

Local climatic changes affect biodiversity responses to land use: A review

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Abstract

Aim: Climate and land-use change, the greatest pressures on biodiversity, can directly influence each other. One key case is the impact land-use change has on local climatic conditions: human-altered areas are often warmer and drier than natural habitats. This can have multiple impacts on biodiversity and is a rapidly developing field of research. Here, we summarize the current state of understanding on the impact that local climatic changes have on biodiversity responses to land-use change, in particular looking at whether human-altered land uses favour species with certain climatic niches.

Location: Global.

Methods: We review studies that have identified links between species' climatic niches and the habitats/land-use types they inhabit. We also critically discuss the methods used to explore this topic (such as the estimation of fundamental vs. realized climatic niches), identify key knowledge gaps by reference to related macroecological literature and make suggestions for further work.

Results: Assemblages of vertebrate and invertebrate species in numerous human-dominated land uses have been found to have higher proportions of individuals affiliated with higher temperatures and lower precipitation levels than assemblages within natural habitats. However, uncertainty surrounds the mechanisms that underlie these observed differences between communities across land-use types, and it remains unexplored as to whether these trends differ geographically or taxonomically.

Main conclusion: Shifts are being observed within human-altered land uses to communities with, on average, warmer and drier climatic niches. A better understanding of the effects of local climatic changes associated with land-use change will enhance our ability to predict future impacts on biodiversity, identify the species most at risk from interactions between climate and land-use change and set up suitable management and conservation plans.

KEYWORDS

biodiversity change, climate, climatic niche, conservation, land-use change, precipitation, temperature, terrestrial, thermal tolerance

1 | INTRODUCTION

Rapid human population growth has resulted in increasing exploitation of the environment and conversion of land for human use (Foley et al., 2005; Laurance, Sayer, & Cassman, 2014; Meyer & Turner II, 1992). Understanding the impact of these changes on biodiversity has become a widely researched topic (Newbold et al., 2015). However, we are still learning about the extensive effects that land-use change has on the local environment, and the subsequent impacts on biodiversity (De Frenne et al., 2019). A rapidly developing field of research, with studies emerging from around the world, is the impact that land-use change has on local climatic systems, and its knock-on effects for biodiversity (e.g. Frishkoff, Hadly, & Daily, 2015; Menke et al., 2011; Piano et al., 2017; Senior, Hill, González del Pliego, Goode, & Edwards, 2017). Conversion of primary (natural, undisturbed) habitats to human-dominated land uses (such as agriculture and urban areas) causes changes to land cover and vegetation structure, which can directly impact local climatic conditions (Sampaio et al., 2007; Senior et al., 2017). Often, areas of land converted for human use are warmer and drier than natural habitats (Britter & Hanna, 2003; Frishkoff et al., 2016). With the importance of integrating thermal biology into landscape ecology recently being highlighted (Nowakowski, Watling, et al., 2018), and the effects of local precipitation changes also beginning to be acknowledged (Frishkoff et al., 2016), it is crucial that these changes in local climatic systems are incorporated into studies aiming to understand species' responses to land-use change.

The climatic changes caused by land-use change can affect local biodiversity, either directly through changes in temperature, precipitation or moisture levels, or indirectly through changes in vegetation structure or resource availability (Barnagaud, Barbaro, Hampe, Jiguet, & Archaux, 2013; Frishkoff et al., 2016). As a result, this can lead to alterations in community composition (Frishkoff et al., 2016). The studies that have investigated the impacts on biodiversity caused by these climatic changes so far have primarily focused on exploring differences in species' climatic affiliations between habitats/land uses. With land conversions set to continue (Foley et al., 2005), understanding their influence on local climatic conditions and the subsequent effects on biodiversity is both timely and vital in order to predict future biodiversity changes and set up suitable management and conservation plans (Oliver & Morecroft, 2014; Tomimatsu et al., 2013).

We aim to enhance understanding of how local climatic changes (mediated by land-use change) influence species' responses to land use. In order to do this, we briefly review how land-use change impacts the local climate (along with how this varies spatially), and then present a recap of key terms commonly used when studying the effect of such climatic changes on biodiversity. Following this, we arrive at the main focus of our review, where we synthesize patterns and identify disparities between studies, discuss the potential mechanisms underlying these trends and compare the methods currently used to explore this topic. Finally, we highlight knowledge gaps within the current literature and suggest directions for future work.

1.1 | The impact of land-use changes on local climatic conditions

Changes in land use result in modifications to landscape composition (i.e. the total amount of different habitat types), landscape configuration (e.g. habitat fragmentation, which is the subdivision of continuous habitat into smaller plots) and/or in changes to land-use intensity (Andrén, 1994; de Chazal & Rounsevell, 2009; Seppelt et al., 2016). Differences in how intensively humans use the land (i.e. "land-use intensity") result from variation in management practices and level of external input (e.g. use of chemicals/fertilizers and extent of labour; de Chazal & Rounsevell, 2009; Seppelt et al., 2016). Taking land used for growing crops as an example, more intensive management practices can include larger fields, monocultures (rather than mixed crops or crop rotation), application of *inorganic* fertilizer, use of irrigation systems and high (relative) annual plant biomass removal (Hudson et al., 2014; Peters et al., 2019). Conversion of natural to human-dominated land uses (such as cultivated or urban land), and from human-dominated land uses back to forest or grasslands (creating secondary vegetation; de Chazal & Rounsevell, 2009) both result in changes to landscape composition.

The extent and type of vegetation cover significantly affect a site's surface temperature, precipitation level and moisture availability (Frishkoff et al., 2016; Hong, Leach, & Raman, 1995; Jiang, Fu, & Weng, 2015; Senior et al., 2017). Removal of vegetation, through deforestation, for example, can lead to decreases in evapotranspiration and surface roughness (deviation from a flat surface) and rises in surface sensible heat flux (heat transfer from the surface into the atmosphere), which lead to less water entering the atmosphere (a reduction in moisture feedback), decreases in precipitation and increases in surface temperatures (Alkama & Cescatti, 2016; Sampaio et al., 2007; Savenije, 1995). Consequently, numerous areas transformed for human use are warmer and drier than primary habitats (Britter & Hanna, 2003; Frishkoff et al., 2016; Senior et al., 2017). Land-use type and precipitation are also linked with variation in moisture level; however, their relationship is complex due to the multitude of factors (such as topography, soil properties and age or species of vegetation present) that also affect moisture levels (Deng, Yan, Zhang, & Shangguan, 2016; Fu, Wang, Chen, & Qiu, 2003).

Within forests, tree canopies buffer temperature extremes, resulting in cooler maximum and warmer minimum temperatures compared to cleared land, such as pastures (De Frenne et al., 2019; Ewers & Banks-Leite, 2013). Accordingly, increases in maximum (hot extremes), mean and minimum (cold extremes) temperatures occur post-deforestation (Alkama & Cescatti, 2016; Findell et al., 2017; Medvigy, Walko, & Avissar, 2012). For example, during the day, urban and agricultural areas have been recorded to be around 13°C warmer than nearby vegetated or forested sites, respectively (Oke, 1973; Senior et al., 2017). Fewer studies have focused on night-time temperatures, but minimum temperatures been recorded to be slightly colder (by around 1°C) in non-forested (e.g. pastures) or deforested areas compared to below forest canopies (Daily & Ehrlich, 1996; De Frenne et al., 2019). Colder minima occur due to a greater

TABLE 1 A summary of the key terms and metrics used in this review, the data sources underlying them, and the main advantages and limitations of the metrics calculated. Superscripts refer to the references at the bottom of the table

Key term	Metrics calculated	Data sources	Main advantages	Main limitations
Fundamental climatic niche	<p>Critical thermal limits</p> <ul style="list-style-type: none"> - Critical thermal maxima (CT_{max}) - Critical thermal minima (CT_{min}) <p>(these limits are used to calculate thermal safety margins)</p>	Physiological tests in the laboratory	<ul style="list-style-type: none"> • Calculated under controlled conditions 	<ul style="list-style-type: none"> • Metrics produced are often incompatible across studies due to different measurement protocols¹ • Critical thermal limits are dependent on other factors as well as temperature (e.g. exposure duration, water supply), which may not be taken into account^{1,2} • Laboratory tests are only possible for a small number of species^{1,2} • Rarely used to calculate precipitation or moisture tolerance limits⁵
<p><i>Example illustration</i></p>	<p>Species temperature indices (which are used to calculate community temperature indices)</p>	<p>Overlying climatic variables on species' spatial distributions (range maps or occurrence data)</p>	<ul style="list-style-type: none"> • Can be calculated for the majority of species⁴ • Can be easily used to produce estimates of precipitation niches⁵ • The indices produced are relatively easy to understand⁴ 	<ul style="list-style-type: none"> • Estimates of climatic limits may be inaccurate due to the influence of dispersal barriers, biotic interactions and resource distribution on species' distributions^{1,6,7} • May underestimate the upper thermal tolerance limits of species found at high latitudes and/or elevations¹ • Relies on accurate species' distribution maps, which are not available for many species⁸ • The mechanisms underlying differences or changes in these metrics can be difficult to identify⁴ • The scale of the climatic data used may influence results⁹
Realized climatic niche				

(Continues)

TABLE 1 (Continued)

Key term	Metrics calculated	Data sources	Main advantages	Main limitations
Climatic niche breadth	Thermal neutral zone	Physiological tests in the laboratory	<ul style="list-style-type: none"> Calculated under controlled conditions 	<ul style="list-style-type: none"> Can lead to overestimates of the risk posed by climatic changes¹⁰ Laboratory tests are only possible for a small number of species^{1,2}
	Standard deviation of a climatic variable across a species' distribution ⁵ OR The difference between the hottest and coldest grid cells in a species' distribution ¹¹	Overlaying climatic variables onto a species' spatial distribution or from climatic measurements taken throughout a species' range	<ul style="list-style-type: none"> Relatively easy to produce for a wide range of species 	<ul style="list-style-type: none"> Metrics produced are often incompatible across studies due to different proxies for climatic niche breadth used Species' distribution maps may contain inaccuracies⁸ The scale of the climatic data used may influence results⁹

¹Araújo et al. (2013); ²Rezende et al. (2014); ³Sunday et al. (2012); ⁴Oliver et al. (2017); ⁵Frishkoff et al. (2016); ⁶HilleRisLambers et al. (2013); ⁷Peterson et al. (2011); ⁸Herkt et al. (2017); ⁹Nowakowski, Frishkoff, Thompson, et al. (2018); ¹⁰Mitchell et al. (2018); ¹¹Barnagaud et al. (2012).

amount of radiation released back to the atmosphere in land uses without a canopy cover (Suggitt et al., 2011).

There is a great variation in the magnitude of local climatic changes following land-use change (Senior et al., 2017). Temperature changes following conversion from primary vegetation depend on the extent of vegetation change (i.e. the ultimate land-use type), with croplands and pastures increasing more in local temperatures than tree plantations when compared to intact primary forest (Senior et al., 2017). Surface runoff levels also differ between land-use types, and less moisture recycling and lower rainfall are linked with greater surface runoff (Savenije, 1995). Accordingly, highly urbanized areas show the greatest decrease in surface moisture when compared to forested areas in comparison to cultivated sites (Jiang et al., 2015). Due to the lack of canopy cover in naturally non-forested areas (such as grasslands), which reduces buffering of temperature extremes (Jarzyna, Zuckerberg, Finley, & Porter, 2016; Villegas, Breshears, Zou, & Royer, 2010), conversions from grasslands to human-dominated land-use types may not result in as large local climatic changes compared to conversion from primary forests. Another source of variation is latitude; boreal habitats experience smaller changes in mean air temperature following forest clearing than temperate or tropical regions, probably due to the effects of snow albedo (Alkama & Cescatti, 2016; Findell et al., 2017).

1.2 | Key terminology

We summarize here a few terms that are key to this subject area (many are also used in related fields). Further on in this review, we critically discuss the advantages and limitations of the methods introduced below (Table 1).

Researchers investigating the effects of climate and its interaction with land-use change on biodiversity often use the term “*climatic niche*” (e.g. Castro-Insua, Gomez-Rodriguez, Svenning, & Baselga, 2018; Dallas, Decker, & Hastings, 2017; Sapes, Serra-Diaz, & Lloret, 2017; Sunday, Bates, & Dulvy, 2012), which aims to reflect the climatic elements of a species' multidimensional niche *sensu* Hutchinson (Hutchinson, 1957; Sapes et al., 2017). Within a species' *fundamental niche* (Hutchinson, 1957), the climatic elements encompass the species' climatic tolerances, which are often estimated through physiological tests (Frishkoff et al., 2015; Peterson et al., 2011). However, the portions of climatic space that a species actually inhabits, its *realized climatic niche*, is also influenced by dispersal barriers and biotic interactions (HilleRisLambers, Harsch, Ettinger, Ford, & Theobald, 2013; Peterson et al., 2011).

To produce estimates of species' fundamental climatic niches, studies often approximate thermal tolerances using laboratory experiments and frequently calculate *critical thermal limits* (e.g. Frishkoff et al., 2015; Nowakowski et al., 2017). These limits are the upper (*critical thermal maxima*) and lower (*critical thermal minima*) temperatures at which an individual is no longer able to accomplish essential behaviours, movement or righting responses, for example (Nowakowski et al., 2017; Tuff, Tuff, & Davies, 2016). These limits are then used to estimate species' *thermal safety margins*, which are

the differences between the species' critical thermal maxima or minima and the maximum or minimum body temperatures experienced within an environment, respectively (Nowakowski et al., 2017; Sunday et al., 2014). These thermal safety margins, based on species' fundamental climatic niches, are then used to explore vulnerability to climate change and the role of physiology versus behaviour by species to avoid temperature extremes (Sunday et al., 2014).

Species' realized climatic niches can be inferred from their observed spatial distribution (e.g. Barnagaud et al., 2013). Studies focusing on realized niches regularly use species or community temperature indices within their analyses (Barnagaud et al., 2013; Devictor, Julliard, Couvet, & Jiguet, 2008). A *species temperature index* is an approximation of the long-term mean temperature experienced by a species throughout all or part of its range (e.g. its breeding range; Devictor, Julliard, & Jiguet, 2008; Pacifici et al., 2017). Species with higher species temperature indices (warmer-dwelling species) are those that live in areas with, on average, warmer temperatures than species with lower species temperature indices. At the community level, a *community temperature index* is the mean (usually weighted by species abundance) of each species' temperature index in an assemblage (Devictor, Julliard, Couvet, et al., 2008; Jiguet, Brotons, & Devictor, 2011). Consequently, assemblages with higher community temperature indices indicate assemblages composed of greater proportions of individuals of warmer-dwelling species, compared to assemblages with lower community temperature indices (Jiguet et al., 2011).

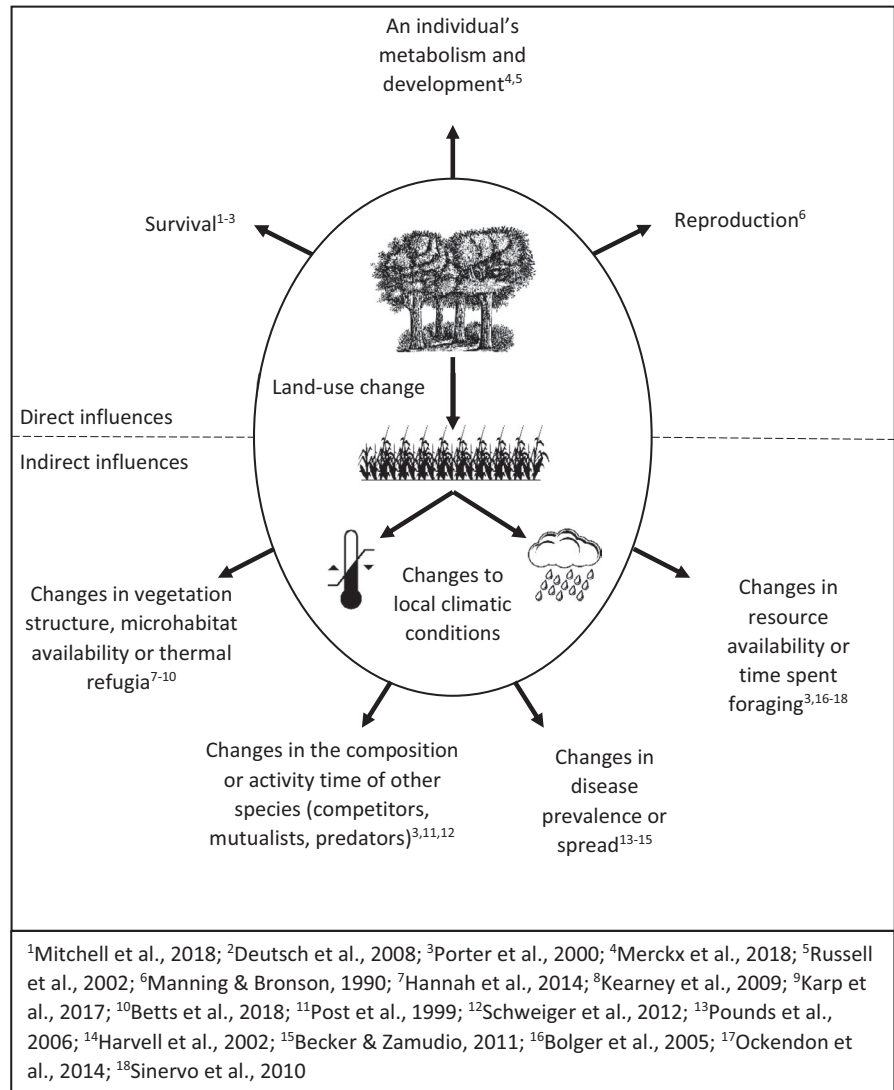
Finally, *climatic niche breadth* describes the breadth of thermal, precipitation or moisture conditions species can tolerate (fundamental niche) or live within (realized niche; Barnagaud et al., 2012; Frishkoff et al., 2016; Khaliq, Böhning-Gaese, Prinzinger, Pfenninger, & Hof, 2017). Using physiological data, previous studies have used estimates of species' *thermal neutral zones* as approximations of thermal niche breadths in endotherms (e.g. Khaliq et al., 2017). The thermal neutral zone is commonly defined as the set of temperatures at which an endothermic species is able to maintain their body temperature without raising their metabolic rate (Khaliq et al., 2017). When calculating realized climatic niche breadths, different methods have been used in the literature; consequently, care has to be taken when comparing these niche breadth results between studies. For example, estimates of climatic niche breadth have been produced from the standard deviation of a climatic variable (e.g. mean annual temperature) over a species range (Frishkoff et al., 2016), as well as from the difference between the average temperature in the hottest and coldest 5% grid cells in which a species is present (Barnagaud et al., 2012).

2 | DIFFERENCES IN SPECIES- AND COMMUNITY-LEVEL CLIMATIC AFFILIATIONS BETWEEN NATURAL AND HUMAN-ALTERED LAND USES

2.1 | Temperature affiliations

Previous research points towards local temperature as an important ecological filter, affecting which species are able to survive within

FIGURE 1 Examples of the impacts local climatic changes mediated by land-use change (for instance, the conversion of a natural habitat to human-dominated land use) may have on biodiversity, which could have knock-on effects for local community composition and/or biotic interactions; the impacts are split into direct influences (where changes in temperature, precipitation or moisture availability affect individuals) and indirect influences (where the climatic changes affect another aspect of an individual's environment, including interacting species, which in turn influences the individual); local climatic changes include changes to temperature, precipitation and/or moisture availability; many of these potential impacts of local climatic changes originate from studies focused on the consequences of global climate change



human-dominated land uses (Frishkoff et al., 2015; Piano et al., 2017). Across a range of amphibian, reptile and bird communities, species within human-altered land-use types, such as pastures, have been found to be affiliated with (realized climatic niche), or able to tolerate (fundamental climatic niche), higher temperatures (i.e. higher species temperature index or critical thermal maxima, respectively) than species within forested primary habitats (Barnagaud et al., 2012; Clavero, Villero, & Brotons, 2011; Frishkoff et al., 2015; Nowakowski et al., 2017). For ectotherms in particular, low heat tolerances and narrower thermal safety margins (in relation to critical thermal maxima) have been linked with greater sensitivity to land-use change (Nowakowski, Watling, et al., 2018). This pattern is not limited to vertebrate assemblages; within invertebrate communities (such as assemblages of carabid beetles and ants), urbanized and agricultural areas contained, on average, warmer-dwelling species (assemblages had higher community thermal indices) in comparison to primary habitats (Menke et al., 2011; Piano et al., 2017). At the individual level, ants from within urban areas were also found to tolerate high-temperature extremes for longer compared to rural-living ants (Angilletta et al., 2007). Changes in community composition with regard to average thermal

niche have also been detected across gradients of land-use change: the community temperature index of French bird communities was found to increase (indicating increases in the proportion of individuals of warmer-dwelling species) along a gradient of decreasing forest cover and increasing fragmentation (Barnagaud et al., 2013). This link between warmer-affiliated species and human-altered habitats also leads to interactions between land-use change and elevation: through thermal niche tracking, lowland tropical forest species have been found to be able to colonize agricultural areas at higher elevations, leading to large differences in community composition between natural and human-altered habitats at higher altitudes (Frishkoff, Gabot, Sandler, Marte, & Mahler, 2019). Taken together, these findings suggest that human-altered habitats are favouring species with warmer thermal niches. Accordingly, the ability to predict species' occurrence in human-altered sites from species' realized thermal niches (using species temperature indices) has also been found to perform better than or as well as other frequently used traits to predict occurrence, such as body size (Frishkoff et al., 2015).

Surprisingly, despite the lack of ability of some human-altered land uses to buffer minimum temperatures (Suggitt et al., 2011),

the few studies comparing estimates of invertebrate cold tolerances found no differences between assemblages in urban and rural habitats (Angilletta et al., 2007; Piano et al., 2017). As the studies investigating differences in minimum thermal tolerance have focused on urban areas as the human-impacted land-use type, this result may be a consequence of the urban heat island effect (Oke, 1973), which may lead to warmer minimum temperatures compared to other human-dominated land uses. In fact, urban areas are often warmer at night than rural, agricultural areas, because the heat absorbed during the day by streets and buildings is released (Kalnay & Cai, 2003; Runnalls & Oke, 2000). Another reason for not finding differences between assemblages in cold tolerances may be because the relative magnitude of difference in cool temperatures between natural and human-altered land uses is much less than the difference in warm temperatures; indeed, the buffering effect of forest canopies has a larger influence on maximum compared to minimum temperatures (De Frenne et al., 2019; Ewers & Banks-Leite, 2013).

2.2 | Precipitation and moisture affiliations

Precipitation niches are also related to association with certain land-use types (Frishkoff et al., 2016). Precipitation (and not temperature) niches were correlated with habitat use in neotropical bird communities; specifically, agricultural land uses were favoured by species associated with drier climates, while those associated with wetter climates favoured forests (Frishkoff et al., 2016). Similarly, invertebrate species usually inhabiting drier climates were found to a greater extent within agricultural and urban assemblages compared with forest assemblages (Menke et al., 2011). These results suggest that human-altered land uses are driving shifts towards communities composed of species that can tolerate drier local climates. However, for some neotropical reptiles and amphibians, realized precipitation niches were not predictive of habitat choices (in this case forested or deforested areas; Frishkoff et al., 2015). This is surprising for amphibians, which are dependent on water availability, and may be because these ectothermic species can find refugia within their tropical habitats (e.g. riparian corridors or remnant trees) and thus persist after changes in local precipitation regimes (Frishkoff et al., 2015). Climate refugia were also found to be important for anole species in pastures, which were areas of low thermal quality where anole body temperatures were often outside preferred thermal ranges (Thompson, Halstead, & Donnelly, 2018). Unfortunately, studies are yet to investigate differences in species' tolerances to moisture availability across land uses, potentially owing to difficulties in acquiring estimates of moisture tolerances (discussed further below) and the complex links between precipitation levels, vegetation cover, soil depth and moisture availability (Deng et al., 2016; Fu et al., 2003).

2.3 | Climatic niche breadths

Climatic niche breadth also varies between land-use types (Piano et al., 2017). For example, beetle assemblages within more urbanized areas

had, on average, wider thermal niches, arising from community-averaged thermal preferences for higher maximum temperatures but similar minimum temperatures, compared to less-urbanized assemblages (Piano et al., 2017). Climatic niche breadth could also be correlated with traits that allow species to be more resilient to environmental change. For instance, thermal and habitat niche breadth were positively correlated for birds within France; in particular, six of the eight species that had the widest thermal niches (classed as climatic generalists) were also those most tightly associated with urban areas (Barnagaud et al., 2012).

3 | POTENTIAL UNDERLYING MECHANISMS

The mechanisms underlying these associations between species' thermal or precipitation affiliations and land-use type are not well known. However, by reference to the literature exploring biodiversity responses to global climate change, we can identify several potential ways in which local climatic changes could affect community composition (Figure 1).

3.1 | Direct influences of local climatic changes

Climatic changes can impact individuals directly, with unfavourable body temperatures reducing fitness, compromising body functions or causing death (Frishkoff et al., 2016; Lovegrove et al., 2014; Mitchell et al., 2018; Porter, Budaraju, Stewart, & Ramankutty, 2000; Welbergen, Klose, Markus, & Eby, 2008). For example, temperature changes can hinder development and reproduction, with colder temperatures leading to greater overnight weight loss in meerkat pups (Russell et al., 2002), and suppressed ovulation in female mice (Manning & Bronson, 1990). Climatic changes can be especially problematic for sessile species and ectothermic species, whose movement, reproduction and development are strongly influenced by ambient local temperatures and humidity (Cahill et al., 2012; Deutsch et al., 2008; Walther et al., 2002). For instance, higher temperatures, which lead to increased metabolic costs, are generally expected to drive shifts towards smaller body sizes in ectotherms (Merckx et al., 2018; Sheridan & Bickford, 2011). Conversely, some species may benefit from warmer temperatures; for some ectothermic species, slight warming may actually increase the length of time that they can spend at optimal core temperatures, which would increase the length of time available for activities such as foraging and reproduction (Kearney, Shine, & Porter, 2009). The direct responses of individuals to climatic changes may lead to changes in the local abundance of certain species, subsequently causing shifts in community composition (Oliver et al., 2017; Porter et al., 2000).

Changes in precipitation and temperature may also have interactive direct effects on individuals. For example, for species within currently arid or semi-arid habitats, further drying may lead to less available drinking water, which can compromise thermoregulation abilities and increase the risks from heat stress (Mitchell et al., 2018). Thus, differences in community composition may result from

declines in species that are unable to tolerate the higher temperatures or lower precipitation levels in human-dominated lands, and increases in species that benefit from the climatic changes.

3.2 | Indirect influences of local climatic changes

Local climatic changes may also influence which species can inhabit an area indirectly (Figure 1; Frishkoff et al., 2016). In human-altered land uses, the vegetation structure may be analogous to natural vegetation in drier and hotter regions, thus favouring species from more arid habitats through bottom-up regulation (Frishkoff et al., 2016; Karp et al., 2017). These sites may also be lower quality habitats with fewer thermal refugia, consequently compromising individuals' abilities to cope with local climatic changes (Betts, Phalan, Frey, Rousseau, & Yang, 2018; Senior et al., 2017). Further, changes in climate may affect food availability (its absolute quantity or seasonal availability), foraging costs or willingness of individuals to forage (Levy, Dayan, Porter, & Kronfeld-Schor, 2016; Porter et al., 2000), which in turn can affect individual's survivorship or reproductive output. For instance, reproductive failure in birds during extreme dry conditions has been attributed to the lack of available food (Bolger, Patten, & Bostock, 2005). As well as prey, climatic changes could indirectly impact species through influences on the demographics of other species within the community, such as mutualists, hosts or competitors (Oliver & Morecroft, 2014; Post, Peterson, Stenseth, & McLaren, 1999; Walther et al., 2002). For instance, if host species decline due to the site's climate no longer being suitable, then species dependent on those hosts may also decline; such mismatches are predicted to occur between host-plant-limited butterfly species under future global climate and land-use change (Schweiger et al., 2012). Again, these impacts can affect each species' abundance within a community, subsequently changing community structure (Porter et al., 2000).

Changes in disease prevalence due to local climatic changes in human-altered land uses may also impact community composition (Pounds et al., 2006). In mammals, a higher prevalence of fungal diseases is hypothesized to occur due to increasing global temperatures (Garcia-Solache & Casadevall, 2010). Conversely, for amphibians, changes in local climate following habitat loss have been suggested to be one mechanism underlying the lower occurrence and prevalence of the chytrid fungus in tropical assemblages in human-altered compared to natural habitats (Becker & Zamudio, 2011). Subsequently, this will affect the composition of amphibian communities in these altered land uses. It is likely that similar local-scale changes in temperature, precipitation level or moisture availability, as a result of land-use change, may also impact the prevalence of other diseases through pathogen growth or survival (Harvell et al., 2002).

After covering several ways biodiversity may be impacted by local climatic changes following land-use change, it is also important to acknowledge that some differences in species' climatic tolerances/affiliations across land uses may not be solely linked to climatic change, but instead (at least to some extent) result from habitat associations (Barnagaud et al., 2012). The past and present location, and thus climatic distribution, of species' preferred habitats may in

part determine their realized climatic niches (Barnagaud et al., 2013, 2012). Species' thermal niche breadths have also been found to be positively correlated with their habitat niche breadth, whereby bird species classed as habitat specialists were also those who experienced less temperature variation across their range (Barnagaud et al., 2012). Consequently, the decline of species with narrow and cool-adapted climatic niches within human-dominated land uses may be due to the negative influence of land-use changes on habitat specialists (Devictor, Julliard, & Jiguet, 2008), rather than directly a result of local climatic changes. The difficulty in separating and identifying underlying mechanisms lies partly in the methods used to establish these patterns (see below; Oliver et al., 2017) and the lack of longitudinal data focusing on changes in community composition following land-use change (leading to a reliance on space-for-time studies).

4 | COMMON METHODS - ADVANTAGES AND LIMITATIONS

The above studies exploring differences in species' climatic affiliations across land-use types analysed either fundamental or realized climatic tolerance estimates, which both have their advantages and limitations (Table 1). Physiological temperature tests, which are used to provide estimates of species' fundamental thermal niches, allow researchers to calculate thermal tolerances under controlled conditions (Frishkoff et al., 2015; Nowakowski et al., 2017). However, there are several potential problems, which can lead to uncertainty regarding how closely the estimated tolerance limits correspond to a species' fundamental niche. First, the measurement protocols used to calculate thermal tolerances often differ between studies, rendering the metrics produced incomparable (Araújo et al., 2013). For example, the rate of temperature increase or decrease within experiments can influence species' thermal tolerances and survival rates, and hence the estimates of fundamental niche generated (Addo-Bediako, Chown, & Gaston, 2000; Hoffmann, Chown, & Clusella-Trullas, 2013). The measure of performance analysed during the temperature changes (e.g. movement or oxygen consumption) also affects the thermal tolerance measures produced (Nowakowski, Frishkoff, Agha, Todd, & Scheffers, 2018). Additionally, using temperature limits to describe thermal tolerances has been criticized due to survival probability depending on the duration of exposure and the intensity of stress (Rezende, Castañeda, & Santos, 2014). Consequently, some researchers suggest using thermal tolerance landscapes instead, which plot the probability of survival as a function of both the duration of exposure and intensity of thermal stress, thus incorporating both aspects influencing thermal tolerance ranges (Rezende et al., 2014). Second, critical temperatures are dependent on other factors that may not be taken into account during experiments, such as water supply (Araújo et al., 2013; Mitchell et al., 2018). Third, calculating thermal tolerances is only possible/desirable for a small number of species, with experiments being time-consuming and expensive (Araújo et al., 2013; Rezende et al., 2014). These tests are far from ideal for threatened species, or species

TABLE 2 The key knowledge gaps in our understanding of how the local climatic changes resulting from land-use change impact communities, along with the conceptual underpinnings for each gap and our hypotheses arising from these. Identifying the mechanisms underlying the responses of animals to local climatic changes is also an area of great uncertainty, but this is not mentioned below because potential impacts/mechanisms are highlighted in Figure 1. Superscripts refer to the references at the bottom of the table

Gap in the literature	Conceptual underpinning	Hypotheses
Geographic variation	<p><i>Tropical versus temperate regions</i></p> <ul style="list-style-type: none"> • The factors influencing species' distribution limits are suggested to differ between tropical and temperate latitudes^{1,2} • Tropical species are suggested to be more sensitive to temperature changes and live closer to maximum temperature tolerance limits than temperate species³⁻⁵ • Temperature differences are greater between open and closed-canopy areas in tropical compared to temperate regions^{6,7} <p><i>Differences between land uses</i></p> <ul style="list-style-type: none"> • The magnitude of change in local climate resulting from land-use change depends on both the starting natural vegetation (e.g. forest vs. grassland) and the final land-use type (e.g. pasture, cropland or urban site)^{8,9} 	<p>Increases in temperature due to land-use change from natural to human-altered sites will have greater negative impacts on tropical than temperate species</p> <p>There will be greater community-level shifts towards species with warmer and drier climatic niches following land-use changes that result in greater local climatic changes (e.g. forested natural habitat to urban areas)</p>
Taxonomic and trait-based variation	<p><i>Endotherms versus ectotherms</i></p> <ul style="list-style-type: none"> • Endotherms can thermoregulate through metabolic control, whereas ectotherms principally rely on behavioural thermoregulation^{7,10} • Temperature and precipitation change directly affect the development, movement, reproduction and biotic interactions of ectotherms^{3,11} • Ectotherms frequently operate when their body temperatures are close to their maximum temperature tolerance limits¹² <p><i>Other trait-based variation</i></p> <ul style="list-style-type: none"> • Traits such as daily activity pattern (e.g. diurnal/nocturnal/crepuscular) and reproductive strategy (e.g. viviparous vs. oviparous species) have been linked to temperature tolerances and may also be linked to precipitation tolerances¹³ 	<p>Temperature and precipitation changes following land-use change from natural to human-altered land uses will have greater impacts on ectothermic than endothermic species</p> <p>Species with traits associated with higher temperature and/or lower precipitation level tolerance limits will be less negatively impacted by the local climatic changes ensuing change from natural to human-altered land uses</p>
Focal climatic variables	<ul style="list-style-type: none"> • Studying differences across land uses in species' precipitation or moisture niches are rare (but see ¹⁴) • The ability of individuals to cope with thermal stress is dependent on water availability^{12,13,15} • It is rare for studies to compare species' cold tolerances across different land-use types (but see ^{16,17}) • Human-altered land uses are often drier and (apart from urban areas) experience colder minimum temperatures compared to natural vegetation^{14,18,19} 	<p>Communities within human-altered sites will, on average, consist of species tolerant of drier climates and (apart from urban areas) colder minimum temperatures</p>
Proximity to climatic tolerance limits	<ul style="list-style-type: none"> • The importance of the proximity of populations to their climatic tolerance limits with regard to the potential risk posed by global climate change has been highlighted³ • Climatic changes are suggested to have greater impacts on populations with narrower safety margins^{3,7,20} • This has rarely been considered in the context of land-use change 	<p>Populations living in environments that are closer to their maximum thermal or minimum precipitation tolerance limits will be more negatively impacted by land-use changes from natural to human-altered land uses</p>

(Continues)

TABLE 2 (Continued)

Gap in the literature	Conceptual underpinning	Hypotheses
Interaction with global climate change	<ul style="list-style-type: none"> Land-use change is occurring alongside global climate change²¹ Global climate change is resulting in, or predicted to generate, hotter temperatures, more extreme heat-waves and greater differences between wet and dry seasons in precipitation levels²² How drivers of change such as global climate change and land-use change will interact poses great uncertainties²³ 	Local climatic changes ensuing land-use change have the potential to interact synergistically with global climate change; for example, with both pressures leading to increased temperatures, we predict that ambient temperatures will be pushed above critical thermal limits for a larger number of species than if the two pressures were acting independently

¹Khaliq et al. (2017); ²MacArthur (1972); ³Deutsch et al. (2008); ⁴Janzen (1967); ⁵Freeman and Freeman (2014); ⁶Kearney et al. (2014); ⁷Nowakowski, Frishkoff, Thompson, et al. (2018); ⁸Senior et al. (2017); ⁹Jarzyna et al. (2016); ¹⁰Sunday et al. (2014); ¹¹Walther et al. (2002); ¹²Kearney et al. (2009); ¹³Clusella-Trullas et al. (2011); ¹⁴Frishkoff et al. (2016); ¹⁵Khaliq et al. (2014); ¹⁶Angilletta et al. (2007); ¹⁷Piano et al. (2017); ¹⁸De Frenne et al. (2019); ¹⁹Kalnay and Cai (2003); ²⁰Nowakowski et al. (2017); ²¹IPCC (2019); ²²Collins et al. (2013); ²³Oliver and Morecroft (2014).

with strict habitat requirements (Hoffmann et al., 2013). Fourth, although widely used to calculate thermal tolerances (e.g. Frishkoff et al., 2015; Nowakowski et al., 2017), using physiological tests to quantify precipitation or moisture tolerances is rare (Sunday et al., 2012). Finally, using a species' thermal neutral zone as an estimate of thermal niche breadth has also been criticized because animals are able to survive outside of this zone and, as such, using this measure may overestimate risk from temperature changes (Mitchell et al., 2018).

To estimate realized climatic niches, climatic tolerances are extracted by overlaying climate databases, such as WorldClim (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005), on species' distribution maps (Barnagaud et al., 2012; Menke et al., 2011), a method that has a set of advantages and limitations. The first advantage is that this method is often the only feasible way to estimate climatic niches for the majority of species (Oliver et al., 2017). This method can also be readily used to produce estimates of precipitation niches (e.g. Frishkoff et al., 2016). However, extracting realized tolerances has several limitations. First, due to the observed conservatism of upper thermal limits across lineages, extracting heat tolerances from distribution maps may underestimate values for species inhabiting higher latitudes or elevations (Araújo et al., 2013). Second, species' realized niches may be constrained by dispersal limitations, biotic interactions such as competition or mutualism, and/or the distribution of resources (Araújo et al., 2013; HilleRisLambers et al., 2013; Peterson et al., 2011), meaning that realized tolerances may not accurately reflect species' actual climatic tolerances (Araújo et al., 2013). Although some studies have developed methods to remove the issue of dispersal when calculating realized niches, for example by focusing on species' responses along regional climatic and land-use gradients (where other variables, such as elevation and temperature, are held constant), then using correlative approaches or differences in species abundances to calculate climatic affinities or niche centres and breadths (Frishkoff & Karp, 2019; Karp et al., 2017). Another biological trait that needs accounting for is migration; species may use migration to avoid severe physical conditions in certain areas (Robinson et al., 2009), so using their entire distribution may provide inaccurate climatic tolerance estimates. Besides these ecological issues, the distribution maps used may have inaccuracies. For

example, maps drawn up following the precautionary principle have a tendency to underestimate species' geographic ranges (e.g. maps produced by the International Union for Conservation of Nature; Herkt, Skidmore, & Fahr, 2017), exacerbated because some biodiversity occurrence data sources lack records for large expanses of land (e.g. the Global Biodiversity Information Facility; Meyer, Kreft, Guralnick, & Jetz, 2015). Yet again, expert-drawn range maps can also overestimate species ranges if they include unoccupied/unsuitable areas between locations where a species exists (Graham & Hijmans, 2006). These limitations may impact the reliability of the climatic tolerances extracted.

Community temperature indices provide a simple index and are a common and powerful method to study changes in average realized climatic niche across or within communities (Bowler & Böhning-Gaese, 2017; Frishkoff et al., 2016; Oliver et al., 2017), but they too have a set of limitations. This practical index allows researchers to study these changes in the absence of standardized surveys of species occurrence, abundance or population sizes across land-use types and spanning climatic gradients (which are rare). However, a drawback of the community temperature index is that, because it is a community-level index, the mechanisms underlying differences in this metric cannot be identified and it can disguise qualitatively different trends between taxa (Barnagaud et al., 2013; Oliver et al., 2017). Further, species' identities and occurrence are not accounted for when calculating community temperature indices, which may result in the presence or absence of an outlier species (which may/may not occur for reasons unrelated to the focal environmental factor) unduly influencing community temperature index results (Bowler & Böhning-Gaese, 2017). Considering which climate variables are used to produce community temperature indices is also important; for example, the choice between using mean or extreme temperatures within a species' range will depend on which is more biologically relevant to the study taxon and question (Parmesan, Root, & Willig, 2000; Sunday et al., 2014). This could cause issues when producing community temperature indices for assemblages, which are composed of a variety of species. Similarly, the spatial scale at which temperature is measured (i.e. landscape vs. microhabitat) and at which the focal taxon perceives the environment also need to be

considered (Nowakowski, Frishkoff, Agha, et al., 2018). Even though there are limitations to these methods of estimating climatic tolerances, they have been used extensively when studying responses to local and global climatic changes, and are able to capture differences in species- and community-level climatic niches across land-use types and over time (Frishkoff et al., 2015; Oliver et al., 2017).

5 | GAPS WITHIN THE LITERATURE

Studying how local climatic changes mediated by land-use change affect local communities is a developing research area. By drawing on principles from related macroecological literature, in particular that on global climate change and factors influencing species' distributions, we highlight below four important knowledge gaps, presenting testable hypotheses where possible (Table 2). Identifying the mechanisms underlying differences in species' climatic niches between land uses is one of the greatest areas of uncertainty and warrants more exploration, but as we have already covered this above, it is not included in this section.

5.1 | Geographic variation

The influence of local climatic changes following land-use change may differ in strength across space, such as between tropical and temperate latitudes, but this is yet to be explored. We hypothesize that such latitudinal variation will occur owing to the fact that the factors impacting species' range limits are thought to differ geographically (Khaliq et al., 2017; MacArthur, 1972). In temperate latitudes, abiotic factors (e.g. climate) are thought to be the primary influence on distribution limits, whereas in the tropics, biotic factors (interactions with other species) are suggested to prevail (Khaliq et al., 2017; MacArthur, 1972; Wiens & Donoghue, 2004). For instance, for birds and mammals, minimum temperature tolerances appear to limit distributions across temperate latitudes, while in the tropics, climatic conditions do not have the same influence (Khaliq et al., 2017). On the other hand, due to the current and historic stability of the tropical climate, species within this region are suggested to have a higher sensitivity to temperature changes (Bonebrake & Deutsch, 2012; Cadena et al., 2012; Deutsch et al., 2008; Janzen, 1967). For instance, tropical species are living closer to their maximum thermal physiological tolerances, with small increases in temperature thought to push these species closer to their heat tolerance limit proportionally faster than in temperate realms (Deutsch et al., 2008). Elevational shifts in tropical montane bird species have also been observed to more closely match increases in temperatures compared to those of temperate montane species, supporting suggestions that tropical species have a higher sensitivity to warming temperatures (Freeman & Freeman, 2014). Conversely, for temperate ectotherms, moderate temperature increases following land-use change may be advantageous, increasing the time they can spend within their optimal temperature limits (Kearney et al., 2009). Temperature also tends to differ more between closed-canopy and open areas at tropical compared to temperate latitudes (although there

is seasonal variation; Kearney, Isaac, & Porter, 2014; Nowakowski, Frishkoff, Thompson, Smith, & Todd, 2018). Consequently, due to the higher sensitivity to climatic changes in the tropics, we hypothesize that increases in temperatures due to land-use change from natural to human-dominated sites will lead to greater negative impacts on species at tropical compared to temperate latitudes.

Additionally, as the magnitude of local climatic change differs depending on both the starting primary vegetation (e.g. forest vs. grassland) and ultimate land-use type (Jarzyna et al., 2016; Senior et al., 2017), grouping together human-altered land uses or only studying a few land uses (such as the focus on natural and urban habitats when comparing cold tolerances) may lead to important differences being missed. There is also currently little research comparing climatic affiliations between communities in non-forested primary habitats and human-dominated land uses (but see Piano et al., 2017). We hypothesize that there will be greater community-level shifts towards species with warmer and drier climatic niches where there are larger changes to local climatic conditions following land-use change from natural habitats; for example, we hypothesize that there will be greater shifts following deforestation to create urban areas in comparison to conversion of grasslands to pastures. Overall, past research points to several mechanisms by which the impact of local climatic changes ensuing land-use change could affect species differently depending on geographic location. It is vital that these differences are understood in order to produce suitable, spatially explicit conservation and management plans and identify species at risk from land-use change within different regions.

5.2 | Taxonomic and trait-based variation

Species are affected differently by climatic changes (e.g. Oliver et al., 2017; Warren et al., 2013), which consequently may lead to species-specific differences in the impact of land-use change. Endothermic and ectothermic species, for example, are influenced differently by changes in ambient climatic conditions (Jezkova & Wiens, 2016; Rolland et al., 2018); thus, their responses to changes in these following land-use change also likely differ. Ectotherms are thought to be more sensitive to climatic changes, a result of the direct effect that shifts in temperature and precipitation have on their development, movement, biotic interactions and reproduction (Deutsch et al., 2008; Walther et al., 2002). Ectotherms have also been found frequently to operate at body temperatures near their maximum temperature tolerance limits (Kearney et al., 2009). The removal of natural habitat, which can provide thermal refugia, may also impact these species differently. For example, ectotherms predominantly rely on behavioural thermoregulation and the presence of microhabitats that can act as thermal refugia, whereas endotherms can thermoregulate through metabolic control (Nowakowski, Frishkoff, Thompson, et al., 2018; Sunday et al., 2014). Thus, we hypothesize that changes in temperature and precipitation level following natural to human-dominated land-use changes will have greater impacts on ectothermic than endothermic species.

Even within endotherms and ectotherms, the strategies used for coping with environmental changes may vary (Khaliq et al., 2017;

Khaliq, Hof, Prinzinger, Böhning-Gaese, & Pfenninger, 2014). For instance, to cope with stressful thermal conditions, birds are suggested to use physiological adaptations as their main strategy, whereas, in mammals, behavioural strategies are more common (Khaliq et al., 2014). Further, the differences in structure of porous insulation (fur or feathers) between and within mammals and birds will also affect their methods of coping with climatic change (Porter et al., 2000). For example, feathers allow birds to seal off airflow from their skin, a quality that is rarely found in fur (Porter et al., 2000), and may consequently impact how animals respond to cold stress. Moreover, wet- and dry-skinned vertebrate ectotherms may differ in strategies to avoid extreme high temperatures, due to the use of evaporative cooling by wet-skinned amphibians that can offset heat gain via solar radiation (though this is likely dependent on moisture availability; Sunday et al., 2014). Insects also are suggested to differ again in their use of behaviour to prevent overheating (Sunday et al., 2014). Consequently, taxonomic groups likely respond differently to local climatic changes following land-use change, but studies rarely explore how differences in species' climatic niches across land-use types vary between taxa. Importantly, to our knowledge, no studies have yet looked at how the climatic niches of mammal communities differ across land uses. Further to this, these differences in how species cope with climatic changes may also lead to taxonomic differences in the predominant mechanisms underlying the impact of local changes in climate. For instance, the loss of thermal refugia may have larger impacts on taxa that are not as mobile and heavily rely on refugia to avoid thermal stress. These research areas are in need of attention.

Species' traits such as daily activity pattern, body mass and reproductive strategy may also influence the impact of local climatic changes. Species active during the day are more likely to be exposed to stress-inducing high temperatures compared to nocturnal species, who instead may face extremes of cold (Kearney & Porter, 2004; Kearney et al., 2009; Navas, 1997). This is reflected in their heat tolerances and preferred body temperatures, which are generally higher in diurnal than nocturnal species (see Clusella-Trullas, Blackburn, & Chown, 2011). Further, if local climatic conditions are more similar between natural and human-altered sites at night than day, nocturnal species may more likely be able to survive within human-altered sites compared to diurnal taxa (Daily & Ehrlich, 1996). Body mass, which has both direct and indirect associations with physiological processes (Gates, 1980; Gillooly, Brown, West, Savage, & Charnov, 2001), is also related to preferred body temperature, although this relationship may vary with precipitation (Clusella-Trullas et al., 2011). In terms of reproductive strategy, oviparous squamate species have been found to be able to tolerate higher temperatures, on average, than viviparous species (Clusella-Trullas et al., 2011). Therefore, these traits likely influence how species react to temperature and precipitation changes and thus to climatic alterations after land conversion. We hypothesize that species with traits associated with the ability to tolerate higher temperatures and/or lower precipitation levels will be less negatively affected by the local climatic changes ensuing land-use change from natural to human-dominated sites.

5.3 | Focal climatic variables and proximity to climatic tolerances

When comparing climatic niches across land uses, there has been a tendency to focus on temperature, in particular mean and maximum temperatures (e.g. Barnagaud et al., 2012; Clavero et al., 2011; Piano et al., 2017), with other climatic variables often neglected. However, precipitation niches are important on their own (Frishkoff et al., 2016) and, in addition, water availability affects the ability of endotherms and ectotherms to cope with thermal stress (Clusella-Trullas et al., 2011; Kearney et al., 2009; Khaliq et al., 2014). For example, amphibians' thermal safety margins are contingent on their hydration status (Sunday et al., 2014). Similarly, studies rarely consider moisture availability (but see Frishkoff et al., 2015), or species' tolerances to this when studying community composition across land-use types. Local moisture availability and precipitation levels are linked (Savenije, 1995), and certain species are dependent on moisture availability (Frishkoff et al., 2015). So, due to human-dominated land uses generally being hotter *and* drier than natural habitats (Frishkoff et al., 2016), if interactions are occurring between thermal and desiccation stress, there may be greater effects on biodiversity after land conversion than expected just from temperature changes (Clusella-Trullas et al., 2011). Therefore, there should be a greater focus on precipitation and moisture availability alongside temperature. Furthermore, due to land-cover type also influencing minimum temperatures (Suggitt et al., 2011), and species' cold tolerances being closely related to the poleward limits of their distributions at temperate latitudes (Khaliq et al., 2017), changes in minimum temperatures (e.g. winter or night-time temperatures) could have a marked influence on species, but relatively little work has explored this possibility (but see Latimer & Zuckerberg, 2017; Piano et al., 2017). Without canopies to buffer minimum temperatures (De Frenne et al., 2019), we hypothesize that, in comparison to natural forested habitats, communities within human-altered land uses will, on average, be able to tolerate lower minimum temperatures (with the exception of urban areas, due to the urban heat island effect).

Another potentially important source of variation in responses to land-use change is a population's proximity to their climatic tolerance limits, a variable highlighted in the global climate warming literature (Deutsch et al., 2008). For example, slight local warming or cooling may have greater impacts on the performance of populations living closer to their hot or cold limits (as they will have narrower thermal safety margins) compared to those populations with larger safety margins (Deutsch et al., 2008; Nowakowski, Frishkoff, Agha, et al., 2018). Very few studies have explored this in the context of land-use change (but see Nowakowski, Watling, et al., 2018). We hypothesize that those populations closer to their maximum thermal or minimum precipitation tolerance limits will be more negatively impacted following natural to human-dominated land-use changes, because human land uses are generally hotter and drier (Frishkoff et al., 2016). Identifying whether these potential sources of variation lead to differences in responses to land-use change will also help identify the mechanisms underlying observed trends.

Intraspecific variation in responses to land-use change across a species' distribution could also result from the impacts of local climatic changes differing between tropical and temperate latitudes, particularly for species with large latitudinal range sizes. Calculating realized climatic niches at the species-level using distribution maps may lead to these intraspecific differences being overlooked. This again highlights the importance of looking at differences between populations in their responses to land-use change.

5.4 | Interaction with global climate change and future projections

Local climatic changes mediated by land-use change are occurring alongside global climate change (Sala et al., 2000), potentially leading to interactions (likely synergistic; Frishkoff et al., 2015; Guo, Lenoir, & Bonebrake, 2018; Kearney et al., 2009). Global climate change is resulting in hotter mean temperatures and more extreme hot events (Collins et al., 2013), so rises in local temperatures due to land-use change will further increase the temperatures to which organisms are exposed (Frishkoff et al., 2016). This may push ambient temperatures above critical thermal limits for a greater number of species than if global climate change was acting independently. Further, species' responses to multiple stressors may be correlated (Vinebrook et al., 2004). Early theories looking at the impacts of correlated sensitivities to multiple stressors assumed that species were only either adversely impacted, or unimpacted (i.e. never benefited) from environmental pressures (Vinebrook et al., 2004). These theories predicted that if species' sensitivities to the stressors were negatively correlated, biodiversity would be severely reduced, but positive correlations would lead to smaller overall impacts on community biodiversity (Vinebrook et al., 2004). However, more recent work has taken into account that species can benefit from environmental change and that the effects of pressures can combine (Frishkoff, Echeverri, Chan, & Karp, 2018). This work has shown that when pressures act simultaneously the outcome for biodiversity is much more complex; for example, positive correlations between sensitivities can lead to either greater or fewer numbers of species lost compared to if the stressors acted independently (Frishkoff et al., 2018). Nonetheless, if climate and land-use change favour the same species, such as those that can tolerate higher temperatures or lower precipitation levels, this may lead to biotic homogenization, which could have detrimental effects for ecosystem functioning (García, Bestion, Warfield, & Yvon-Durocher, 2018; Karp et al., 2017; Mori, Isbell, & Seidl, 2018). Previous work has also indicated that human land conversion can lead to phylogenetic homogenization, by favouring clades that are more tolerant to land-use change (Nowakowski, Frishkoff, Thompson, et al., 2018), which could also be exacerbated by global climate changes. The uncertainty surrounding how community biodiversity will be affected when environmental pressures act simultaneously further highlights the need to understand the mechanisms underlying how these pressures affect different species.

Finally, a crucial area yet to be investigated is the *future* impact of land-use change, its effect on local climatic conditions and the

interaction with global climate change. Some papers have made predictions regarding the impact of land-use and climate change on biodiversity (Mantyka-Pringle et al., 2015; Newbold, 2018; Segan, Murray, & Watson, 2016), but haven't accounted for local climatic changes resulting from habitat disturbances. Unfortunately, current predictions of species vulnerability are likely unreliable, due to the limitations in current methods (Sunday et al., 2014), the lack of understanding of the mechanisms underlying differences in climatic niches across land uses (Barnagaud et al., 2013) and the likely geographic and taxonomic variation. Furthermore, disentangling the effects of global climatic changes, local climate changes due to land-use change and the other effects of land-use change can be challenging (Oliver & Morecroft, 2014), which adds extra complications when trying to understand responses. However, with ongoing exploration into these topics, being able to predict how these drivers of change will impact biodiversity will form an essential part of conservation planning.

6 | CONCLUSIONS

Local climatic conditions are affected by land use, with human-dominated land uses often found to have hotter and drier local climates compared to areas of primary vegetation (Britter & Hanna, 2003; Frishkoff et al., 2016). Reflecting this, studies from around the globe have demonstrated that communities of vertebrates and invertebrates within human-dominated land uses are composed of warmer- and drier-dwelling species in comparison to communities within natural, undisturbed habitats (Frishkoff et al., 2015, 2016; Menke et al., 2011). However, further work is needed to understand the mechanisms underlying these community differences, such as the relative strength of direct versus indirect influences of temperature and precipitation changes. As well as the underlying mechanisms being a major gap in our current knowledge, we also highlighted several other key areas in need of attention, such as how trends may differ geographically and/or taxonomically. Additionally, species within human-altered land uses are facing other pressures, such as global climate change, which may lead to complex synergistic interactions and is another area requiring further research (Collins et al., 2013; Frishkoff et al., 2016; Sala et al., 2000). Overall, this is a rapidly developing field with exciting research being carried out that will help us to identify which species or populations may be at risk from land-use change, ways to minimize these negative impacts, and thus aid future conservation planning.

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There are no data associated with this manuscript.

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BIOSKETCHES

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