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Land-use change: incorporating the frequency, sequence, time span, and magnitude of changes into ecological research

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The frequency and extent of human-induced land-cover changes is escalating worldwide. Recurrent turnover of land-cover types will affect ecosystems over and above major, one-time changes (eg deforestation). Here, we show how a deeper appreciation of the temporal dynamics of land-cover change is needed to understand its effects on ecosystems. We distinguish between four key components of land-change regimes: (1) frequency of land-cover changes over a period of time, (2) the sequence of land-cover types, (3) the time span over which each land-cover type extends, and (4) the magnitude of difference between land-cover types. We synthesize the impacts of these four components on ecological communities, showing that frequent land-cover changes are likely to favor species that are habitat and dietary generalists. Greater attention to the complex dynamics of land-cover changes is critical for a better understanding of the future impacts that human-generated land-use changes will have on global biodiversity.

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Seventy-five percent of the area of Earth's ice-free terrestrial biomes is affected by humans (Ellis 2011). Human-induced landscape change is one of the greatest threats to biodiversity conservation globally (Foley *et al.* 2005). Most research on land-cover change has focused on the consequences of singular, major changes, particularly from natural to human-dominated ecosystems. However, human land use is not a static process; rather, individual land uses and the resultant vegetation cover types undergo constant change (eg clearing for agriculture → grazing → cropping → land abandonment → regrowth of secondary forests), and these histories of change often differ among landscapes (Foster *et al.* 2003). The legacy of different land-use histories can fundamentally shape ecological communities occupying contemporary landscapes (Foster *et al.* 2003; Lindborg and Eriksson 2004; Lunt and Spooner 2005).

In a nutshell:

- The extent of human land-cover change is increasing dramatically and threatens biodiversity around the world
- To better understand the effects of land-cover changes on biota, we must explicitly recognize that certain components of change – frequency, sequence, time span, and magnitude – will strongly affect ecological communities
- More frequent land-cover change will result in landscapes dominated by generalist species that can readily adapt to shifting environments
- Conservation of ecosystems in human-dominated landscapes requires both the development of appropriate indicators for measuring the spatial and temporal components of change and consideration of how these components affect organisms

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In human-modified systems, land-cover changes can occur frequently, rapidly, and over vast areas, driven by changing environmental and socioeconomic conditions (Figure 1; Martínez-Casasnovas *et al.* 2005). For example, between 2006 and 2007, the area converted to maize (*Zea mays*) crop production in the US increased by 7 million ha at the expense of other agricultural commodities (Goldemberg and Guardabassi 2009), while in China, 3.18 million ha of cropland was converted to urban, forest, and grassland environments between 1990 and 2000 (Yan *et al.* 2009). Such large, one-time changes can have a substantial impact on biota; for instance, farmland abandonment in the Mediterranean region of southern Europe has altered avifaunal composition (Gil-Tena *et al.* 2009), and expansion of oil palm (*Elaeis guineensis*) plantations in Borneo imperils orangutan (*Pongo* spp) conservation (Nantha and Tisdell 2009).

While it is important to recognize the effects of such one-time changes in human land use, a more detailed focus on the spatiotemporal dynamics of land-cover change is crucial for gaining a better understanding of the consequences for ecosystem function (Zhao *et al.* 2009). This is particularly urgent given mounting evidence that the pace and extent of human-induced land-cover change is increasing. In Australia, the frequency of land-cover change increased markedly from 1990 to 2008, even though the area that was cleared of native vegetation declined over the same period (Figure 2). In forest and grassland/shrubland environments of the western US, the area of land lost to or gained from other types of land cover increased consistently from 1973 to 2000 (Sleeter *et al.* 2012); indeed, overall areal extent of such change from 1992 to 2000 (3%) was almost twice that seen between 1973 and 1980 (1.6%). In the "Corn Belt"

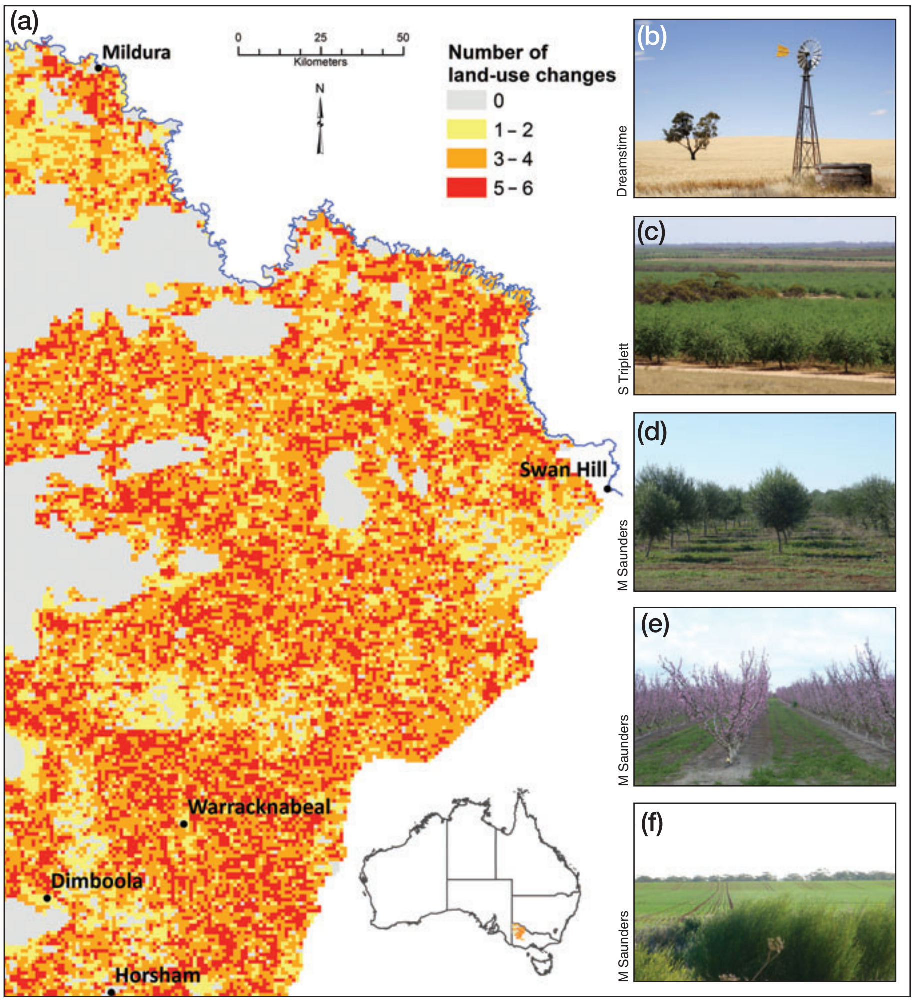


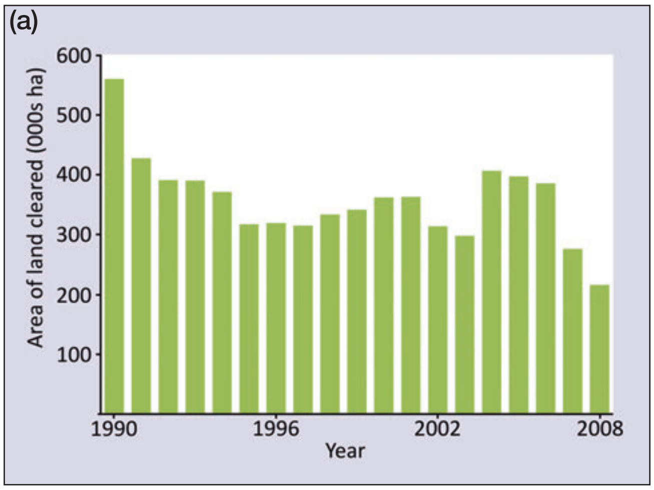
Figure 1. *A land-cover time series from 1992–2006 in north-western Victoria, Australia. (a) The map shows the number of land-cover changes that have occurred in each 1-km^2 pixel throughout the 50 000-km^2 region. Some of these changes reflect a transformation from dryland cropping, such as (b) wheat, to a diversity of irrigated horticultural crops, including (c) almonds, (d) olives, (e) citrus and stone fruit, (f) garden vegetables, and vineyards. (Data source: The Australian Collaborative Land Use and Management Program; Australian Bureau of Agricultural and Resource Economics and Sciences, http://adl.brs.gov.au/landuse/index.cfm?fa=main.downloadData.)*

of the western US, Wright and Wimberly (2013) identified increased rates of conversion of grassland to corn and soybean (*Glycine max*) crops from 2006 to 2011 (5–30% of grassland area converted), primarily driven by a doubling in the market value of these crops.

Understanding how interactions between the spatial and temporal components of land-cover change influence ecosystem dynamics is a fundamental challenge for ecologists and land managers seeking to halt the decline in biodiversity. It is well recognized that the extent, composition, and configuration of landscape elements can greatly affect biota (Bennett *et al.* 2006). McIntyre and Hobbs (1999) synthesized these ideas through a scheme that categorized landscapes, at a specific point in time, as intact, variegated, fragmented, or relictual. Different disturbance processes (eg grazing or cropping) led to different landscape types. The authors also recognized that areas of non-native vegetation within a landscape (often termed "the matrix") can influence biotic responses (see also Prugh *et al.* [2008]), and there is increasing recognition that landscapes should be viewed as mosaics of multiple land covers (Bennett *et al.* 2006; Fahrig *et al.* 2011). This is a substantial advance over a simple patch–matrix view of landscapes because it recognizes the ecological importance of all landscape elements, as well as their interactions. However, most studies continue to view mosaics at a single point in time, even though mosaics constantly shift over time as land cover changes (Forman and Godron 1986).

Previous researchers have also considered the temporal dynamics of biophysical or ecological processes. These studies include documenting interannual variation in climate or primary productivity (eg Cao *et al.* 2004) and, in some cases, relating fluxes to the responses of biota – for instance, how climate change will influence geographic range dynamics (Parmesan and Yohe 2003) or how energy variability affects species richness (Rowhani *et al.* 2008). In agricultural landscapes, mapping of crop dynamics is increasingly common as time series of land-cover data from satellite imagery become more accessible (Veldkamp and Lambin 2001; Martínez-Casasnovas *et al.* 2005).

The idea that landscapes with different land-use histories will yield different biota is generally well established (Fjeldså and Lovett 1997), although the effects of the temporal dynamics of land-cover change on plants and animals remain poorly understood (Lambin *et al.* 2003). Manning *et al.* (2009) introduced the concept of "landscape fluidity" – "the ebb and flow of different organisms within a landscape through time" – to highlight the importance of temporal landscape dynamics on ecological processes. Building on both established spatial and temporal ecological theory, we present a framework that distinguishes four key components of land-cover change and how they may impact biota: (1) the frequency of change, (2) the sequence of changes, (3) the time span of land covers, and (4) the magnitude of change. Our goal is to develop a more nuanced but generalizable approach to understanding



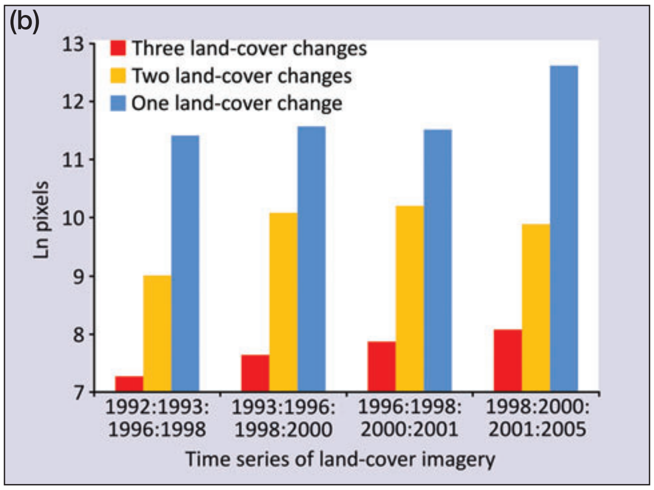


Figure 2. *Two contrasting patterns of land-cover change across continental Australia and Tasmania: (a) clearing of native vegetation has declined from 1990–2008; (b) the increasing frequency of land-cover change for four overlapping time spans: the log number of 0.01 × 0.01 decimal degree grid cells that experienced one, two, or three land-cover changes, determined by overlaying four digital data layers for each time span. (Source: The Australian Collaborative Land Use and Management Program, http://adl.brs.gov.au/landuse. Data source for native vegetation clearance rates: Australian Bureau of Statistics, www.abs.gov.au.)*

the impacts of land-cover changes that focuses explicitly on biotic responses to the temporal aspects of such change.

■ Four major components of anthropogenic land-cover change

(1) Frequency of land-cover change

This refers to the number of times land cover has changed over a defined period. Our conceptualization of frequency of change is analogous to disturbance frequency, which has underpinned studies of ecological community dynamics and has been incorporated into various theoretical frameworks (eg Connell and Slatyer 1977; Huston 1994; Hubbell 2001). The disturbance response of vegetation depends on the functional traits and relative abundance of individual life forms (McIntyre *et al.* 1999); disturbances such as fire or grazing may favor annual grasses and herbs but negatively impact larger perennial grasses (McIntyre *et al.* 1999). Despite recognition of the importance of disturbance frequency in shaping biotic composition, it has received little attention in studies of the effects of anthropogenic landscape change on biota.

To persist in landscapes that are undergoing frequent changes in land cover (eg Figure 1), organisms must have the ability to occupy a variety of different land-cover types; this will favor habitat and dietary generalists that can respond to, and exploit, a changing resource base. Land-cover change has already been linked to an increase in the number of generalist species among bird communities (Le Viol *et al.* 2012). Vagility (the ability to move around) is also likely to influence a species' capacity to adapt to frequent land-cover changes; more mobile species have greater potential to move to and from a site, depending on its suitability and the connectivity of the surrounding landscape. Conversely, relatively sessile and sedentary organisms will persist only if they can tolerate numerous, repeated changes to their surroundings.

(2) Sequence of land-cover changes

This pertains to the order in which different land covers have occurred in a particular location over a given time period (eg "forest → pasture → cereal crops → irrigated horticulture → unmanaged shrubland"). This cumulative process will likely affect the composition of contemporary biota because it reflects the temporal changes seen in the structure of vegetation and abundance of resources, two principal drivers of population dynamics.

The importance of sequential land cover for population dynamics can be seen in crop rotation for pest management. To avoid losses caused by the potato nematode (*Globodera* spp), farmers often plant potato (*Solanum tuberosum*) crops only once in a 5-year period in a given location (Barker and Koenning 1998), while different crop types may be planted in the same fields in the interim. This sequence reduces the population size of nematodes through the removal of a key resource – the host plant (ie potato). Similarly, the sequence of land-cover types will have a strong influence on ecological communities. By way of illustration, if a native woodland is replaced by crops grown on trees (eg fruit tree orchards) for 30 years, and then replaced by cereal crops grown for another 30 years, that location would have experienced a continuous 30-year period of unsuitability for all tree-canopy-dwelling organisms. Conversely, if cereal crops replaced native woodland and were grown for 15 years, followed by crops grown on trees for 30 years, then cereal crops once more for another 15 years, the longest period of unsuitability for all canopy-dwelling organisms would be 15 years, even though the two scenarios both represent 30 years of cereal and treed crops over a 60-year period, with annual crops being the current land cover.

(3) Time span of land covers (time since land-cover change)

Ecologists have long recognized the importance of disturbances in shaping ecosystems, where time interval is critical to understanding the impacts of disturbance regimes (eg Pickett and White 1985). For instance, a prolonged interval between fires can lead to localized extinctions of fire-dependent vegetation through species senescence (Morrison *et al.* 1995). A change in land cover is akin to a disturbance process. As such, the temporal properties of disturbance regimes are highly relevant to understanding the impacts of land-cover change on biota.

In the context of land-cover change, the disturbance event itself may benefit colonizing species, but changes in community composition will depend on the new type of land cover, the time since the change (ie the life span of the current land cover), and the functional traits of organisms. In southern Australia, when Monterey pine (*Pinus radiata*) plantations replace native eucalypt forests, initial land clearance favors bird species that are specialists of open-country habitat, but as plantations mature, different bird communities occupy different age and structural classes of pine (Luck and Korodaj 2008). Thus, time since conversion, which in the pine plantation example is mirrored in tree age, is vital for understanding current ecosystem properties.

Closely related to this concept is the idea of time lags, where localized extinctions are often a delayed consequence of past land-use changes, perhaps due to habitat destruction (Kuussaari *et al.* 2009; Metzger *et al.* 2009). Where a new land cover reduces elements required for a species' survival, the population of that species will decline, but this may happen incrementally over time as individuals successively emigrate or die. Conversely, when species benefit from land-cover change, the time necessary for populations to increase will depend on the species' colonization ability, competitiveness, fecundity, and other traits, as well as on the landscape context. For instance, Jonason *et al.* (2011) reported a positive relationship between time since transition to organic farming and butterfly species richness and abundance.

(4) Magnitude of land-cover change

This is a measure of the difference between land covers at a given location (eg in terms of vegetation structure; see "Practical considerations and future research needs" below). Major differences in land covers (such as forest to urban) generally represent a large magnitude of change, which, we argue, will have greater impact on the dynamics of local ecosystems than lower magnitude changes, such as switching from wheat (*Triticum* spp) to barley (*Hordeum* spp) crops. For example, converting primary rainforest to agricultural land often results in substantial loss of biodiversity and the establishment of comparatively simple ecological communities (Laurance *et al.* 2011). Conversely, other large-magnitude changes, such as urban development of agricultural land, can lead to overall increases in species diversity (Luck and Smallbone 2010).

Understanding how differences in the magnitude of land-cover change affect biota can help to focus and prioritize management strategies to improve biodiversity conservation. For example, retaining native canopy trees within shade coffee plantations reduces the magnitude of differences – in terms of vegetation structure and plant community composition – between a plantation and the rainforest it replaced, as compared to plantations without shade trees; shade coffee plantations may also support a greater diversity of native animal species than non-shade plantations (Perfecto *et al.* 1996). Peh *et al.* (2006) showed that forest bird species richness in agricultural landscapes was highest in rubber plantations as compared with oil palm plantations and open country because rubber plantations were structurally more similar to the original forest ecosystems.

■ Integrating the components of land-cover change and their impacts on biota

Case study

We focus on land-cover changes that have occurred in north-western Victoria, Australia (Figure 1), to illustrate each of the major components of change and how these can influence biota. This region is characterized by a patchwork of remnant native vegetation, livestock grazing lands, and various annual and perennial crops, similar to many managed agricultural landscapes worldwide. It was first settled by Europeans in the late 19th century. Following initial large-scale clearance of native vegetation for grazing and cereal cropping, sizeable water diversions were made from the Murray River into the surrounding agricultural land to develop irrigated agriculture. This allowed the planting of various annual and perennial crops, including nuts, citrus, stone fruit, garden vegetables, and vineyards. Over the past decade, almond plantations have increased substantially in the area because of the high economic return for the crop, suitable environmental conditions, and strong international demand.

Fluctuations in water availability, climate, and socioeconomic factors – especially the variation in demand, and thus value, of agricultural commodities – have influenced the frequency of land-cover change in this part of Australia. Frequency of change has increased over time, characterized largely by a transformation from primarily cereal cropping to more diverse land-cover types as irrigation spread and trends in global markets increasingly influenced land-use options (Taylor *et*

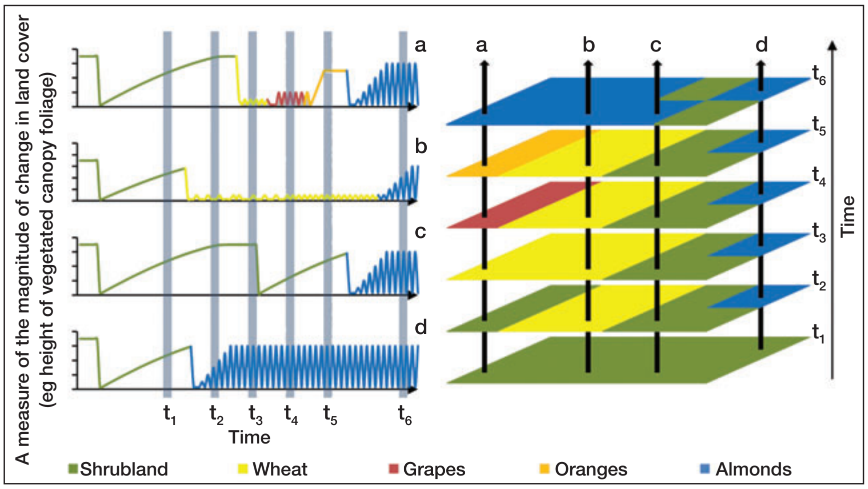


***Figure 3.** A conceptual model of the major components of land-cover change, illustrating different land-change regimes across four locations (a–d). Each location supports a mature almond plantation but varies in historical patterns of land-use change. Differences in the magnitude of changes are illustrated by disparities in the height of the vegetated canopy foliage for the different land-cover types (left panel), including seasonal cycles in canopy foliage and disturbances in native shrublands (eg fire). Patterns of land-cover change show variation in the time since change to the current land cover, time spans of historical land covers, and frequency of land-cover changes. Regarding land-cover changes, location "a" experienced five, "b" experienced four (one of which was a variation in cropping rotation), "c" experienced one that was recent, and "d" experienced one that was older. The spatial context of each pattern varies across locations through time (right panel), indicated by six time slices (t_1–t_6).*

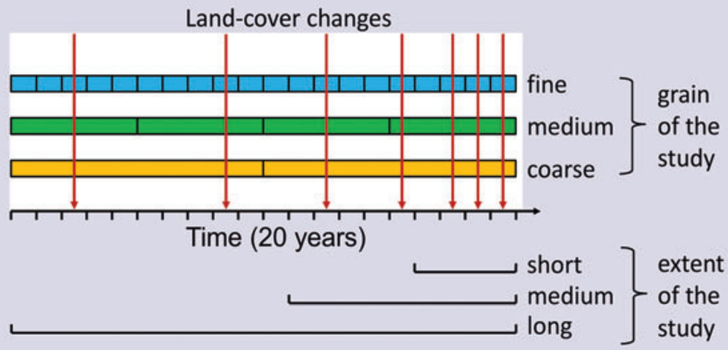
al. 2006). The initial clearance of native woodland for cereal cropping represented a major change in land-cover structure; however, the spread of tree horticulture has reduced the structural differences and, sometimes, the disparities in resource availability between remnant woodland and agricultural land, with concomitant effects on local biota.

The ecological effects of this change are exhibited by the regent parrot (*Polytelis anthopeplus*), a bird listed as endangered across southeastern Australia by Australian state government agencies (Baker-Gabb and Hurley 2011). The regent parrot relies on native forests and shrublands for nesting and foraging, and clearance of its habitat has caused substantial population declines (Baker-Gabb and Hurley 2011). One reason for these declines is a dissimilarity in the vegetation structure between native habitat and cereal crops. However, despite the considerable differences in vegetation structure, there may be a smaller disparity in food availability because regent parrots also feed on cereal crops. This underscores why the indicators used to measure the magnitude of land-cover differences must be carefully selected (see "Practical considerations and future research needs" below), because separate indicators may yield distinct interpretations of biotic responses.

A further twist in this case involves the recent and rapid spread of almond plantations in the study region. Being a perennial, treed crop, almonds more closely resemble the structure of the native woodland than do cereal crops. Moreover, almonds are frequently consumed by regent parrots (Triplett *et al.* 2012). Almond plantations therefore provide both roosting and feeding habitat for this species and may facilitate their movements through the landscape, thereby providing more support for parrot populations than other land-cover types. The time span and sequence of land covers is critical here as well; almond trees younger than 5 years of age generally produce few nuts, and their sparse canopy is less appealing to roosting parrots. Yet almond plantations that directly replace cereal crops would result in less temporal disruption of non-native food resources for regent parrots compared to a "wheat → citrus → almond" sequence (citrus orchards are common in the region but are not used as a food resource by the regent parrot). This underscores the importance of the process of land-cover change – not just the current land-cover type – to population changes in biota.

We illustrate the complex changes that have occurred in the region in Figure 3, which depicts four different regimes of change for landscapes that now support almond plantations. We use the height of the vegetated canopy to represent one measure of the magnitude of change from one land-cover type to another, relative to the original vegetation. Our conceptual model also captures natural disturbance events, such as fire, which can lead to at least temporary modifications of native vegetation, although the major land-cover type itself does not change. Additionally, we highlight differences among landscapes in terms of the duration of land covers, frequency of land-cover change, and sequence of land-cover types (Figure 3).

The changes that are occurring in our study region also affect many other species. For example, over 4 years of research, we have recorded numerous parrot species roosting and feeding in almond trees and have identified more than 40 species of birds using the crop in some way (unpublished data, GWL, PGS, DMW). Complete and rapid removal of almond plantations from this region – a genuine possibility under future scenarios of reduced water availability – could have serious repercussions for regent parrots and other species in this part of Australia, depending on how the land-cover transformation is managed and what form of land use replaces the almond plantations. Further information on the implications of land-cover change is urgently needed to effectively manage species conservation in these novel and dynamic ecosystems (Hobbs *et al.* 2009).



Grain / Extent	Fine (annually)	Medium (5 yearly)	Coarse (10 yearly)
Short (5 years)	4/5 (0.8)	1/5 (0.2)	Grain cannot be > extent
Medium (10 years)	5/10 (0.5)	2/10 (0.2)	1/10 (0.1)
Long (20 years)	7/20 (0.35)	4/20 (0.2)	2/20 (0.1)

Figure 4. *Estimates of the frequency of land-cover change (ie number of changes per unit of time) are influenced by the temporal grain (frequency of sampling) and temporal extent (duration of study). A coarser temporal grain (yellow bar) represents less frequent sampling, resulting in a decrease in the observed frequency of change. Red arrows indicate land-cover changes.*

Interactions with spatial and temporal scale, and thematic resolution

The conceptualization and application of our framework intersects with scale and resolution issues for each component of land-cover change. Land-cover change studies can be defined by their spatiotemporal grain and extent, as well as their thematic resolution. The grain is the finest unit of a study and the extent is the total breadth of a study. A study using 1-ha plots spread over a 1000-km^2 area has a spatial grain of 1 ha and a spatial extent of 1000 km^2. That study may take one sample per year (temporal grain = 1 year) and continue for 20 years (temporal extent = 20 years). The thematic resolution is the level of detail at which landscape elements are recorded. A finer thematic resolution may classify land covers as *Eucalyptus camaldulensis* woodland, *Eucalyptus largiflorens* woodland, almond orchards, and apple orchards, whereas a coarser resolution may classify these land covers as simply "native woodland" and "treed horticulture".

Researchers must carefully consider the effects of the spatiotemporal grain and extent and thematic resolution when interpreting results (Table 1). For example, the frequency of land-cover change is strongly dependent on the temporal grain and extent used for sampling. Studies that examine finer temporal grains (eg annual rather than decadal) are likely to capture a greater frequency of change (Figure 4). By contrast, while investigations with longer temporal extents (eg a 50-year versus 10-year sampling period) will identify more land-cover changes, they may yield lower or higher frequencies of change, depending on the distribution of changes through time: lower if most changes occurred recently (as in Figure 4) or higher if most changes occurred early in the study period. Smaller spatial grains will capture more spatially discrete land-cover changes, thus identifying smaller areas of higher frequency of change as compared to larger grains. Frequency of change will not co-vary with spatial extent because change frequency should be measured at the spatial grain (sampling unit). A finer thematic resolution will capture a greater number of land covers and, thus, will capture more discrete land-cover changes. Consequently, studies with a finer thematic resolution are likely to observe a greater frequency of changes (Table 1). For instance, the thematic land-cover classification of "annual crops" would not detect a "wheat → corn → soy" sequence in land-cover change, because all are annual crops.

Linking patterns to drivers and processes of land-cover change

Emphasizing the major components of temporal change directs attention toward the process and drivers of change. For example, by focusing on the frequency of land-cover change, researchers and land managers may ask why certain locations are experiencing rapid and frequent changes while others are relatively stable. This is exemplified in a recent study by Wright and Wimberly (2013), where substantial changes in the market values of corn and soy were shown to be driving elevated rates of grassland conversion in the US.

Documenting land-cover sequences over time also raises critical questions about how and why exogenous and endogenous factors have driven the particular sequence of events and the processes associated with each land cover. For example, a land-cover sequence of "native vegetation → wheat → barley → grazing on salt-tolerant shrubs → revegetation with deep-rooted perennials" may reflect a landscape where soil salt levels have increased over time due to rising water tables, thereby limiting land-use and production options. Similarly, recording the time span of particular land uses provides insight into the environmental and socioeconomic conditions that influence longevity in the type of land cover. In particular, human-managed land covers that persist for long periods may indicate a level of compatibility between the form of land use and local conditions or the application of sustainable management practices by land users.

■ Practical considerations and future research needs

There are several practical considerations that should be acknowledged when implementing our approach and for guiding future research. The first is how to measure the different components of land-cover change. For magnitude of change, indicators should adequately represent differences between land covers that are likely to be rele-

Table 1. Scale considerations in the study of each component of land-cover change

		Frequency	*Sequence*	*Time span*	*Magnitude*
	Definition	The number of land-cover changes per unit time	The sequence of land-cover changes over time	The length of time that a land cover is present	A measurable difference between land covers (eg vegetation structure, food availability, soil moisture capacity)
Scale considerations	Temporal grain (frequency of sampling)	Finer temporal grain studies (eg annual sampling) will capture more land-cover changes per unit time than those using a coarser grain (eg decadal sampling)	Finer temporal grain studies will capture more land-cover changes and thus will result in more accurate land-cover sequences	Finer temporal grains will lead to more accurate recording of the start and end points of the time spans of land covers	Finer temporal grains will lead to more accurate measures of magnitude because variations in magnitude are more likely to be detected (eg a coarse temporal grain may not detect changes in deciduous vegetation)
	Temporal extent (duration of study)	Longer temporal extents will capture more land-cover changes, but the frequency of change can increase or decrease depending on when changes occurred (see Figure 4)	Longer temporal extents will capture more land-cover changes and improve understanding of long-term sequences	Longer temporal extents will result in more accurate recording of the duration of time spans because the probability of capturing start and end points is increased	Longer temporal extent will improve the accuracy of measures of magnitude because indicators of magnitude that vary over longer time frames will be detected (eg ongoing structural vegetation changes with crop age)
	Spatial grain (area of the sampling unit)	Observed frequency of change should increase with finer spatial grains because there is a greater likelihood of encountering spatially discrete changes	Finer spatial grains will capture more spatially discrete changes and result in more detailed land-cover sequences	If finer spatial grains capture more spatially discrete changes, this will result in a decrease in the observed time span of changes, as these will be recorded more frequently	Finer spatial grains will capture more accurate measures of variation in magnitude, as coarser grains require averaging values across larger areas
	Spatial extent (total area sampled)	Frequency is measured at the spatial grain of a study; although increasing spatial extent will likely capture more land-cover changes, it should not affect the observed frequency of land cover for a given grain size	Increasing spatial extent will capture a broader array of sequences as additional land covers are encompassed by the study area	Time span is a measure characterized at the grain of the study and therefore should not interact with spatial extent	Larger spatial extent will capture more variability within land-cover types and therefore greater variability in measures of magnitude of differences between land-cover types
	Thematic resolution (level of refinement in land-cover classification)	Finer thematic resolution will likely capture more changes and thus result in a higher observed frequency of change	Finer thematic resolution will improve the detail of land-cover sequences	Finer thematic resolution will result in a decrease in the observed time span of land-cover changes because a greater variety of land covers will be recognized	Finer thematic resolution will capture more detailed measures of the magnitude of change

vant to the taxa of interest. For example, the composition of bird communities is often related to vegetation structure (MacArthur 1958), the presence of nesting resources such as tree hollows (Gibbons and Lindenmayer 2002), and food availability (Watson and Herring 2012). Ectothermic animals can be strongly reliant on structural elements that affect their ability to thermoregulate (Kearney *et al.* 2009), while the composition of plant communities is affected greatly by the hydrological properties of soils (Araya *et al.* 2011).

Similarly, the spatial and/or temporal scale and thematic resolution at which each component of land cover is measured should be dictated by the key ecological characteristics of the focal organisms, such as range size and generation time. For organisms with annual life cycles (eg many invertebrates), a temporal grain of less than 1 year may be required for measuring land-cover change components such as frequency and sequence. For species with large home ranges, magnitudes of land-cover change measured over smaller spatial extents (eg square meters) may have little relevance to the ecology of the species.

It is important to identify the key ecological characteristics of organisms that are likely to affect their responses to each land-cover change component (Figure 5). As a case in point, the time span of land covers will interact with various ecological characteristics (eg generation time, population size, phenology) to influence biotic response. Frequency of change interacts with many ecological characteristics, underscoring the importance of further research on this landscape process (Figure 5). Given the sparse information available to the components of land-cover change, it is difficult to make concrete predictions about how each component will affect biota. Nevertheless, we hypothesize that more frequent land-cover change will favor species that are habitat and dietary generalists, at the expense of more specialist

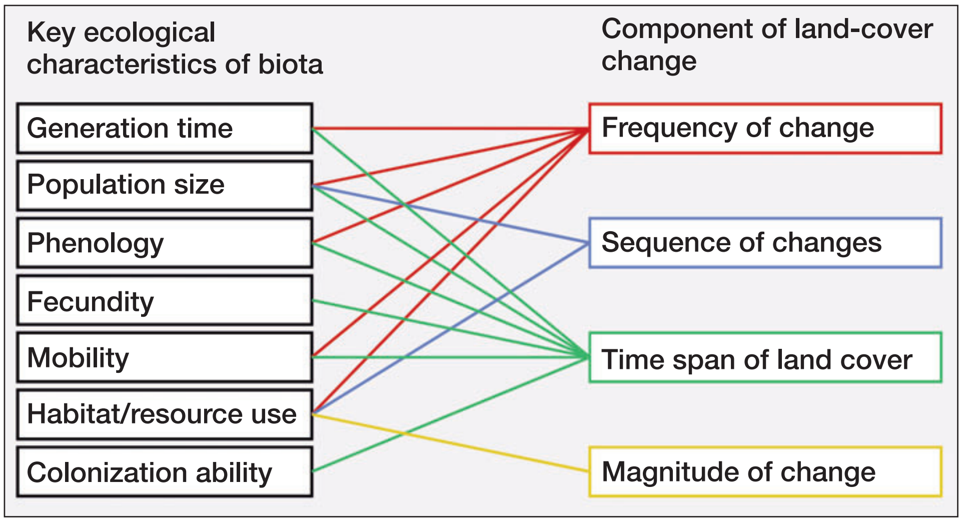


***Figure 5.** The key ecological characteristics of organisms that are likely to interact with the four components of land-cover change to cause changes in biotic communities.*

species, because generalists are able to adjust to and utilize a greater number of land-cover types (Le Viol *et al.* 2012). More mobile species can better track spatially and temporally variable resources and so are less likely to be affected by more frequent changes. While the sequence of land-cover changes will also influence contemporary community composition, this will largely depend on interactions with the type of land covers present at each point in time.

Future research should focus on spatially and temporally explicit regimes of land-cover change and how they interact with the ecological characteristics of organisms to explain their responses. Studies of frequency, sequence, and time span of land covers conducted at large spatial extents and over longer time periods will be more useful in documenting shifting mosaics of land use and the implications of interacting spatial and temporal patterns on ecosystem dynamics. Selecting an appropriate thematic resolution is crucial to defining what is actually meant by land cover and will strongly influence interpretations of all components of land-cover change.

We primarily focus on landscapes dominated by agriculture and at larger scales to illustrate our approach, but the issues we raise are equally applicable to other landscape types. For example, in urban landscapes, the magnitude of difference between urban environments, the age of suburbs (which reflects the magnitude of change and time span of land covers), and the sequence of land-cover changes (eg agriculture to urban, forest to urban) all influence the composition of urban plant and animal communities (Luck and Smallbone 2010).

Human-modified landscapes dominate a large portion of Earth and are increasingly characterized by temporally dynamic mosaics of land-cover types. Understanding how these shifting mosaics influence ecological communities and how to manage ecosystems accordingly remains an ongoing challenge. Land managers and policy makers must recognize the effects that different temporal components of land-cover change can have on biota. Management decisions (eg converting annual crops to perennial tree crops) will affect the magnitude and temporal dynamics of land-cover change, which will subsequently influence the persistence of native biota in the landscape. We hope that the concepts presented here will enhance the recognition of the temporal elements of land change and promote management that better integrates the dynamics of human affected ecosystems.

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