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Temporal Lag in Ecological Responses to Landscape Change: Where Are We Now?

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Abstract

Purpose of the Review The loss or gain of biodiversity and/or ecosystem functions and services can occur with a substantial delay following landscape change. We have first revisited the key concepts used to refer to those delayed ecological responses to landscape change and then reviewed the literature aiming to summarize (i) methodological approaches used to empirically evaluate the existence of delayed ecological responses, (ii) empirical evidences of delayed ecological responses, and (iii) current understanding of the main mechanisms that can explain those delayed responses.

Recent Findings We identified that key concepts used to refer to delayed ecological responses are very confusing as many different terms are used to refer to a single delayed ecological response. So, we propose here a unified vocabulary to support future research. Our review showed that there is plenty of empirical evidence that delayed ecological responses to landscape change are common in nature. However, current knowledge is mostly restricted to biodiversity responses to adverse landscape changes. Few studies have investigated for ecosystem functions and/or services delayed responses or delayed ecological gains after landscape structure improvements such as increase in habitat amount. We verified that some progress occurred in recent years. We identified the use of three new methodological approaches to empirically evaluate the existence of delayed ecological responses, and we also verified an increase in our understanding about the mechanisms that explain delayed ecological responses. As expected, we observed high levels of support for delayed ecological responses in landscapes that have undergone recent changes and for habitat specialist species. Other hypotheses have been less frequently tested. Some of them have a low level of support (no clear relationship between strength of landscape change and delayed responses), while others have a good level of support but still need more evidences (relationships between species longevity and dispersal capability with delayed responses).

Summary Our understanding about delayed ecological responses to landscape change is still at an early stage and seems to be increasing slowly while human-altered landscapes are increasing rapidly worldwide. There are still important knowledge gaps to be filled. Beyond providing better support for some explanatory hypotheses, we still need to explore (1) ecosystem functions and services delayed responses to landscape change, and (2) the delayed ecological gains after positive landscape changes.

Keywords Colonization credit · Ecosystem function debt · Ecosystem service debt · Extinction debt · Immigration credit · Species credit

Introduction

Accumulating evidence suggests that biodiversity losses and gains can occur with a substantial delay following landscape change [e.g., 1, 2]. Recently, some studies have also shown that such temporal lags in biodiversity responses may produce a lag in biodiversity-dependent ecosystem functions and/or services responses to landscape change [e.g., 3, 4]. It is thus crucial to assess the extent of these delays and understand their main drivers to evaluate the real ecological consequences of landscape change. Understanding delayed ecological responses is also important to guide and evaluate actions to effectively

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prevent extinctions or ensure the recovery of species and/or ecosystem functions and services.

The pioneer studies about the delayed effects of human-induced changes in landscapes in the late 1990s and early 2000s have largely focused on species local extinctions, more specifically on "extinction debts," i.e., the number of extant species (or populations for single species) that are expected to eventually become extinct due to past adverse environmental changes [2]. Extinction debts have been empirically evaluated using five main methodological approaches (see Box 1 in [2]) and accumulated evidence suggests at least five explanatory hypotheses. The first hypothesis considers that extinction debts should decline through time following landscape change (Fig. 1a). Therefore, extinction debts are most likely to exist in landscapes where an adverse change occurred recently [e.g., 5]. This hypothesis could be considered as an obvious implication or assumption of any delayed response. The second hypothesis considers that extinction debts are more likely to occur at landscapes that have undergone an adverse modification with intermediate intensity (Fig. 1b [6]). This nonlinear expectation arises because landscapes with intermediate modifications may support many species that persist for long time periods close to their species-specific extinction thresholds [7]. By contrast, a severely impacted landscape is more likely to result in immediate extinctions, and in a slightly transformed landscape many species are able to persist above their extinction threshold with little adverse impact. Finally, the three remaining hypotheses consider that extinction debts should vary depending on life history traits of the species, particularly their habitat specificity (Fig. 1c), longevity (Fig. 1d), and dispersal capability (Fig. 1e). Habitat specialist species are predicted to show delayed extinction when compared to habitat generalist species, as generalists are not expected to be restricted to habitat patches and should be more resilient to landscape changes [e.g., [8]]. Short-lived species are predicted to disappear faster than long-lived species since the former will have passed through many generations after a landscape change while the latter will have spent fewer generations near a critical extinction threshold and might persist longer [9]. Sessile or dispersal-limited species are also predicted to show delayed responses to landscape change while mobile species with good capabilities for dispersal are expected to show faster responses [8].

Although those hypotheses were raised for extinction debts, they might also apply to the inverse process of species gains after beneficial landscape modifications, such as increase in habitat amount or habitat restoration [10]. Those gains are mentioned with different terms in the literature, usually used as synonyms or with similar meanings: species credit, colonization credit and immigration credit (see section "Key Concepts on Delayed Ecological Responses to Landscape Change"). Such gains should also depend on time since modification and on the landscape level of modification. The chances for colonization are probably lower when a beneficial landscape modification has occurred recently [10] as successful colonization might occur after several generations of population growth. Furthermore, it is also well known that intermediate landscape conditions are more effective for restoration actions, as the recovery of too degraded landscapes is slower, and well-preserved landscapes usually do not need any restoration initiative [11]. In other words, it is expected that the existence of credits is most likely in landscapes that

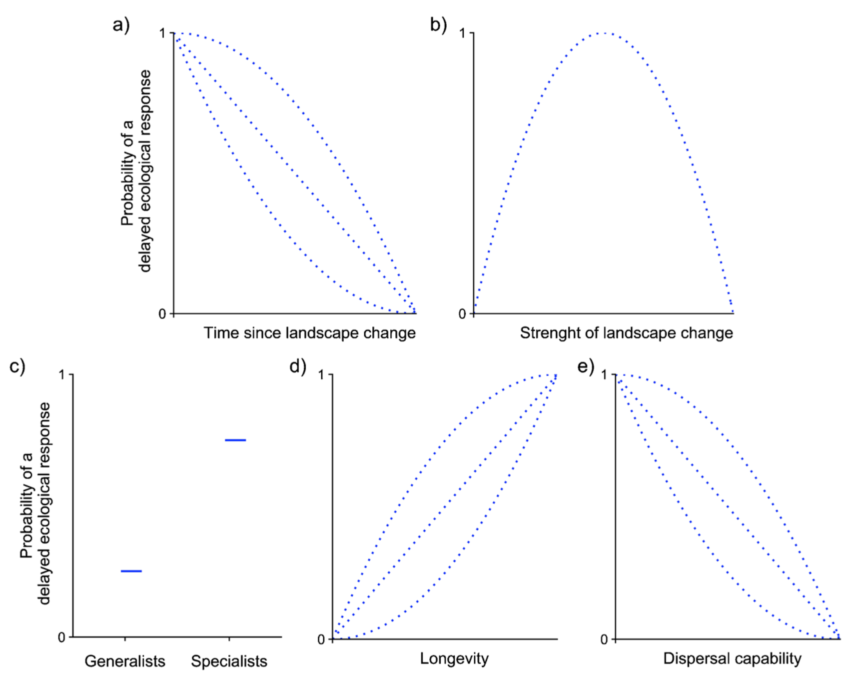


Fig. 1 Hypotheses about the probability of a delayed ecological response after landscape change depending on: **a** time since landscape change (hypothesis 1), **b** the strength of landscape change (hypothesis 2), and species traits such as **c** habitat specificity (hypothesis 3), **d** longevity (hypothesis 4), and **e** dispersal capability (hypothesis 5)

have recently undergone an intermediate positive modification [10]. Habitat generalists or species with high dispersal capacities are not expected to respond to an increase in habitat amount or habitat restoration since they are not restricted to habitat patches, so time delayed responses are only expected for habitat specialist species or species with more restricted dispersal ability. As a successful colonization might occur after several generations of population growth, delayed colonization should be more likely to occur for long-lived species than for short-lived species. Thus, both extinction and colonization processes might depend on time following landscape change, strength of the landscape change and species life history traits, and as a consequence, the existence of ecosystem function and service debts and credits might also depend on those same drivers.

Despite the existence since 2009 of those hypotheses to explain ecological responses' delays to landscape modifications, mainly from the seminal work of Kuussaari and colleagues, we do not have until now an extensive compilation of evidences that support (or not) those hypotheses. Here, we first revisited the key concepts used to refer to delayed ecological responses to landscape change, and then reviewed the literature of temporal lag in ecological responses to landscape change presenting a "state of the art" of the research on this topic. We summarize which approaches have been used to evaluate the existence of delays, the empirical evidences of those delays, and identify when delayed ecological responses to landscape change are likely to occur through the studies that have tested the five main explanatory hypotheses of delayed responses. Finally, we provide directions for future research as a way to improve our knowledge about temporal lag in ecological responses to landscape change.

Key Concepts on Delayed Ecological Responses to Landscape Change

The term *extinction debt* was coined by Tilman et al. [12] to describe the time-delayed deterministic loss of species, from the best to the poorest competitors, following habitat destruction. However, in subsequent literature, extinction debt has been considered a phenomenon that is not dependent on the competitive interactions assumed by Tilman et al. [12] and today a more widespread definition considers that an extinction debt is the number of extant species (or populations for single species) that are expected to eventually become extinct due to past adverse environmental changes [2] (Table 1). Extinction debt is paid during the relaxation time [13] as extinctions are gradually realized.

In 2000, Hanski highlighted that the only remedy to avert extinction debt payment was to improve environmental conditions to enhance its capacity to retain biodiversity. But Hanski [1] considered that, just as in the case of extinction debt, it will take some time before the positive effects become evident and suggested that the number of species that will eventually benefit from these measures should be called *species credit*. According to Hanski, species credit consists of (i) species that have already gone extinct from a landscape and may return (species credit in the narrow sense), or (ii) species that are declining towards extinction and may recover by rescue-effect, becoming more abundant and thus less threatened (in this case, the species credit is avoiding extinction debt, and thus no delayed extinction will actually occur) [1].

Two years later, Nagelkerke et al. [14] proposed the term *colonization credit* to refer to "the slow reappearance of species after landscape restoration," that is, the first element of Hanski's species credit. However, in 2010, Cristofoli et al. [15] used the same term, i.e., colonization credit, to refer to "the number of species yet to colonize a patch, following landscape changes, until the patch reaches the equilibrium between species richness and patch spatial properties." Cristofoli et al.'s colonization credit is subtly different from the one of Nagelkerke et al. (and, consequently, from Hanski's species credit first element) as it does not consider necessarily species that exist previously in the patch and were extinct, i.e., both recolonization and colonization are possible. More recently, Jackson & Sax [16] introduced the term *immigration credit* which, according to them, completely differs from Hanski's species credit as it mostly refers to generalist species colonizing new low quality habitat patches, while Hanski's species credit refers to doomed species that are likely to benefit from a positive environmental change by recolonization (first element of Hanski's species credit) or immigration (second element of Hanski's species credit). We understand that Jackson & Sax's immigration credit is the same phenomenon described by Cristofoli et al. [15] as colonization credit.

Finally, Essl et al. [17] introduced the term *invasion debt* to refer to the future realization of invasions as it can take a considerable amount of time for invasive species to establish after the date of first introduction. We understand that invasion debt sensu Essl et al. [17] can be considered the number of invasive species that are expected to eventually become part of the species pool due to past non-native species introduction and, as suggested by Vilà & Ibáñez [18], *invasion credit* seems to be a better term to refer to this expected gain of invasive species.

Those different definitions of delayed species gain to landscape change can potentially generate confusions. To facilitate communication and avoid misunderstandings, we propose a unified vocabulary distinguishing three credit situations after landscape change (Table 1). Firstly, the credit refers to species that has gone locally extinct and can reappear. Secondly, the credit refers to threatened species that has not gone extinct and can be rescued by immigrants. Thirdly, the credit refers to the colonization by new species, including invasive species. In the first case, we suggest to use the term *recolonization credit*,

Table 1 Proposed terminology to refer to delayed ecological responses to landscape change. For more detailed information, see section "Key Concepts on Delayed Ecological Responses to Landscape Change"

Delayed ecological response	Description
Extinction debt	Number of extant species (or populations for single species) that are expected to become extinct due to adverse landscape changes.
Species credit	Number of species that will benefit from landscape restoration. Species credit refers to recolonization credit, immigration credit and colonization credit, independently or simultaneously.
Recolonization credit	Number of species that has gone locally extinct and are expected to recolonize due to landscape restoration.
Immigration credit	Number of threatened species that are declining towards extinction and may recover by rescue-effect due to landscape restoration.
Colonization credit	Number of new species yet to colonize a focal habitat due to landscape restoration.
Invasion credit	Number of new invasive species yet to colonize a focal habitat due to landscape restoration. Invasion credit is a specific type of colonization credit.
Ecosystem function debt	Number of ecosystem functions that are expected to become extinct due to adverse landscape changes.
Ecosystem function credit	Number of ecosystem functions yet to be added and/or restored after landscape restoration.
Ecosystem service debt	Number of ecosystem services that are expected to become extinct due to adverse landscape changes.
Ecosystem service credit	Number of ecosystem services yet to be added and/or restored after landscape restoration.

while in the second and third cases we propose to use *immigration credit* and *colonization credit*, respectively. The invasion credit sensu Vilà & Ibáñez [18] is thus understood here as a type of colonization credit. Finally, the term *species credit* should be used as an umbrella term, to refer to any of those situations independently or simultaneously.

As ecosystem functions and services often directly depend on biodiversity [19], extinction debt and species credit after an environmental change will likely create a debt or a credit of ecosystem functions and/or services. More recently, some studies have shown the existence of delayed changes in ecosystem functions and/or services after an environmental change [3, 4, 20–22].

In 2002, Gonzalez & Chaneton [23] introduced the term *functioning debt* to refer to "a delayed alteration in ecosystem attributes driven by the decline of species persisting in remnant patches". Later, Isbell et al. [3] and Haddad et al. [21] used the term *ecosystem functioning debt* and *ecosystem function debt*, respectively, to refer to the same phenomenon highlighted previously by Gonzalez & Chaneton [23]. Additionally, Valiente-Banuet et al. [4] applied the concept of extinction debt of species to ecological interactions and defined the *extinction debt of ecological interactions* as "any future interaction loss that has to be realized due to a current or past environmental disturbance." This concept refers thus to "interactions 'committed to extinction' owing to lags between habitat loss and the complete extinction of the interaction." We understand that Valiente-Banuet et al.'s extinction debt of ecological interactions is part of the phenomenon described by Gonzalez & Chaneton [23], since ecological interactions are important for ecosystem functioning. We suggest the use of the term *ecosystem function debt* for any ecosystem function that is expected to eventually become extinct due to past adverse environmental changes (Table 1).

The other side of the coin would be an *ecosystem function credit*, a term that could be used to refer to any ecosystem function that is expected to be added and/or restored after immigrations and/or recolonizations (Table 1). In 2017, Genes et al. [22] introduced the term *credit of ecological interactions* to refer to the number of interactions that can be restored in a focal area by species recolonization (in their case, by reintroduction), which is a counterpart of Valiente-Banuet et al.'s extinction debt of ecological interactions. However, they have not considered that some ecological interactions might not be functional anymore not because a species is missing but just because it is present in low abundance. So ecological interactions can also be restored by immigrant arrivals (e.g., rescue-effect, population reinforcement). From our point of view, Genes et al.'s credit of ecological interactions is a type of an ecosystem function credit.

As a result of the delayed effects of species loss and gain on ecosystem functioning, there could be an *ecosystem service debt* [3] and an *ecosystem service credit*. Ecosystem service debt is a gradual loss of benefits that people obtain from natural ecosystems, as defined by Isbell et al. [3]. Ecosystem service credit, its counterpart, has never been mentioned in the literature, but we define it as the gradual gain of benefits that people could obtain from natural ecosystems (Table 1).

Systematic Mapping of the Literature

To set up a "state of the art" of the research related to delayed ecological responses to landscape changes, we performed a systematic mapping of the literature [24]. We surveyed scientific articles from the Thomson Institute for Scientific Information database (ISI; http://www.portal.isiknowledge.com/), covering the period of January 2009 to August 2017. We chose this period to evaluate the state of the knowledge after the seminal article of Kuussaari et al. [2] that reviewed the extinction debt topic. We used the keywords “extinction debt” OR “species credit” OR “colonization credit” OR “colonisation credit” OR “immigration credit” OR “ecosystem function debt” OR “ecosystem service debt” OR “ecosystem function credit” OR “ecosystem service credit” OR “time lag*” in title, abstract, and keyword fields. We limited the search for scientific articles (avoiding gray literature, e.g., technical reports) not only due to access facility but also to consider only consolidated results that had been peer-reviewed.

To eliminate unrelated articles unwittingly included in the reference list after the survey, we defined a sequence of two filtering procedures. First, we read the titles, keywords, and abstracts of each article in order to identify and exclude publications that were not related to time lag in ecological responses to landscape change. In the second filtering, we checked the entire content of all remaining articles, excluding irrelevant and non-empirical publications while simultaneously recording the ecological concepts used by the authors and also classifying the selected articles into a set of predefined categories and its respective levels (Table 2). Each selected article was classified with respect to: characteristics of the publication (journal and year), study area (ecosystem, drivers of landscape change, temporal window of landscape change), study object (taxa, level of organization or ecosystem function/service, ecological metric), methodological approach, delayed ecological responses (type of response: debt, credit and none; magnitude and delay time), and hypothesis evaluated.

In the classification process, each article can contribute to more than one result if it has investigated the existence of delayed ecological responses for different taxa or study areas, for example. Thus, the number of responses for each category is sometimes higher than the number of articles. To assure consistency in all steps of the classification described above, each article was assessed by the two reviewers (PKL and MSL) at least once. This task intrinsically had some level of subjectivity, mainly when the information sought was not explicit in the article, for example in the categories of habitat specificity, delayed ecological response, delay magnitude and time, and ecological hypothesis. When there were doubts or a lack of concurrence between reviewer’s classification, articles were discussed by both to reach a consensus. All information extracted from the selected articles is provided in Table S1.

From a total of 489 articles matching our search term, only 96 (~ 20%) were selected as studies related to delayed ecological responses to landscape change. The number of articles per year increased with time and varied between five in 2009 to 16 in 2016 (Fig. 2a). These articles were published in 45 different journals with very different scopes, ranging from very broad ecological and conservation journals (e.g., Biological Conservation, Ecography, Landscape Ecology) to taxa related journals (e.g., Journal of Vegetation Science, Plant Ecology, Insect Conservation and Diversity), but many journals (n = 25; 46%) had only one article selected (Table S2). This growing tendency and more diffuse pattern of publication may indicate this theme is attracting an increasing attention from a broad range of researchers, studying different ecological systems and biological levels of organization.

Almost one third of the articles report studies that have been realized in grasslands ($n = 32$), followed by temperate ($n = 25$; 26%) and tropical forests ($n = 12$; 12%). Other ecosystems covered less than 10% of the studies (Fig. S1). The most common driver of landscape change was habitat loss or fragmentation (70%) followed by habitat gain or an increase in habitat connectivity (14%), habitat degradation (6%), and restoration (4%) (Fig. 2a). As a consequence, delays of losses, such as extinction debt, were much more studied than the ones related with gains. However, there is a growing trend to study delays related to habitat gain or restoration (Fig. 2a). Studies focused essentially on biodiversity ($n = 91$), but there is a recent initiative to go beyond that, focusing on delayed responses of ecosystem functions and services ($n = 5$). Almost half of the articles studied plants ($n = 53$; 49%), followed by invertebrates ($n = 18$; 17%) and vertebrates ($n = 16$; 15%; Fig. S2). Species richness was, by far, the most used ecological metric covering almost half of the results ($n = 55$, 47%). Articles reporting studies with populations ($n = 16$, 15%) were more common in plants ($n = 7$; 6%) and vertebrates ($n = 6$, 6%; Fig. S2).

Empirical Evaluation of Delayed Ecological Responses to Landscape Change

Since 2009, delayed ecological responses to landscape change were empirically evaluated in the literature using seven different approaches. The four most frequently used approaches were already described as ways to empirically evaluate extinction debt by Kuussaari et al. [2], but three other new approaches appeared more recently. Each of those approaches has different requirements and abilities to estimate the existence, duration and magnitude of delayed ecological responses as summarized in Table 3. The most frequently used methodological approach (*past* vs. *current landscape information*; $n = 56$, 55%) assumes the existence of delayed ecological responses to landscape change if current ecological response is better explained by past than by current landscape information. The methodological approach that monitors the ecological response to landscape change through time (*time series data on ecological response*) and the one that compares current ecological responses at stable and unstable landscapes (*stable* vs. *unstable landscapes*) were used almost equally ($n = 19$, 19%; $n = 16$, 16%, respectively). Delayed ecological responses to landscape change was also empirically evaluated using a known relationship between past habitat

Table 2 Systematic mapping categories and their respective levels and definitions used to extract information from each paper analyzed

Category	Description
Journal	Journal where the article was published
Year	Year of publication
Ecosystem	Categories for ecosystem types, following IPBES (https://www.ipbes.net/glossary/units-analysis)
Tropical forests	Tropical and subtropical, dry and humid forests
Temperate forests	Temperate, boreal forests and woodlands
Heathlands, scrub, and tundra	For example, Mediterranean scrubland, tundra
Savannas and grasslands	For example, Xeric grasslands, alpine meadows
Drylands and deserts	Arid and semi-arid ecosystems
Wetlands	For example, Peatlands, mires, bogs
Cultivated areas	For example, Cropping, aquaculture, intensive livestock, farming
Inland surface waters	Water bodies such as rivers, lakes and estuaries
Coastal	Coastal and near shore marine or inshore ecosystems
Marine	Including deep water and offshore ecosystems
Urban/semi-urban	Cities and areas under urban influence
Multi-ecosystems	More than one ecosystem evaluated
Landscape change driver	Human direct drivers of landscape change that could have led to a delayed ecological responses (modified from Essl et al. 2015)
Negative drivers	
Habitat loss/fragmentation	Habitat loss or increase in the fragmentation level of the remaining habitat
Habitat degradation	Pollution, selective logging or any other practice decreasing habitat quality but not its amount
Change in disturbance regime and biophysical conditions	Anthropogenic changes in natural disturbance frequencies and intensities or in cycles and stocks of matter and energy not directly related to habitat loss or degradation
Overharvesting	Selective removal of species (e.g. hunting, collecting wild plants)
Invasions	Anthropogenic translocation, introduction and spread of alien species
Positive drivers	
Habitat gain/connectivity	Active or passive increase of habitat amount, possibly increasing connectivity as well
Habitat restoration	Active or passive increase in habitat quality
Changes in disturbance regime and biophysical conditions	Cessation of anthropogenic changes in natural disturbance frequencies and intensities or in cycles and stocks of matter and energy not directly related to habitat loss or degradation
Strength of landscape change	The strength (in percentage of change) of landscape change that could have led to a delayed ecological response
Temporal window	Temporal window (in years) considered to evaluate landscape change and its ecological impacts
Level of organization	Ecological level of organization of the operational response variable considered in the study
Population	One or more (meta)populations of a single species
Community	One or more (meta)populations of more than one species
Ecosystem	Functions and/or services evaluated in one or more ecosystems
Categories for taxa-oriented studies	
Taxa	
Plants	Populations and communities of lower and/or higher plants
Fungi/Lichens	Populations and communities of fungi or lichens
Invertebrates	Populations and communities of invertebrates
Vertebrates	Populations and communities of non-human vertebrates
Multi-taxa	More than one of the taxa described above
Habitat specificity	Indicate if the studied taxa is a habitat specialist or generalist
Generalist	Species that are not restricted to certain habitat types
Specialist	Species restricted to certain habitat types.
Longevity	Taxa longevity reported in the article, either in years or as an index for comparison with other taxa in the same study
Categories for ecosystem studies	
Ecosystem function	Ecosystem function studied (e.g., ecological interactions)
Ecosystem service	Ecosystem services studied (e.g., primary production, nutrient cycle)
Ecological metric	Metric used to describe community diversity, population size or ecosystem function/service
Methodological approach	Methodological approaches used to empirically evaluate delayed ecological responses to landscape change (see Table 3 for definitions)
Delayed response	Which delayed ecological response was identified?
None	No time lag in ecological responses to landscape change was detected
Debt	Delayed loss of species (extinction debt) or ecosystem functions and services (ecosystem function or service debt)
Credit	Delayed gain of species (species credit) or ecosystem functions and services (ecosystem function or service credit)
Delay magnitude	The magnitude of the delayed ecological response identified: the number or percentage of species, ecosystem functions or services expected to be extinct (debt size) or to be gained (credit)
Delay time	Depending on the methodological approach it can be the time (in years) for debt payment or for credit receipt, or the time that the study detected the lag
Hypotheses evaluated	Which hypotheses about the probability of delayed ecological responses were tested by the studies? (Fig. 1) Possible answers: yes for corroborated hypothesis; no, if not corroborated; and not tested
Hypothesis 1	The probability of a delayed ecological response decreases with time elapsed since landscape change (this hypothesis could be considered as an assumption or a mandatory implication of any delayed response)
Hypothesis 2	The probability of a delayed ecological response has a non-linear relationship with the strength of the landscape change
Hypothesis 3	The probability of a delayed ecological response is larger for habitat specialist species than generalists
Hypothesis 4	The probability of a delayed ecological response increases with longevity/generation time
Hypothesis 5	The probability of a delayed ecological response is larger for sessile species or species with limited dispersal than for mobile species or species with good dispersal capabilities

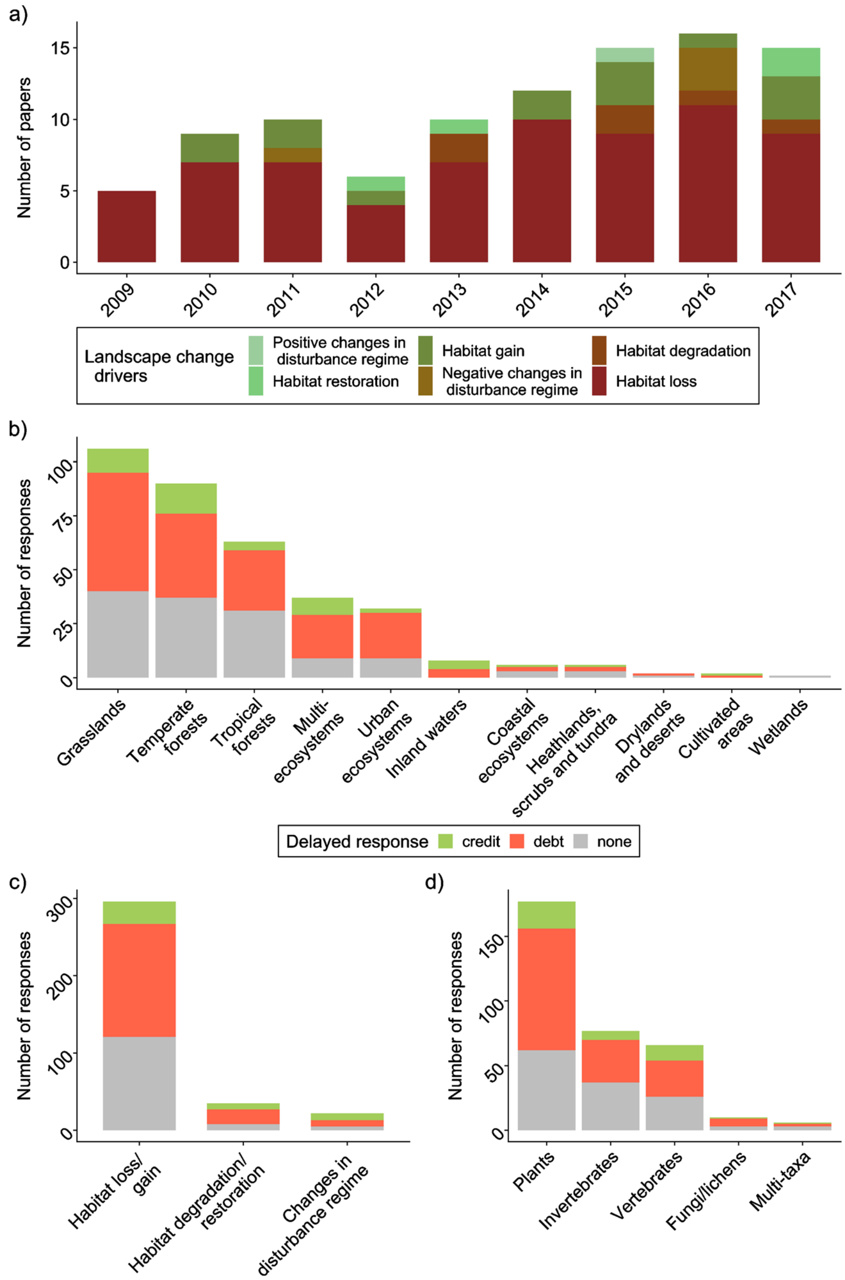


Fig. 2 Number of papers published per year between January 2009 and August 2017 investigating temporal lag in ecological responses to different drivers of landscape change (**a**). Number of delayed responses for each ecosystem (**b**), main landscape change driver (**c**), and taxa (**d**) reported

characteristics and past ecological pattern/process to calculate the predicted ecological response for current habitat characteristics and compare it to the actual observed ecological response (*past and current relationship between ecological response and habitat characteristics*; $n = 6$, 6%). Another methodological approach is to compare observed species distribution with the expected distribution using habitat suitability models, and then assuming a delayed ecological response when those distributions are different (*observed* vs. *expected species distribution*; $n = 2$, 2%). Other authors consider threatened species as an unpaid extinction debt (*species conservation status*; $n = 1$, 2%). Finally, another methodological approach considers how species loss or gain alters ecosystem functions and services (*biodiversity and ecosystem functioning and services relationships*; $n = 1$, 2%; Table 3).

Four studies have used three new methodological approaches that are different from the five presented by Kuussaari et al. [2]. In the first new methodological approach, Procter et al. [36] and Gijbels et al. [37] compared observed species distribution with expected distribution as determined by measures of habitat suitability and assumed that missing species from habitats deemed suitable represented a credit (*observed* vs. *expected species distribution* methodological approach, Table 3). We understand that through this methodological approach one can also observe species occurring in

Table 3 Methodological approaches used to empirically evaluate delayed ecological responses to landscape change between January 2009 and August 2017. Type of data: data required; Indicative of delayed ecological response: result that indicate the existence of a delayed ecological response. Delay time estimative: how the delay time is estimated. Delay magnitude estimative: how the delay magnitude is estimated. Example: studies that have investigated delayed ecological response by each methodological approach

Type of data	Indicative of delayed ecological response	Delay time estimative	Delay magnitude estimative	Example
A. Past vs. current landscape information ($n = 56$, 55%)				
Current ecological pattern/process Past and/or current landscape information	Past landscape information is (still) important in explaining current ecological pattern/process	Time interval between past and current landscape information is an indicative of time lag	Difference between the ecological response predicted by past landscape information and the one predicted only by current landscape information	[10, 17, 25–29]
B. Stable vs. unstable landscapes ($n = 16$, 16%)				
Current ecological pattern/process at stable and unstable landscapes	When a significant difference exist between current ecological pattern/process at stable and unstable landscapes	Time since unstable landscape has being modified	Difference between current ecological pattern/process at stable and unstable landscapes	[15, 30]
C. Time series data on ecological response ($n = 19$, 19%)				
Ecological pattern/process through time after landscape change	Existence of a considerable time interval until the ecological response reaches an equilibrium or an expected value	Time since landscape change until the equilibrium or the expected value	Differences between observed ecological pattern/process before landscape change and equilibrium or expected value	[22, 31–33]
D. Past and current relationship between ecological response and habitat characteristics ($n = 6$, 6%)				
Past and current ecological pattern/process Past and current habitat characteristics	When current observed ecological response differ from current predicted ecological response based on the known relationship between past habitat characteristics and ecological response	Can be estimated assuming an exponential change in the ecological pattern/process through time (Diamond 1972)	Difference between current observed and predicted ecological response	[34, 35]
E. Observed vs. expected species distribution ($n = 2$, 2%)				
Current observed and expected species distribution under habitat suitability	Suitable habitats unoccupied or habitats that are unsuitable but occupied	Time since landscape change	Differences between current observed and expected species occurrences	[36, 37]
F. Species conservation status ($n = 1$, 1%)				
Conservation status of each species in the community	When there are threatened species in the community, i.e. it is assumed that threatened species are an extinction debt	Time since landscape change	Number of threatened species still present in the community	[38]
G. Biodiversity and ecosystem functioning and services relationships ($n = 1$, 1%)				
Biodiversity and ecosystem functioning relationships Ecosystem functioning and services relationships	When there is a delay in biodiversity responses, there is a delay for related functions and services	Estimated as the time it takes for delayed biodiversity responses to affect ecosystem functioning and services provision	Difference between current observed functions or services and their predicted potential value	[3]

habitats deemed unsuitable and that these species can be considered a debt (Table 3). In the second new approach, Niissalo et al. [38] consider threatened species (i.e. species occurring in a single location or in extremely small populations) as an unpaid extinction debt (*species conservation status* methodological approach, Table 3). This approach seems to be supported by *past and current relationship between ecological response and habitat characteristics* that have predicted extinction debts in a magnitude similar to the number of species present in Red-Lists [e.g., 39, 40]. Finally, Isbell et al. [3] developed a third new approach, which quantifies biodiversity-dependent ecosystem service debts after habitat destruction (*biodiversity and ecosystem functioning and services relationships*, Table 3).

As different methodological approaches can lead to different results, it has been recommended to compare the performance of different methodological approaches to identify the existence of delayed ecological responses and/or estimate its magnitude [2]. Despite the existence of this recommendation for almost 10 years, only four studies used more than one methodological approach to investigate extinction debt [30, 34, 41, 42] but just one [30] was, in fact, interested in comparing results obtained by the different methodological approaches. These four studies have detected the existence of an extinction debt with the two different methods used by each, i.e., *past* vs. *current landscape information* and *stable* vs. *unstable landscapes* [30, 41, 42] and *past* vs. *current landscape information* and *past and current relationship between ecological response and habitat characteristics* [34]. However, only one of those studies [30] has estimated the extinction debt magnitude using the two different methodological approaches and found that both methods estimated a similar value. Therefore, it seems that there is congruence between different methodological approaches in identifying the existence of an extinction debt, but no conclusive data for their congruence in estimating the magnitude of this debt. It is thus important that future research evaluates the performance of different methodological approaches in identifying and, particularly, estimating the magnitude of delayed ecological responses.

An interesting methodological advance in the field was the mapping of extinction debt magnitudes [34, 42, 43]. Those maps infer extinction debts for each habitat patch as the difference between current (or predicted) species richness and expected species richness. This spatial representation of extinction debt magnitudes can be a useful tool for identifying areas that need urgent actions, and thus for setting restoration priorities for rescuing many living-dead species and preventing future biodiversity losses [44]. This same reasoning can be extended for debts in ecosystems functions and services or even for credits as a way to accelerate the gain of species and ecosystem functions and services.

Empirical Evidence of Delayed Ecological Responses to Landscape Change

From a total of 353 results from the 96 selected studies, 219 (62%) have found evidence of temporal lag in ecological responses to landscape change: 173 (79%) have found evidence for debt (163 extinction debt, one ecosystem function debt and nine ecosystem service debt) and 46 (21%) for credit (42 for species credit, one for ecosystem function credit and three for ecosystem service credit). Debts were mainly detected in grasslands (32%), after habitat loss (84%) and for plants (54%). Credits were mainly detected in temperate forests (30%), after habitat gain (63%) and for plants (46%) (Fig. 2b–d).

Studies for which the delay magnitude was reported as a percentage of species expected to be extinct (debt size) or to be gained (credit size), we found that extinction debt magnitude is larger for invertebrates than for plants and is highly variable for vertebrates (Fig. 3a). The size of the extinction debt also seems to vary according to the methodological approach used: the higher values were obtained by *past and current relationship between ecological response and habitat characteristics*, intermediate and highly variable values by *time series data on ecological response* and lower values by *past* vs. *current landscape information* and *stable* vs. *unstable landscapes* (Fig. 3b). On the other hand, for species credit magnitude *stable* vs. *unstable landscapes* and *time series data on ecological response* indicate similar values (Fig. 3b).

For the studies where the time delay was reported, we found a large variation among taxa. Extinction of fungi/lichens takes longer to be paid (e.g., > 100 years) than extinction debt of plants, invertebrates and vertebrates (delays around 20–50 years), with the lowest delays observed for vertebrate species (Fig. 3c). Species credit of invertebrates and vertebrates are realized faster than species credit of plants and, in general, time for species credit to be realized is shorter than time for extinction debt payment (Fig. 3c, d). The length of time for species credit to be realized do not vary too much when estimated by different methodological approaches; however, time for extinction debt payment is clearly longer when estimated by *past and current relationship between ecological response and habitat characteristics* (Fig. 3d).

When Are Delayed Ecological Responses to Landscape Change Likely to Occur?

From the 96 selected studies, 40 have tested at least one explanatory hypothesis for delayed ecological responses resulting in 62 hypotheses testings. All tests considered delayed biodiversity responses to landscape change; none considered delayed responses of ecosystem functions and services. Most hypothesis testings were done considering

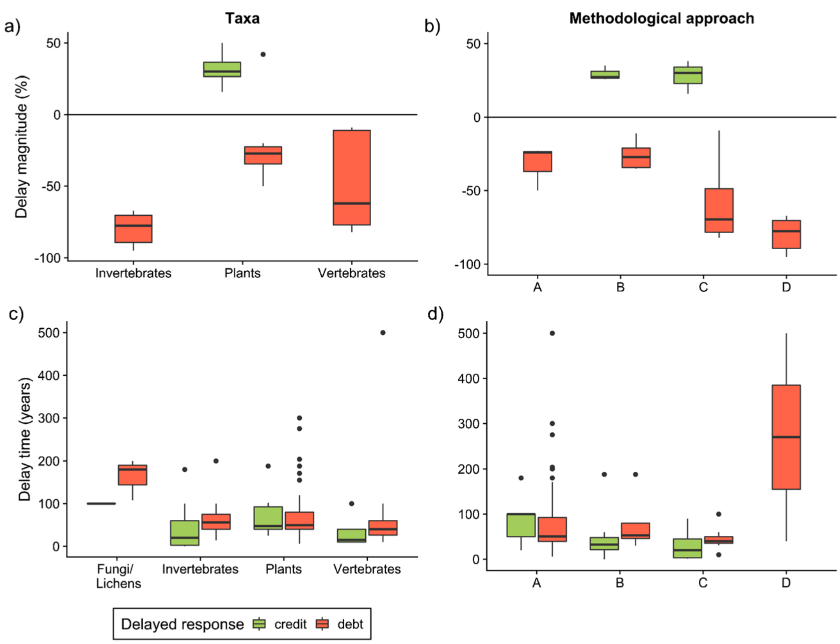


Fig. 3 Upper panel: Delay magnitude in percentage of change in the number of species expected to be extinct (red boxplots, negative percentages) or to be gained (green boxplots, positive percentages) for **a** different taxa and **b** methodological approaches ($N = 31$). Lower panel: Delay time in years for a debt to be paid or for a credit to be received for **c** different taxa and **d** methodological approaches ($N = 114$). Data only for taxa-oriented studies. Only the methodological approaches with more than one result are considered: A, past vs. current landscape information; B, stable vs. unstable landscapes; C, time series data on ecological response; D, past and current relationship between ecological response and habitat characteristics. See Table 3 for methodological approaches description

extinction debt ($n = 49$) and just a few considered species credits ($n = 13$).

Extinction debts, in fact, declined through time following landscape change (number of tests = 14, 79% of support) and there was an indicative that the same may also apply to species credit ($n = 2$, 50%, Fig. 4). The effects of the strength of the landscape change on the probability of a delayed ecological responses to landscape change was tested very few times ($n = 4$) and only one test gave support to this hypothesis (Fig. 4).

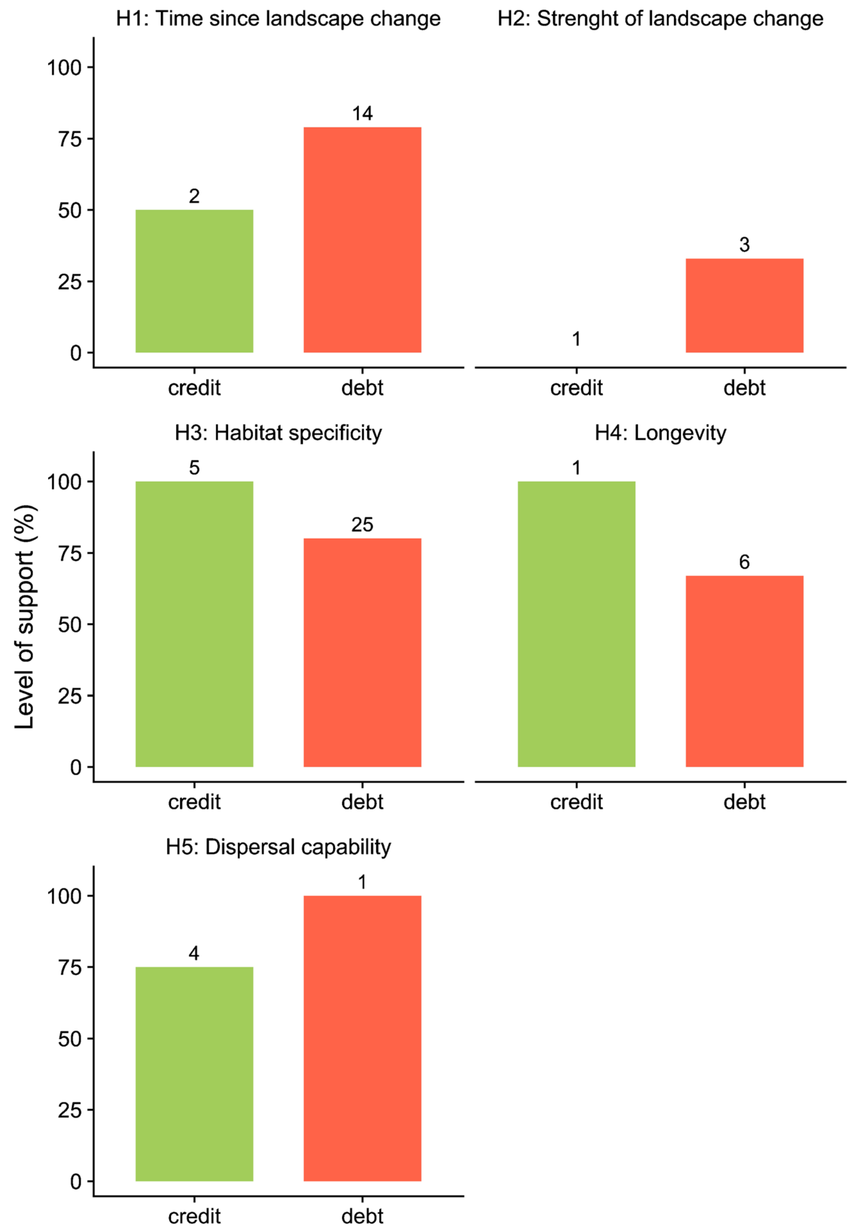
Extinction debt is definitely more likely for habitat specialist species than generalists ($n = 25$, 80%), and the probability of species credit is also larger for specialists ($n = 5$, 100%, Fig. 4). Although the hypothesis that delayed ecological responses may be more likely for long-lived than short-lived species was tested few times, extinction debt was indeed more likely to occur for long-lived species ($n = 6$, 67%) and a test suggested that species credit is also more probable for long-lived species ($n = 1$, 100%, Fig. 4). The hypothesis considering that sessile and/or dispersal-limited species are more likely to show delayed responses to landscape change than mobile species with good capabilities for dispersal was tested only five times, but there is a high level of support for it (Fig. 4).

Priorities for Future Research

Despite the progress that has been made over the past 9 years, our review highlight important gaps in our understanding about delayed ecological responses that provide directions for future research. First, our knowledge is mostly restricted to biodiversity responses. Given the increasing need to understand the effects of biodiversity losses on the functioning of ecosystems and their effects on human well-being, we also need to consider delayed responses of ecosystem functions and services. Depending on the degree of functional redundancy in the community and the role that endangered species have, we can raise different hypotheses about the delays in functions and services. If the degree of redundancy is high and the function of the threatened species can be replaced by other species, then the effects of landscape changes on functions and services could be low and postponed for a long time. On the other hand, in the opposite situation (low redundancy, loss of key species), effects on functions and services should be more intense and immediate. Testing those kinds of hypotheses is an important challenge to be explored in the future.

Second, we still poorly understand how landscape and species traits influence the magnitude and duration of ecological delays. There were only 62 hypothesis testings in the last 9 years. Regarding landscape drivers, there is a weak support for the hypothesis linking the strength of landscape change to delayed responses. Is there an intermediate level of disturbance promoting delays with higher magnitude or duration? In this context, how are habitat fragmentation/connectivity, land use intensity, matrix permeability, and landscape heterogeneity related to delays? Regarding species traits, the number of studies investigating the effects of longevity and dispersal capability on delayed ecological responses is still limited. Furthermore, the majority of the studies published since 2009 have only investigated how

Fig. 4 Level of support for debts or credits is the percentage of tests supporting each of the five hypotheses in relation to the total number of tests (numbers above each bar)



group of species differing in a single-trait differ in their response to landscape changes. This approach ignores that there are interactions or correlations among traits. For example, dispersal ability is often (negatively or positively) correlated with reproductive capacity, and reproductive capacity is strongly related to response to landscape change. Sometimes, the correlated and not the measured trait may be the driver. To derive a general understanding of the underlying mechanisms in building delayed responses, it is essential to focus on combinations of traits (i.e., functional groups) and their effects on species persistence after landscape change, as suggested by Koyanagi et al. [45].

Third, most studies investigated temporal lag in ecological responses to adverse landscape changes ($n = 77$, 80%), and only a few explored delays after positive landscape changes ($n = 17$, 18%) or both ($n = 2$). Given the urgent need to reverse the effects of negative landscape changes, the understanding of delays after positive changes is necessary. This "delay knowledge" can help us to act in a more effective way in three complementary manners: (i) by reducing expectations around immediate improvements of restoration actions; (ii) by identifying favorable landscapes or conditions for a faster gain of species and ecosystem functions and services; and also (iii) by identifying areas where losses should occur more quickly, and thus where actions should be prioritized to avoid further losses [44]. For example, based on hypothesis 2 (Fig. 1b), delays are not expected when landscape connectivity is too high or low: landscapes with very high connectivity should not be at risk of species loss (low local risk of extinction, high recolonization potential), and landscapes with very low connectivity should present immediate extinctions (high local risk of extinction, low recolonization potential). Given these circumstances, we would expect that the ideal conditions for landscape restoration are those with intermediate levels of connectivity [11].

Fourth, there are clear taxonomic and geographical biases in the study of temporal lag in ecological responses to landscape change, which hinders the generalization of observed patterns. Particularly, most studies were realized with plants, in grasslands or temperate forests, and after habitat loss and fragmentation processes. This pattern is certainly a reflection of the concentration of the research groups interested in this topic at North America and Europe. We believe that more studies on tropical forests and on urban/semi-urban ecosystems are necessary. Tropical forests contain an untold diversity of species, for which it is important to know how much time we still have to avert extinctions and ecosystem functions and services losses. As there is a rapid trend of urban expansion [46], we also need to understand in which time frame there will be an impact on urban biodiversity and ecosystem functions and services to try to avert it.

Fifth, we still need more studies evaluating the performance of different methodological approaches in identifying delayed ecological responses to landscape change and its size and duration. As the methodology *time series data on ecological response* probably leads to a higher potential accuracy in inferring temporal lags in ecological responses to landscape change, future research should focus in evaluating the performance of the other methodological approaches comparing its results with the results obtained by this approach.

Finally, Kuussaari et al. [2] indicated the need of quantitative meta-analysis to summarize knowledge about extinction debt. This meta-analysis is still missing but we believe that it would be more useful to consider not only extinction debt but also the other types of delayed ecological responses to landscape change that we have discussed here.

Conclusion

With this systematic literature mapping, we provide terminological, methodological, and empirical contributions to the understanding of delayed ecological responses to landscape changes. To avoid further misunderstanding, we have proposed a unified vocabulary that can facilitate the communication and foster research in this topic (see Table 1). We also identified progress in how we are empirically evaluating the existence, magnitude, and duration of delayed ecological responses. Three new methodological approaches were proposed after the seminal paper of Kuussaari et al. [2]. The first one compare observed species distribution with expected species distribution under habitat suitability and assumes that missing species from suitable habitats can be considered a credit and that species occurring in unsuitable habitats can be considered a debt. The second one considers threatened species as an unpaid extinction debt. And, finally, the third one assumes that a delay in biodiversity responses may produce a lag in biodiversity-dependent ecosystem functions and/or services responses to landscape change and estimates those lags based on the biodiversity and ecosystem functioning and the relationship between ecosystem functioning and services. Furthermore, new modeling procedures are allowing to map delay magnitudes [34, 42, 43], with potential applications to the identification of priority areas for conservation or restoration actions.

We showed that temporal lag in ecological responses to landscape change is common (62% of the 353 results) but still poorly studied (only 96 articles were published in 9 years). We showed a high level of support for the effect of time since landscape change and habitat specificity on the probability of delayed ecological responses. Delayed ecological responses are in fact more likely to exist in landscapes that have undergone recent changes and for habitat specialist species.

On the other hand, there are still important knowledge gaps to be filled, related to the effects of landscape change intensity, species dispersal and longevity on delayed responses, besides the understanding of delayed responses for ecosystem functions and services, and also after positive landscape changes (delays in ecological gains). Thus, although delayed ecological responses are highly relevant, and there is a growing literature providing empirical evidence of ecological delayed responses, the mechanisms that can explain the magnitude and duration of these delays are still to be better explored.

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Compliance with Ethical Standards

Conflict of Interest We have no conflicts of interest.

Human and Animal Rights This article does not contain any studies with human or animal subjects performed by any of the authors.

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