with an extent relatively larger than components found at the field scale (*n* = 183; Figure 2). Studies that tested at least two different types

TABLE 1 Definitions of the non-production vegetation elements encountered in this review

Non-production vegetation element	Description
Mixed	A mix of different non-production vegetation element types
Reserve	A large area of native vegetation outside of agricultural production
Corridor	A linear non-production vegetation element, specifically described as facilitating the movement of animals, pests or diseases within a landscape
Patch	A nonlinear (e.g. round or rectangular) woody or non-woody non-production vegetation element, with a relative size greater than the field scale
Riparian margins	Usually linear non-production vegetation element alongside rivers or creeks
Shelterbelts	Linear non-production vegetation elements planted on farms for shelter and shade
Hedgerows/borders	Linear non-production vegetation elements occurring between fields
Scattered individuals	Multiple individual trees within a farm
Plots	Small-scale (within field) experimental plantings
Single trees	An individual tree
Understorey	Non-production vegetation planted underneath orchard or other crop vegetation

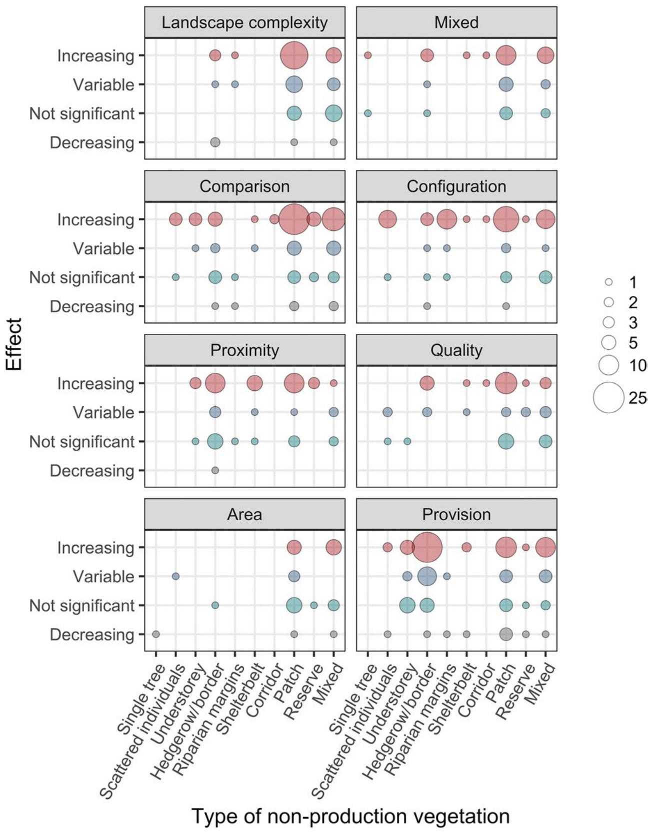


FIGURE 2 The outcomes of studies, grouped by the types of non-production vegetation and their tested effects, as stated in each of the 500 research questions posed by the 342 reviewed articles, including those both inferring and directly measuring processes. Effects (Table 2) were assessed relative to the presence of non-production vegetation, or variation in the relative amount, structural complexity, connectedness and/or condition, of non-production vegetation elements in the study areas. The outcomes of these tests were classified as 'increasing' (*n* = 287; ecosystem processes were significantly improved); in the case of 'disservices', the process was lessened or prevented), 'decreasing' (*n* = 26; processes were lessened or prevented; in the case of 'disservices', the process was increased or enhanced), 'not significant' (either a non-significant [*n* = 74] or unclear [*n* = 26] effect) and 'variable' (*n* = 83; where the outcome varied by vegetation type, taxon/taxa involved, landscape configuration or season)

of non-production vegetation elements ('mixed'; *n* = 109) and hedgerows or field margin plantings ('borders'; *n* = 98) were also studied more frequently than any of the other types, including corridors (*n* = 5; Figure 2), which are often presented as important connecting elements in agriculture landscape (Correa Ayram, Mendoza, Etter, & Salicrup, 2016). Whether or not non-production vegetation was present in the landscape ('provision'; *n* = 103) and the comparison of different non-production vegetation types (*n* = 95) were the most commonly tested effects of non-production vegetation (Table 2) on agroecosystem processes. Hedgerows/borders and shelterbelts showed relatively more increasing (rather than variable, decreasing or non-significant) effects than other vegetation types, across a range of tested effects (Figure 2).

TABLE 2 Description of the main categories of non-production vegetation effects on agroecosystem processes and examples of how they were studied in reviewed articles

Effect category	Explanation of non-production vegetation effect on agroecosystem process
Provision	The presence of a non-production vegetation type as compared to it not being present; for example, farms with and without remnant forest patches
Area	The relative amounts of non-production vegetation types; for example, larger areas of remnant forest relative to smaller areas of remnant forest
Quality	Non-production vegetation complexity, diversity, age or stature effects on a given process; for example, older hedgerows relative to young hedgerows
Proximity	Effect of distance to non-production vegetation, connectivity of patches or level of fragmentation; for example, inside a farm forest patch compared to edge and field
Configuration	Non-production vegetation shapes and/or arrangements in the study area (field, farm or landscape) that affect connectivity among vegetation elements; for example, effect of more connected arrangements of vegetation in the landscape relative to more disconnected arrangements
Comparison	Comparison of effects among different types of non-production vegetation, including field areas where non-production vegetation is absent; for example, woody patches versus linear elements versus marginal strips versus field only, typically representing a gradient of structural and/or compositional complexity
Landscape complexity	Effect of the diversity of types and amounts of non-production vegetation at the landscape scale; for example, landscape with more heterogeneous mix of large and small vegetation patches compared to one with small amounts of homogeneous vegetation
Mixed	A mixture of the above effects

4 | AGROECOSYSTEM PROCESSES ARE MOSTLY INFERRED, NOT DIRECTLY MEASURED

The ability to draw strong conclusions regarding the effects of non-production vegetation on agroecosystem processes is dependent on the degree to which processes are measured directly as opposed to whether indicator or proxy variables are used to represent those processes. In our review, very few studies directly measured the effects of non-production vegetation on agroecosystem processes. Only 17% (*n* = 84) of the 500 research questions from the 342 reviewed articles directly measured effects on processes, while 83% (*n* = 416) were posed using variables that have only been hypothesized to represent ecosystem function, such as biodiversity and soil physicochemical properties. There is only variable and/or weak evidence for many hypothesized causal relationships between such proxy variables and ecosystem functions, such as the links between biodiversity and soil carbon, decomposition rates or herbivory (van der Plas, 2019) or the links between indicators of soil properties and processes such as nutrient cycling and water quality (Bünemann et al., 2018). In other cases, links have been shown to be weak or absent. For example, land use types are often used as a proxy for abiotic function, but this has been shown to be unreliable (Bünemann et al., 2018) and there have been suggestions that more work needs to be done to model soil processes before causal relationships can be determined between processes and easy-to-measure indicator or proxy variables (Vereecken et al., 2016). Recent work has suggested, for instance, that microbial communities characterized by rapidly evolving and cost-effective molecular methods and databases can be used as highly sensitive bio-indicators of ecosystem processes (Astudillo-García, Hermans, Stevenson, Buckley, & Lear, 2019). Thus, our results suggest that greater research emphasis needs to be put on directly measuring ecosystem functions in agroecosystems associated with non-production vegetation and disentangling their relationships with other variables such as biodiversity and abiotic properties. However, further research is required to characterize which ecosystem processes are reliably measured and monitored using proxy indicators, as compared to direct process measurements, and how this might be influenced by agroecosystem context.

The research questions that used direct measurements of ecosystem processes rather than inferred links (*n* = 84 out of 500) examined a limited range of taxa and ecosystem processes and used relatively few methods to measure those processes (Table 3), revealing significant research gaps in this field. For example, 43% of studies on ecosystem processes related to fauna in non-production vegetation elements looked at invertebrate biocontrol and natural enemies of crop pests, such as parasitoids (*n* = 26 out of 61 studies); indeed, the majority of these were invertebrate-related studies (*n* = 38), while the remainder studied birds (*n* = 11), mammals (*n* = 8), multiple taxa (*n* = 3) and reptiles (*n* = 1). For soil- and water-related ecosystem processes, 19 out of 20 studies looked at ecosystem cycling processes such as decomposition, carbon cycling and nutrient cycling; no studies directly measured soil erosion, a key process in agroecosystems often touted to be positively affected by non-production vegetation. Only three weed studies directly measured processes by monitoring weed invasion over time; all other studies, including 30 on weeds and 17 on diseases inferred processes sampling the presence and/or abundance of weed- and disease-related taxa in different non-production vegetation elements and the production matrix.

Of the research questions that addressed directly measured processes, the majority (79%; *n* = 66) showed increases in the presence, level or rate of the ecosystem process due to the presence, or relatively higher amount, structural complexity, connectedness and/or condition, of non-production vegetation; this is compared to few study questions that showed variable (*n* = 8), decreasing (*n* = 3) or minimal or inconclusive (*n* = 7) effects (Figure 3). For process-based study questions where effects were not directly measured, but were inferred (*n* = 132), there were relatively fewer positive effects (57%), and more variable (19%) and minimal/inconclusive (20%) effects.

TABLE 3 The number of research questions directly testing different agroecosystem processes and the methods used to measure each process type. Ecosystem cycling refers to measurements of the flux and cycling of water, carbon or nutrients. Habitat selection refers to measurements of mobile animals that moved into (or, in the case of weeds, were excluded from) non-production vegetation elements. Spillover refers to the movement of animals out of non-production vegetation elements. Matrix invasion refers to the spread of weeds into non-production vegetation elements. Direct observation refers to methods that monitored animal movement such as GPS trackers and capture–recapture studies. Soil emission measurements refer to studies that used experimental methods, such as incubation, to record respiration and gas exchange of soils

Study type	Process measured	Method	*N*
Soil and water	Ecosystem cycling	Litter bag experiments	6
Soil and water	Ecosystem cycling	Soil emission measurements	9
Soil and water	Ecosystem cycling	Isotope measurements	1
Soil and water	Ecosystem cycling	Mass balance measurements	1
Soil and water	Ecosystem cycling	Multiple methods	1
Soil and water	Ecosystem cycling	Piezometer experiment	1
Soil and water	Soil sedimentation	Sediment accumulation	1
Fauna	Animal movement	Direct observation	8
Fauna	Animal movement	Population genetics	2
Fauna	Biocontrol	Food consumption amount or rate	15
Fauna	Habitat selection	Direct observation	6
Fauna	Pest animal movement	Direct observation	1
Fauna	Pest competition	Direct observation	1
Fauna	Pest habitat selection	Direct observation	4
Fauna	Pest herbivory	Food consumption amount or rate	5
Fauna	Pest predation	Direct observation	1
Fauna	Pest predation	Food consumption amount or rate	1
Fauna	Predation	Food consumption amount or rate	4
Fauna	Predation	Direct observation	2
Fauna	Spillover	Food consumption amount or rate	9
Fauna	Spillover	Direct observation	2
Weeds	Habitat provision	Individual counts	1
Weeds	Matrix invasion	Tree ring counts	1
Weeds	Matrix invasion	Individual counts	1

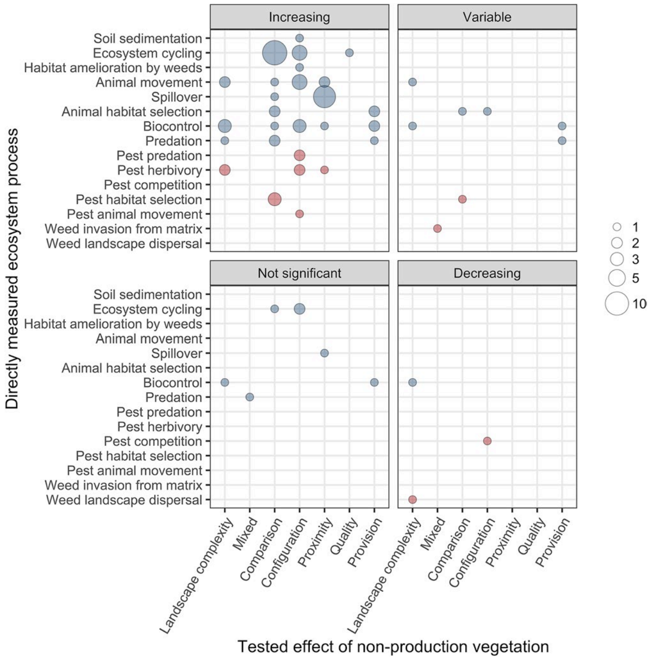


FIGURE 3 Cross-tabulation results for 84 reviewed studies where processes were directly measured, relating the stated, tested effects of non-production vegetation and measured ecosystem processes, grouped by study outcome. As per Figure 2, outcomes of these tests were classified as 'increasing', 'decreasing', 'not significant' or unclear effect and 'variable'. Red circles represent ecosystem disservices and blue circles represent ecosystem services

These results suggest that, despite the relatively minimal use of direct process measurements, there is quantitative support for the idea that non-production vegetation beneficially affects agroecosystem processes, and that direct process measurements may result in stronger inference.

Across all tested vegetation effects, ecosystem cycling (*n* = 19), biocontrol (*n* = 15), spillover (*n* = 11) and animal movement (*n* = 10) were the processes most frequently measured directly, with almost all of these (82%) showing positive (increasing) outcomes. Certainly, the last two decades has seen a proliferation of studies on the role of non-production vegetation in supporting beneficial invertebrates in agroecosystems, in terms of providing habitat and resources (e.g. Knapp & Řezáč, 2015; Saunders, Peisley, Rader, & Luck, 2016), facilitating their movement into adjacent farmland (e.g. Inclán, Cerretti, & Marini, 2015), and for generally enhancing pollinators and the biocontrol of invertebrates that impact on crop production (e.g. Pywell et al., 2015). There were clear positive effects of several different types of non-production vegetation elements, in comparison to production areas, on ecosystem cycling, such as decomposition, soil respiration and nitrogen mineralization (Figure 3). Conversely, our review also revealed gaps in the types of processes investigated. For example, few studies directly measured processes related to pest competition and movement, the dispersal and invasion of weeds into the production matrix, and other abiotic processes, such as soil erosion and sedimentation (Figure 3). Our results also showed that processes related to non-production vegetation were not commonly directly tested at landscape scales (e.g. landscape complexity effect, Figure 3), with many effects tending to be inferred indirectly via correlations with indices of land use intensity and composition.

We advocate for landscape-scale studies that are set up a priori as 'natural experiments' (e.g. Jonsson et al., 2012), where landscapes are purposefully chosen to test specific hypotheses regarding the effects of the types, amounts and/or configurations of non-production vegetation on specific processes (e.g. Tscharntke et al., 2012). Preferably, the process of interest could be directly measured within this design (as opposed to using proxy variables for the process), such as using GPS-based measurements of animal dispersal and habitat use. Furthermore, taxa or conditions could be manipulated experimentally at more local scales within the overall design to test for landscape-scale non-production vegetation effects on processes. For instance, Cosentino, Schooley, and Phillips (2011) manipulated the immediate moisture environment of a salamander species, and tracked their movements, through two production and two non-production vegetation types in a replicated landscape experiment to determine and test if this species preferentially use particular vegetation types to avoid desiccation while moving across the agricultural matrix between habitat patches.

5 | AVAILABLE METHODS SHOULD BE HARNESSED TO IMPROVE THE DIRECT MEASUREMENT OF PROCESSES

In all, 11 methods were employed across the 84 research questions emerging from studies directly measuring non-production vegetation effects on ecosystem processes (Tables 3 and S3). Of these 11 methods, only six methods were used in more than one study, and mainly comprised direct observations and food consumption amounts or rates for faunal studies and litter bag experiments and soil flux measurements for soil and water studies. This suggests that both the biotic and abiotic methods typically employed are limited to those that are easier to conduct in the field; for instance, vegetation effects on invertebrate predation are likely easier to document than those on competition, and disease transmission and soil gas flux measurements are relatively straightforward compared to those of erosion rates or nutrient and water flow dynamics.

There is a range of underused methods available for measuring ecosystem processes that could be usefully applied in agroecosystem research. For instance, landscape genetics methods, which are used extensively in natural habitats (Manel & Holderegger, 2013), could be employed more widely in agroecosystem studies to reconstruct the movement, current gene flow and past history of mobile native fauna in the fragmented habitats of agroecosystems (e.g. Jaffé et al., 2016). Furthermore, landscape genetics approaches could be successfully employed to provide in-depth, direct understanding of the processes driving host–parasite interactions and infectious diseases in agroecosystems (e.g. Biek & Real, 2010); we note that such methods were not used by any of the disease studies captured in our review and that, instead, landuse types were mainly used as correlative indicators of disease movement in landscapes. Temporal studies that track the movement of native and pest animals, weeds and diseases through agroecosystems would allow us to assess the role of non-production vegetation elements in providing both connectivity for native species (affecting ecosystem resilience) and pathways for the spread of unwanted organisms. For example, non-invasive and low-cost methods for direct tracking of native and invasive animals are available such as the use of rubidium as an isotope tracer to track native invertebrate movement (Payne & Dunley, 2002), or GPS technologies to quantify the movement of mobile macrofauna (e.g. Neilly & Schwarzkopf, 2017). Temporal studies involving experimental tracers could also be used to assess how non-production vegetation elements affect ecosystem processes such as sedimentation and run-off (e.g. Mabit et al., 2018), and the potential level of below-ground connectivity between different ecosystem components. Indeed, the roles of non-production vegetation elements for farm-to-catchment scale water flow and movement were particularly understudied in the literature we reviewed.

Experimental studies similarly provide strong inference for tests of process under manipulation; even large-scale manipulative experiments can be logistically easier to conduct in agroecosystems than in native ecosystems (e.g. Resasco, Bruna, Haddad, Banks-Leite, & Margules, 2017). Experimental approaches in agroecosystems could also include subsequent measurements of social and economic outcomes, such as crop yield, meat yield as outputs, social outputs (e.g. Maseyk, Dominati, White, & Mackay, 2017), thus expanding the scope of the experiment to test for effects of non-production vegetation elements on provisioning ecosystem services. Greater natural history and species-level understanding are needed to build knowledge of the processes that support resilient ecosystems (Oliver et al., 2015), and enable the scaling up of key processes using appropriate modelling to predict landscape-level ecosystem outcomes. For example, Padullés Cubino, Buckley, Day, Pieper, and Curran (2018) collected a comprehensive set of data on flammability traits for both natural and grazed tussock grasslands in New Zealand; using these data, they were able to scale up plant-scale flammability for these communities to determine the potential impacts of weed invasion in the grazed landscapes on potential flammability.

6 | THE ROLE OF NON-PRODUCTION VEGETATION IS EMBEDDED WITHIN THE SOCIAL–ECOLOGICAL CONTEXT

This review has shown that non-production vegetation can support the processes that underpin functional biodiversity in agroecosystems. However, fundamentally, agroecosystems are a human creation and so our choices and subsequent behaviours, such as maintaining or restoring non-production vegetation patches in agricultural landscapes, ultimately determine the structure and functioning of these landscapes (Figure 4a; Landis, 2017). Our review shows that there are gaps in our understanding of the broad range of agroecosystem processes that are likely to be affected by non-production vegetation elements. However, if we aim to achieve sustainable and resilient agroecosystems, research efforts to expand biological knowledge must be embedded in the 'cultural context' of agroecosystems, or we risk missing the role of people and the influence of their decisions in maintaining or disrupting the key biological processes and relationships (Figure 4b). For instance, although recent research showing that not all vegetation is equally flammable (Wyse et al., 2016) and some species can act as 'green firebreaks' (Cui et al., 2019), our review did not reveal any studies on how variation in non-production vegetation affects flammability in agroecosystems. Nonetheless, climate change is increasing landowners' concerns about the risk of fire occurrence and spread in their farm landscapes, and such landowners may make decisions about woody vegetation management on their farms that result in less-than-optimal biodiversity outcomes (Jellinek, Parris, Driscoll, & Dwyer, 2013). In some agroecosystems, cultural practices and knowledge can influence the way non-production vegetation is conserved or used in the landscape, such as for securing reliable sources of timber, fuel, food, medicine (e.g. Altieri & Toledo, 2002; García-Serrano & Del Monte, 2004; Huambachano, 2018) and for other benefits such as tourism (Addinsall, Weiler, Scherrer, & Glencross, 2017); conversely, land use and management changes imposed from the top down (e.g. by policy) that, for instance, encourage increased landscape homogenization and intensification, can have unforeseen negative impacts on the provisioning of cultural ecosystem services (Hanaček & Rodríguez-Labajos, 2018). The challenge, then, is to reconcile relevant ecological knowledge, land management policies, and human perspectives and behaviours to inform future research into poorly studied agroecosystem processes.

People make land management decisions, including those involving non-production vegetation, for a wide variety of reasons including economic consideration, personal values, and their knowledge of biodiversity and its role in the farming landscape (Norton & Reid, 2013; Welsch, Case, & Bigsby, 2014). For example, a primary driver of land management decisions is the economics of the farm business, but this is not always in conflict with good functional biodiversity management (Smith & Watson, 2018) and further can be incentivized by local and national government policy (Hanley, Banerjee, Lennox, & Armsworth, 2012). How we value biodiversity both intrinsically, such as for the enjoyment of native bird song, and extrinsically, such as for the provision of pollination or harvestable material or for soil nutrient mitigation, has been shown to provide both incentive for good biodiversity management and economic benefits (Cáceres, Tapella, Quétier, & Díaz, 2015). Traditional ecological knowledge and the cultural importance of particular species or habitats can positively influence the maintenance and enhancement of non-production vegetation and associated biodiversity (e.g. Ruiz-Mallén & Corbera, 2013). Likewise, fear of native species such as large mammalian predators, or other forms of human wildlife conflict, can impact on the management and use of non-production vegetation in farming landscapes (Sitati, Walpole, & Leader-Williams, 2005). Pest or disease vector taxa provide an economic incentive for

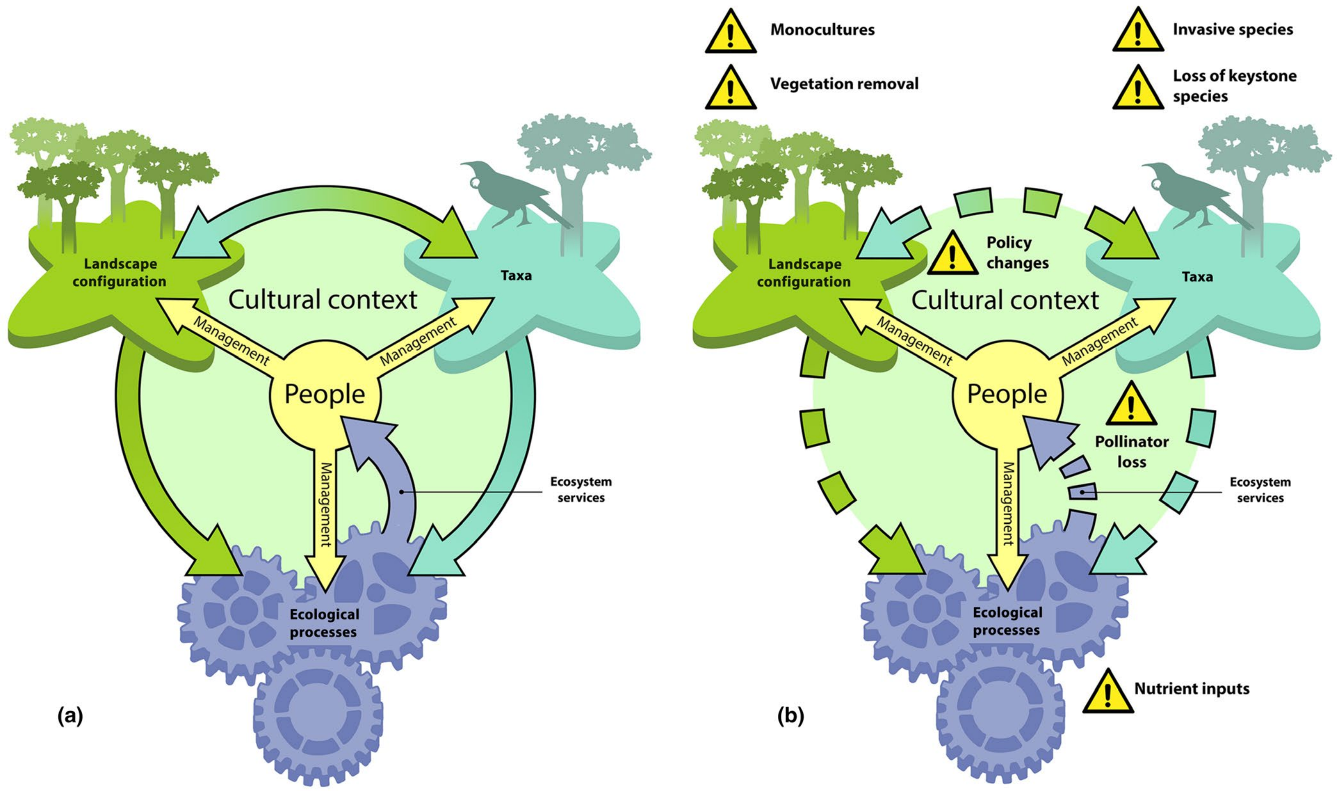


FIGURE 4 (a) People create agroecosystems and the management of these agroecosystems depends on the cultural context, which underpins landowners' decision-making. This human centre-point drives three components of multi-functionality and ecosystem resilience: (1) the taxa present in the agroecosystem, including the species composition of the non-production vegetation elements, (2) the landscape configuration (including amount, arrangement and condition) of the non-production vegetation elements in the landscape and (3) the ecological processes that are operating; taxa and landscape configuration interact to determine the ecological processes, and ultimately the delivery of ecosystem services for humans. (b) Disruption, due to management decisions, policy changes, and/or human-caused biotic and abiotic alterations, can occur for any of the components and result in the degradation of agroecosystem function (dashed arrows) and a loss of multi-functionality. Disruptors that cause a reduction in ecosystem function in an agricultural landscape could include, for example, the widespread reliance on single crop species ('monocultures'), high numbers of invasive animal and plant species that either outcompete, or cause direct mortality of, native species, and the loss of high-trophic-level animal species ('keystone species') that would normally have a top-down regulatory influence on energy and nutrient exchange in the local food chain. To better understand how to maintain or enhance resilience, future research needs to be transdisciplinary, and focussed at multiple scales and on under-emphasized processes (see Box 2)

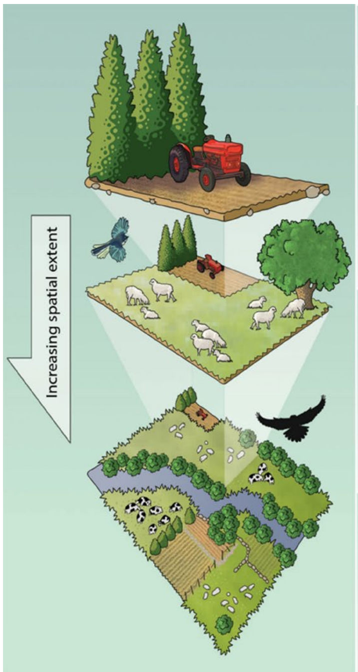
management and control; where such species also negatively affect native biodiversity, this provides a win–win for farming and good biodiversity management. For instance, the control of the invasive brushtail possum *Trichosurus vulpecula* in New Zealand, which is both a vector for bovine tuberculosis infection in cattle and a rapacious predator on native birds, has led to significant economic and ecological gains (Byrom, Innes, & Binny, 2016). Conversely, economic returns reaped via the management of non-production vegetation for one ecosystem function (e.g. pollination) can at times occur at the expense of other processes (e.g. biocontrol) (Shackelford et al., 2013). Thus, management decisions in agroecosystems arise from such complexities related to the social-ecological context and often result in trade-offs between competing viewpoints (Saunders et al., 2016), potentially disrupting one or many parts of the system (e.g. Figure 4b). Considerably more work is required to fully understand the contribution of these perspectives and decisions to enhancing agroecosystem processes for purposes other than maintaining diversity and preventing extinctions.

7 | A FRAMEWORK FOR FUTURE RESEARCH

In light of this cultural and ecological context (i.e. land management decisions are at the farm level, processes occur at multiple scales and management actions need social license), ecological understanding needs to be built within a framework that encompasses these three main components: the composition and configuration of non-production vegetation elements in the landscape, the role of important taxa/functional groups and how these taxa are supported by non-production vegetation, and the interplay of these components with management decisions (Lawton et al., 2010; Saunders et al., 2016). However, research should not be limited to a narrow set of topics to inform landscape design, but on as many processes as possible (Landis, 2017). The recent concept of 'Nature-based Solutions' (e.g. Cohen-Shacham et al., 2019) offers a transdisciplinary approach that aims to provide guidelines and standards by which non-production vegetation could be used as a mechanism

BOX 2 Filling the gap: A synthetic approach for building understanding of non-production vegetation effects on agroecosystem processes

The main components of resilient agroecosystems are likely to operate at, and interact across, different spatial scales. Therefore, the scale of observation and the methods used differs for different processes and ecosystem components (taxa, configuration of non-production vegetation, agroecosystem processes and people). Appropriately matching the scales of observation and measurement of processes is critical to deepening our understanding of agroecosystem function.



Spatial grain of observation	Methods for strong inference	Taxa	Landscape configuration	People and management	Processes supported by non-production vegetation needing greater research attention
Local, field	Small-scale experiments	Micro-organisms, invertebrates, reptiles, weeds,	Linear features (hedgerows, herbaceous borders, riparian margins), single trees	Field management decisions (tilling, pesticides and herbicides, fertilising, irrigation)	Mutualisms and facilitation, e.g., pollination, seed dispersal; competition between non-production plants and crop plants, animal competition; fine scale variability in soil processes and plant-water relations
Within-farm	Larger-scale experiments, direct observations, e.g., camera traps, GPS trackers, isotope markers	Small or limited-range mobile animals, weeds, diseases,	Multiple linear features, scattered trees and small patches; variable habitat composition, structure, and quality	Farm planning e.g., stocking rates and locations	Nutrient and water movement; soil erosion; habitat patch connectivity for a range of taxa (diseases, weeds, mammals, reptiles and birds in particular); non-invertebrate food webs
Landscape	Population genetics, direct observations, landscape-scale experiments	Larger or highly-mobile animals	(Dis)connected non-production vegetation elements, including reserves, corridors	Catchment-level planning e.g., water use	Long-distance dispersal, e.g., migration and seed dispersal; large-scale connectivity; water, nutrient and carbon budgets; interactions with abiotic conditions (soil type, climate) and finer-scale factors (species composition, vegetation configuration, etc.)

to increase the resilience of modified ecosystems to global change while addressing societal challenges. We advocate for such transdisciplinary research approaches that can be used to effectively evaluate the role of non-production vegetation for capturing a broad range of cultural, economic and ecological outcomes across multiple scales; such research is necessary for informing decision-making that will achieve sustainable and resilient systems that support higher functional biodiversity. We also suggest an important component of such research will be to determine if the provisioning of non-production vegetation will sufficiently enhance ecosystem processes, and downstream outcomes, to counteract the economic cost of lost production land (e.g. Magrach, Champetier, Krishnan, Boreux, & Ghazoul, 2019).

Because agroecosystem decision-making operates at the farm level, while functional biodiversity often operates at coarser scales (Kleijn et al., 2019), multi-level thinking is required to manage functional biodiversity across spatial scales (Box 2). The spatial scale at which ecosystem measurements should be taken needs to consider: (a) the scale of the organisms or the processes under study, (b) the size and arrangement of the non-production vegetation elements to be evaluated and (c) the logistical or other constraints of the methods used to measure the process. Where possible, pilot studies or prior information from the literature (e.g. Welsch et al., 2019) should be used to justify the spatial scale of sampling. Furthermore, fragmented landscapes cannot sustain all species because some, for instance, require large home ranges; however, where multi-functionality is the goal, rather than solely conservation of individual species, resilient systems need not contain maximal landscape biodiversity to be able to adapt to recover after perturbations such as drought or fire, or adapt to shifting conditions such as increasing temperatures or rising nutrient inputs (Lindenmayer et al., 2008). Instead, the focus should be on restoring, enhancing and manipulating non-production vegetation elements to create connected, structurally complex agricultural landscapes with a diversity of species across key functional groups at multiple scales (Fischer, Lindenmayer, & Manning, 2006).

8 | CONCLUSIONS

Non-crop vegetation elements in agroecosystems make a positive contribution to biodiversity and ecosystem functioning. Nonetheless, there are significant gaps in our understanding that can be filled by studies focussing on disentangling the role of different taxa (or functional groups) across non-production vegetation elements, incorporating a wider variety of processes and spatial scales, and employing novel and underused methods. Indeed, if we are to increase and enhance functional biodiversity, future efforts should be focussed on measuring and monitoring relevant biotic and abiotic ecosystem processes at landscape scales within the context of farm management scenarios. This will lead to new insights into how the types, amounts and arrangements of non-production vegetation elements, mediated by decision-making on farms, can result in resilient agroecosystems into the future.

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CONFLICT OF INTEREST

There are no conflicts of interest.

AUTHORS' CONTRIBUTIONS

B.S.C., J.L.P., M.C.S., D.A.N. and H.L.B. conceived the ideas and designed methodology; B.S.C., J.L.P., A.B., M.F., C.M., C.S., F.S. and H.L.B. collected the data; B.S.C., J.L.P. and H.L.B. analysed the data; B.C. and H.L.B. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The compiled literature review data used for this study have been made publicly available on the Dryad Digital Repository: https://doi.org/10.5061/dryad.8931zcrmn (Case et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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