The impacts of tropical forest disturbance on species vital rates

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Article Impact Statement: Empirical research on demography across taxa and regions is lacking and between-species variation in demographic responses to land-use change is considerable.

Abstract

Tropical forests are experiencing enormous threats from deforestation and habitat degradation. Much of our knowledge on the impacts of these land-use changes on tropical species comes from studies examining patterns of richness and abundance. Demographic vital rates (survival, reproduction and movement) can also be impacted by land-use change in a way that increases species vulnerability to local extinction, but in many cases these impacts may not be manifested in short-term changes in abundance or species richness. We assessed current knowledge and research effort concerning how land-use change affects species vital rates in tropical forest vertebrates. We find a general paucity of empirical research on demography across taxa and regions, with some biases towards mammals and birds, and land-use transitions including fragmentation and agriculture. There is also considerable between-species variation in demographic responses to land-use change, which could reflect trait-based differences in species sensitivity, complex context-dependencies (e.g. between-region variation) or inconsistency in methods used in studies. Efforts to improve our understanding of anthropogenic impacts on species demography are underway, but there is a need for increased research effort to fill knowledge-gaps in under-studied tropical regions and taxa. The lack of information on demographic impacts of anthropogenic disturbance makes it difficult to draw definite conclusions about the magnitude of threats to tropical ecosystems under anthropogenic pressures. Thus, determining conservation priorities and improving conservation effectiveness remains a challenge.

Tropical deforestation and degradation

Despite a wealth of research identifying tropical deforestation and degradation as primary drivers of global biodiversity loss (Barlow *et al*. 2016, Gibson *et al*. 2011), most empirical work examines patterns of species richness and abundance across spatial or temporal gradients of anthropogenic impact (Gibson *et al*. 2011; Burivalova *et al*. 2014). Importantly, such patterns can mask underlying impacts on species that persist following land-use change. For example, forest degradation following selective logging might not affect a species' abundance in the short-term, but long-term population viability could be reduced via declines in survival or reproductive success (Srinivasan *et al*. 2015). Core drivers of overlooked impacts include when populations in degraded habitats are buffered by immigration from surrounding areas (Gilroy & Edwards 2017), when high-quality habitats are occupied by dominant individuals that force others to occur in higher abundance in marginal habitats (Holt 1985), or when degradation causes declines in habitat quality without influencing the relative attractiveness of the habitat ('ecological traps', Gilroy & Sutherland 2007).

To generate a robust understanding of the true long-term impacts of anthropogenic-induced land-use change on ecological communities requires understanding how underlying demographic vital rates, such as survival, reproductive success and movement (dispersal) change. Dispersal rate, for instance, can determine the ability of populations to persist in degraded and fragmented habitats (Fahrig 2007), and to traverse inhospitable barriers (Lees & Peres 2009). Vital rates can thus better indicate the state of a population, as both population stability and viability are driven by demography (Saether & Bakke 2000; Haridas *et al*. 2013).

Here, we examine the state of current understanding of the impacts of tropical land-use change on species' vital rates to identify knowledge gaps and assess any general trends in responses. Such understanding can give us a better picture of the long-term resilience of species in degraded habitats. We assess demographic vital rates of terrestrial vertebrates (birds, mammals, reptiles and amphibians) in the tropics, exploring patterns of research effort across regions and taxonomic groups for four key land-use changes: forest conversion to agriculture, forest fragmentation, selective logging, and fire.

Literature review methods

We reviewed studies that assessed the impacts of anthropogenic disturbance on survival, reproductive success and movement in tropical forest vertebrate species (birds, mammals, reptiles and amphibians). For survival, we only included studies that calculated empirical estimates of survival rates from observed data (e.g. mark-recapture, telemetry studies). For simplicity, we define measures of reproductive success as any assessment of fecundity, breeding success or recruitment rate (including population growth rate). We defined movement studies as those considering dispersal rates (i.e. movements resulting in successful or unsuccessful gene flow) or temporary movement (e.g. foraging movements), since foraging is important for survival.

Using the online Web of Science database, studies were found using the key words: [degradation OR deforestation OR "habitat change" OR "land use" OR "habitat conversion"] AND [survival OR dispersal OR movement OR "population growth" OR "birth rate" OR "death rate" OR fecundity OR "breeding success" OR "clutch size" OR "reproductive success" OR "brood size" OR productivity OR lambda OR demography]. The search was refined by [tropic*] and either [logging], [agriculture], [fragmentation] or [fire]. This search was conducted from 6th October 2016 to 20th November 2016. In total, 3076 studies were found using this keyword search. Of these, we selected studies for inclusion only if they were: (i) conducted in the tropical region (between 23.43706° N and 23.43706° S); (ii) conducted in closed-canopy tropical forests, excluding studies in open, grassland dominated systems like Cerrado; (iii) studied only terrestrial tropical vertebrates; and (iv) assessed the impacts of anthropogenic disturbances using any measure of survival, demography and movement in their analyses. The COMADRE database (Salguero-Gomez *et al*. 2016) was also used to supplement the search. Of 71 studies found in the tropics, 64 studies met our criteria (see Appendix S1 for full list of studies; Fig 1 for distribution of studies across tropics). The remaining seven were conducted in open, grassland dominated systems. These 64 studies were separated into the different vital rates (survival, reproductive success, movement) and then classified by land-use disturbance (selective logging, agriculture, fragmentation, fire), tropical region (Neotropics, Afrotropics, Indomalayan tropics, Australasian tropics/Oceania) and study area elevation (lowland, sub-montane, montane). Studies that reported results for multiple rates, regions or land-use classes were counted for each class separately.

Impacts of anthropogenic disturbances on vital rates

Pan-tropically, we found a total of seven studies reporting impacts of anthropogenic disturbances on forest vertebrates using measures of survival, 22 using reproductive success and 40 using movement (see Table 1 for summary; Fig. 1). Overall, these totals highlight a paucity of information on how anthropogenic changes affect the vital rates of vertebrate biodiversity across the tropics. Studies were largely restricted to birds and mammals, with only 3% concerning amphibians and none on reptiles (Fig. 2d). For all three vital rate classes, deforestation for agriculture and forest fragmentation were the predominant anthropogenic impacts addressed by research, with far fewer studies considering selective logging or fire (Fig. 2). In the following sections, we examine general patterns and trends evident from studies concerning each anthropogenic impact class.

Forest conversion to agriculture

The rate of forest conversion to farmland in the tropics was around 7 million hectares annually from 2000 to 2010 (FAO 2016) and it is well established that this conversion produces strong negative impacts on tropical biodiversity (Edwards *et al.* 2014; Gibson *et al*. 2011). Agricultural conversion typically removes important food sources, breeding habitats and refugia from inhospitable climates (Fitzherbert *et al*. 2008). Nevertheless, low intensity farmland and polyculture landscapes can support a surprising amount of wildlife (Karp *et al*. 2011), particularly if crop plants themselves provide diverse food sources (Wickramasinghe *et al*. 2004).

Survival: We found only three studies assessing the impact of forest conversion to agriculture on survival rates (Newell 1999; VanderWerf 2004; Peery & Pauli 2014). In two cases, conversion did not significantly affect survival: Hawaiian ‘Elepaio *Chasiempis sandwichensis* (VanderWerf 2004) and Hoffmann’s two-toed sloths *Choloepus hoffmanni* (Peery & Pauli 2014), as the agricultural lands in question apparently provided sufficient resources to fulfil niche requirements, and the species exhibited plasticity in their foraging behaviors (Vaughan *et al*. 2007). However, studies showed that deforestation reduced the survival of two other mammal species, due to increased predation and poor habitat quality in the agricultural systems.

Reproductive rates: We found eight studies evaluating the impacts of deforestation on reproductive rates, again concerning bird and mammal species. The effects of deforestation on reproductive rates were species-dependent where four studies showed declines in breeding success of birds and mammals, three did not detect any impacts on avian nest survival and one study on Hoffmann's two-toed sloths *Choloepus hoffmanni* and brown-throated three-toed sloths *Bradypus variegatus* found variations in population growth rates. Conversion to agriculture can have little impact on reproductive rates if species are able to utilize resources within the novel habitat (Sekercioglu *et al*. 2015), or if other limiting factors such as predator populations are controlled by human activities (Bobo & Waltert 2011).

Movement: We found nineteen studies examining the impacts of animal movements in agricultural lands after deforestation; two on amphibians, and the rest on birds and mammals. Again, these studies found a varied range of effects of conversion on movement, from less (Ibarra-Macias *et al.* 2011) to no effect (Medina *et al*. 2007) to more movement (Powell *et al*. 2016). Factors that can cause changes in movement behavior include increased competition, increased predation (Lees & Peres 2009; Shadbolt & Ragai 2010) and higher mortality risks from inhospitable microclimates (Lees & Peres 2008). Alternatively, species movement can be unaffected by agriculture if farmlands provide adequate resources (Luck & Daily 2003) or if species are already highly vagile (Estrada *et al*. 1993).

Forest Fragmentation

Deforestation fragments the remaining forest, creating abundant edges impacted by hotter, windier and drier climates (Laurance *et al*. 2002). Detailed autoecological studies have shown that many forest-dependent species are unable to persist within forest patches and/or cross gaps (Ferraz *et al*. 2003; Lees & Peres 2009), such that smaller and more isolated fragments have strong negative impacts on species diversity and abundance (Ferraz *et al*. 2003; Russildi *et al*. 2016). Furthermore, increased edge effects mean that fragmentation can alter the community composition of landscapes, with shifts from interior-specialists to edge-specialists and generalists (Laurance *et al*. 2002; Magnago *et al*. 2014, Pfeifer *et al*. 2017).

Survival: We found four studies assessing species survival on birds in fragmented forest landscapes. Fragmentation resulted in reduced survival in 24 species, relative to contiguous forest, likely caused by increased predation, reduced resources, and higher mortality risks when vagile species traverse the matrix (Shadbolt & Ragai 2010; Lees & Peres 2008). Conversely, eight bird species exhibited no negative effects from fragmentation. The survival of white-starred robins *Pogonocichla stellata* in Southeast Kenya, for example, was similar in all fragment sizes (Githiru & Lens 2006). However, the major causes of mortality varied with fragment size: mortality associated with dispersal was more prominent in larger fragments, whereas mortality from nest predation was more important in smaller fragments.

Reproductive rates: We found fifteen studies assessing the impacts of forest fragmentation on reproductive rates, 14 using birds and one using mammals (Umapathy *et al*. 2011). The majority of these studies examined reproductive success using nest predation experiments. Common detrimental effects of fragmentation on reproductive rates include increased nest predation (Stirnemann *et al*. 2015) and negative population growth rates (Korfanta *et al*. 2012). Conversely, fragmentation had little effect on breeding rates in a few cases. Reproductive rates can be robust to fragmentation if key resources remain intact inside fragments, or if vagile species can utilise the matrix to meet their foraging needs (Lees & Peres 2009).

Movement: Forest fragmentation impacts on movement were examined in 28 studies, considering birds and mammals with only one study on frogs (Robinson *et al*. 2013). Some species exhibited changes in their movement patterns in fragmented landscapes relative to contiguous forests. For instance, understorey birds in Central Amazonian Brazil have their movement restricted by open narrow roads and these roads act as territorial boundaries (Develey & Stouffer 2001). This could be due to intolerance of crossing fragment edges (Laurance *et al.* 2004), higher predation risks or increased competition from matrix-tolerant species that invade forest edges (Lees & Peres 2009; Shadbolt & Ragai 2010). However, other studies showed limited effects of fragmentation on movement. This could reflect species using the matrix for refuge (Robinson *et al*. 2013) or food (Estrada & Coates-Estrada 2002; Luck & Daily 2003), allowing species to traverse the matrix (Manning *et al*. 2006; Lees & Peres 2009).

Selective Logging

Over 20 percent of tropical forests were degraded by selective logging from 2000 to 2005 (Asner *et al*. 2009), yet selective logging has minimal negative impacts on biodiversity, often allowing the retention of similar species richness to primary forest (Gibson *et al*. 2011; Putz *et al*. 2012; Edwards *et al*. 2014), including species of conservation concern (Edwards *et al*. 2011). However, selective logging changes community composition (Chapman *et al*.

2000; Edwards *et al*. 2011, 2014) and can have more adverse effects on biodiversity at higher logging intensities (Burivalova *et al*. 2014; Martin *et al*. 2015) or when using poor ('conventional') logging techniques (Bicknell *et al*. 2014).

Survival: We found only one study that evaluated the impacts of selective logging on avian survival (VanderWerf 2004). No impact of selective logging was found on the survival of Hawaiian 'Elepaio bird populations (VanderWerf 2004) despite logged sites having a lower estimated carrying capacity. In this case, populations appeared to buffer disturbance impacts by increasing their territory sizes.

Reproductive rates: We found four studies examining the impacts of selective logging on reproductive rates, again all concerning birds. These showed varying responses to logging, including increased nest predation rates (Cooper & Francis 1998; Pangau-Adam *et al*. 2006) due to increased forest access for predators (Andren & Angelstam 1988) and mesopredator release after logging (Crooks & Soule 1999). Positive or neutral responses were also found in some cases, including no change in breeding success in logged habitats relative to unlogged (VanderWerf 2004; Yap *et al*. 2007).

Movement: We found seven studies examining the effects of selective logging on mammal and bird movements. Again, these studies found varying responses, with some species exhibiting no change and others showing inhibitions or movement changes. Species movement can be affected by selective logging if the exposed forest gaps and logging roads have harsher microclimates that deter species, or if changes in forest structure alter movement strategies (Cunha & Vieira 2002). Alternatively, movement can remain unaffected if logged forests provide suitable habitat or if there is plasticity in species behaviours (Wells *et al*. 2008).

Forest Fire

Forest degradation increases fire risk by increasing fuel load and exposing the forest to more wind and sun, which increases desiccation (Peres *et al*. 2006, Nepstad *et al*. 2008). El Niño drought-induced fires severely degraded ~20 million hectares of tropical forests in 1997-98 (Cochrane 2003) and millions of hectares in 2015-16. Burning can result in severe tree mortality, leading to the replacement of forest interior animals and hardwood emergent trees with generalist wildlife and pioneer plants (Barlow & Peres 2004; Brando *et al*. 2014). Fire typically reduces bird species abundance and richness, changing community composition (Barlow & Peres 2004, 2008; Slik & Van Balen 2006).

We found no studies assessing survival and reproductive rates with respect to fire-prone tropical forest landscapes. One study showed significant changes in movement behaviour of northern bettongs after fire (Vernes & Haydon 2001), indicating behavioural plasticity in movement in response to habitat alteration, though the potential consequences for demography were unclear. It is crucial that we better understand the implications of fire on species vital rates, given the drastic effects of fire on tropical forest structure, resources, and biodiversity.

Research effort by region & elevation

Our review highlighted some important regional and elevational biases in research (Fig 1). Survival, reproductive rate and movement studies spanned all tropical regions, but there was a preponderance of studies from the Neotropics (total=35; survival=3; reproductive rate=7; movement=25), with less than half the number of studies in the Afrotropics (total=16; survival=2; reproductive rate =8; movement=6), less than a third in the Indomalayan tropics (total=10; survival=0; reproductive rate=5; movement=5) and less than a quarter in the

Australasian/Oceanic tropics (total=8; survival=2; reproductive rate=2; movement=4) (Fig. 1; Table 1). All three vital rates were studied at all elevational classes, although more studies were conducted in the lowlands (50) compared to sub-montane (16) or montane elevations (11), despite uplands harbouring high endemism and extinction risk (Appendix S2). This trend is expected, however, being broadly in line with the total area covered by each elevational class across the tropics.

Discussion & Future Directions

Deforestation and forest degradation are key drivers of the current extinction crisis (Gibson *et al*. 2011; Barlow *et al*. 2016), but most knowledge of their impacts on biodiversity comes from one-off censuses conducted across a short time frame used to generate estimates of species richness and abundance patterns (Gibson *et al*. 2011; Burivalova *et al*. 2014; Edwards *et al*. 2014; Barlow *et al*. 2016). However, species richness and abundance may change over time if the degraded habitat is in extinction debt or if it recovers. Importantly, these abundance-based metrics can sometimes mask more severe underlying longer-term impacts on species persistence (Srinivasan *et al*. 2015; Gilroy & Edwards 2017). The fact that so few studies have been carried out in the tropics suggests that anthropogenic impacts might be underestimated. This might mean that the true biodiversity impact of anthropogenic disturbances like selective logging and low-intensity agriculture are much more significant than currently recognized, and thus that greater efforts are needed to assess impacts on demographic vital rates.

We find wide variation in observed vital rate responses to anthropogenic change across tropical vertebrates. This might reflect the variation in species-specific responses to disturbance, with many species possessing traits allowing them to persist in novel environments, whilst others are more vulnerable (Isaac & Cowlishaw 2004). However, we caution against making definite conclusions regarding these trends due to the different natures of these studies and varied methodologies, which makes direct comparison impossible. Furthermore, vital rate responses can vary regionally among populations of the same species (Frederiksen *et al*. 2005). Vital rate changes in species have been linked to both abiotic (soil nutrients, light availability, etc.) and biotic (competition, predation, etc.) processes at local scales, which brings further complexity to efforts in understanding and predicting land-use impacts (Ehrlen & Morris 2015). Many studies had small sample sizes (eg. Suarez-Rubio *et al*. 2015), because rarer or more elusive species were targeted, or study species inhabited inaccessible areas.

It is common practice to extrapolate a species' vital rate responses from a few locations to a wider area (Sæther *et al*. 2005), since it is not possible to sample every species in every location. However, the robustness of these extrapolation approaches has seldom been tested, and it is unclear which metrics are best used for extrapolating across populations. Coutts *et al*. (2016) showed that extrapolation is possible but at limited spatial scales, finding that demographic rates cannot be robustly extrapolated further than 20 km geographically. Extrapolation between species is further limited, with robust extrapolation unlikely for species pairs where phylogenetic distance exceeds 10 million years since the last common ancestor (Coutts *et al*. 2016). While this does not mean that it is impossible to apply the responses of one population over a larger range or to use rules of thumb derived from one species to make predictions about others, it suggests that more studies are required, sampling over larger areas and across more taxa, if we are to properly understand how underlying vital rates respond to land-use change.

We focused only on terrestrial vertebrates, though the research paucity identified will likely extend to other taxa. Land-use change impacts on tropical plant demography, in particular, may be critically important in determining long-term ecological resilience following anthropogenic impact. Terrestrial vertebrates are important pollinators and dispersers for plants and are likely to drive the vital rates of plants (Kremen *et al*. 2007; Peres *et al*. 2016). For example, fragmentation can be detrimental to plant vital rates (Bruna *et al*. 2002; Laurance *et al*. 1998) if their pollinators and seed dispersers are negatively affected (Regan *et al*. 2015, Peres *et al*. 2016) or seed predation increases (Curran & Webb 2000; Scariot 2000).

It is difficult to reliably compare between demographic studies as there is a lack of consistency in the methods and metrics used. This lack of consistency combined with the paucity of vital rate data make it difficult to understand or predict patterns in species' demographic responses to environmental change (Sutherland *et al*. 2013). One effort to promote the standardization of data is the COMPADRE Plant Matrix (Salguero-Gomez *et al*. 2015) and COMADRE Animal Matrix (Salguero-Gomez *et al*. 2016) databases. These open data repositories contain matrix population models for both plant and animal species that aim to encourage more comparative studies. So far, COMPADRE has facilitated more than 35 comparative studies since its establishment in 1990 (eg. Stott *et al*. 2011). By compiling and standardizing vital rate data, ecologists will be better able to identify gaps in our knowledge and thus broaden the coverage of data across species and geographical locations.

A role for indirect evidence?

As direct measurement of species vital rates to determine the long-term risk posed by tropical forest disturbance are relatively rare, a key question is the degree to which it is possible to use indirect evidence to infer impacts. One method is to use count-based abundance and density trends to infer demographic change (Durant *et al*. 2011), especially when data are collected over a long-time series (Durant *et al*. 2011; Keith *et al*. 2015). However, long-term trends in abundance and density may still mask negative demographic impacts in situations that involve source-sink dynamics (Gilroy & Edwards 2017), where population density can be maintained despite reductions in population growth rate by immigration of individuals from surrounding habitat (Pulliam 1988). Furthermore, density can be higher in disturbed habitats, despite declining demographics, from processes such as competitive exclusion ('dominance hierarchies', Holt 1985), the crowding effect (Debinski & Holt 2000) or individuals mistaking poorer quality habitats as being more attractive ('ecological traps', Gilroy & Sutherland 2007).

Another potential method is to use observed contractions in species ranges due to land-use change as a predictor for increased species' extinction risk (Harris & Pimm 2008). For instance, incorporating geospatial data by refining species geographical ranges using elevation maps and the extent of remaining habitat cover could improve the accuracy of predictions in species extinction risk analyses (Ocampo-Peñuela *et al*. 2016). Using this approach, Ocampo-Peñuela *et al*. (2016) assessed the extinction risk posed by land-use change for 586 tropical forest bird species from six regions (Southeast Asia, Sumatra, Madagascar, Colombia, Central America and Brazil) and showed that 210 species were more at-risk than previously thought .

Evaluating change in suitable habitat quality and area can also allow inferences of changes in species abundance and ranges to be drawn, providing insights into resilience under changing habitat conditions (Jennings 2000, Harris & Pimm 2008). Such regular assessments are especially important for tropical species, where land-use change occurs rapidly (Barlow *et* *al*. 2016). Although Negret *et al*. (2015) only conducted a one-off assessment of the range size of black tinamou (*Tinamus osgoodi hershkovitzi*), it revealed that their habitats are increasingly degraded by logging, hunting and agricultural activities, thus threatening the species with extinction despite populations currently occurring at high densities. Such data are important for providing a better understanding of the future resilience of species.

In conclusion, the current paucity of data makes it difficult to draw definite conclusions about the state of many tropical forest ecosystems, potentially influencing the robustness of conservation prioritization and management efficacy. We call for significant increases in long-term research efforts to measure demographic responses in a far wider variety of taxa, regions and habitat types across the tropics. Such data are also critical to assess the reliability of predictions made from indirect evidence, and may ultimately permit greater confidence, under certain circumstances at least, in the use of those forms of data to infer demographic change. Both would greatly aid the development of conservation approaches to reduce the impacts of land-use change through more sustainable natural resource use and improved protected area design throughout the tropics.

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Supporting Information

Complete list of studies on vital rates (Appendix S1) and number of studies with positive, negative and varying responses to land-use change, grouped by elevation (Appendix S2) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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TABLE 1. Number of studies with positive, negative and varying responses to land-use change, grouped by land-use type, region and taxa.

Land-use	Survival	Reproductive success	Movement	Response
Agriculture	1	3	7	Positive
	1	4	7	Negative
	1	1	5	Varies
Fragmentation	1	6	8	Positive
	2	7	9	Negative
	1	2	11	Varies
Logging	1	2	3	Positive
	0	2	3	Negative
	0	0	1	Varies
Fire	0	0	0	Positive
	0	0	1	Negative
	0	0	0	Varies
Region	**Survival**	**Reproductive success**	**Movement**	**Response**
Neotropics	0	2	9	Positive
	1	3	7	Negative
	2	2	9	Varies
Afrotropics	1	4	2	Positive
	1	4	3	Negative
	0	0	1	Varies
Indomalayan tropics	0	2	3	Positive
	0	2	2	Negative
	0	1	0	Varies
Australasian tropics/ Oceania	1	1	1	Positive
	1	1	2	Negative
	0	0	1	Varies
Taxa	**Survival**	**Reproductive success**	**Movement**	**Response**
Birds	2	8	3	Positive
	2	9	7	Negative
	1	2	9	Varies
Mammals	0	1	11	Positive
	1	1	6	Negative
	1	1	2	Varies
Reptiles	0	0	0	Positive
	0	0	0	Negative
	0	0	0	Varies
Amphibians	0	0	1	Positive

	0	0	1	Negative
	0	0	0	Varies

Figure Legends

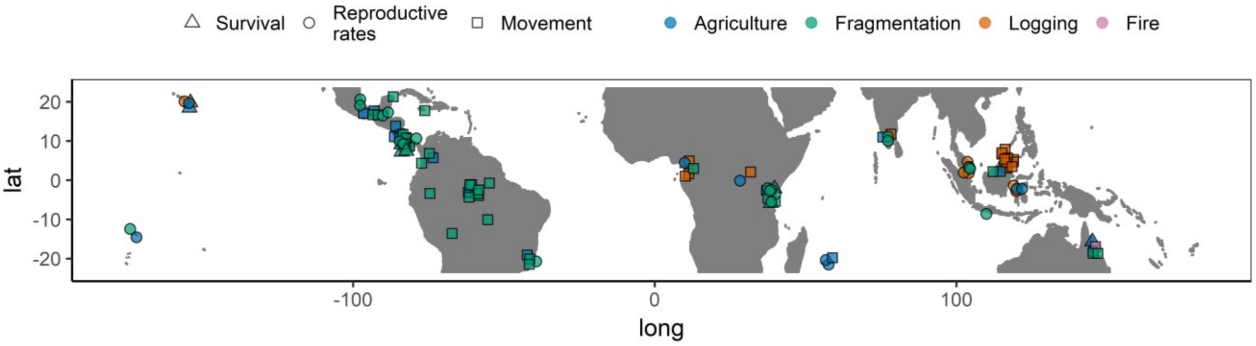

FIG 1. Distribution of vital rates studies across regions by land-use type (agriculture, fragmentation, selective logging, and fire) and vital rate category (survival, reproductive rates and movement).

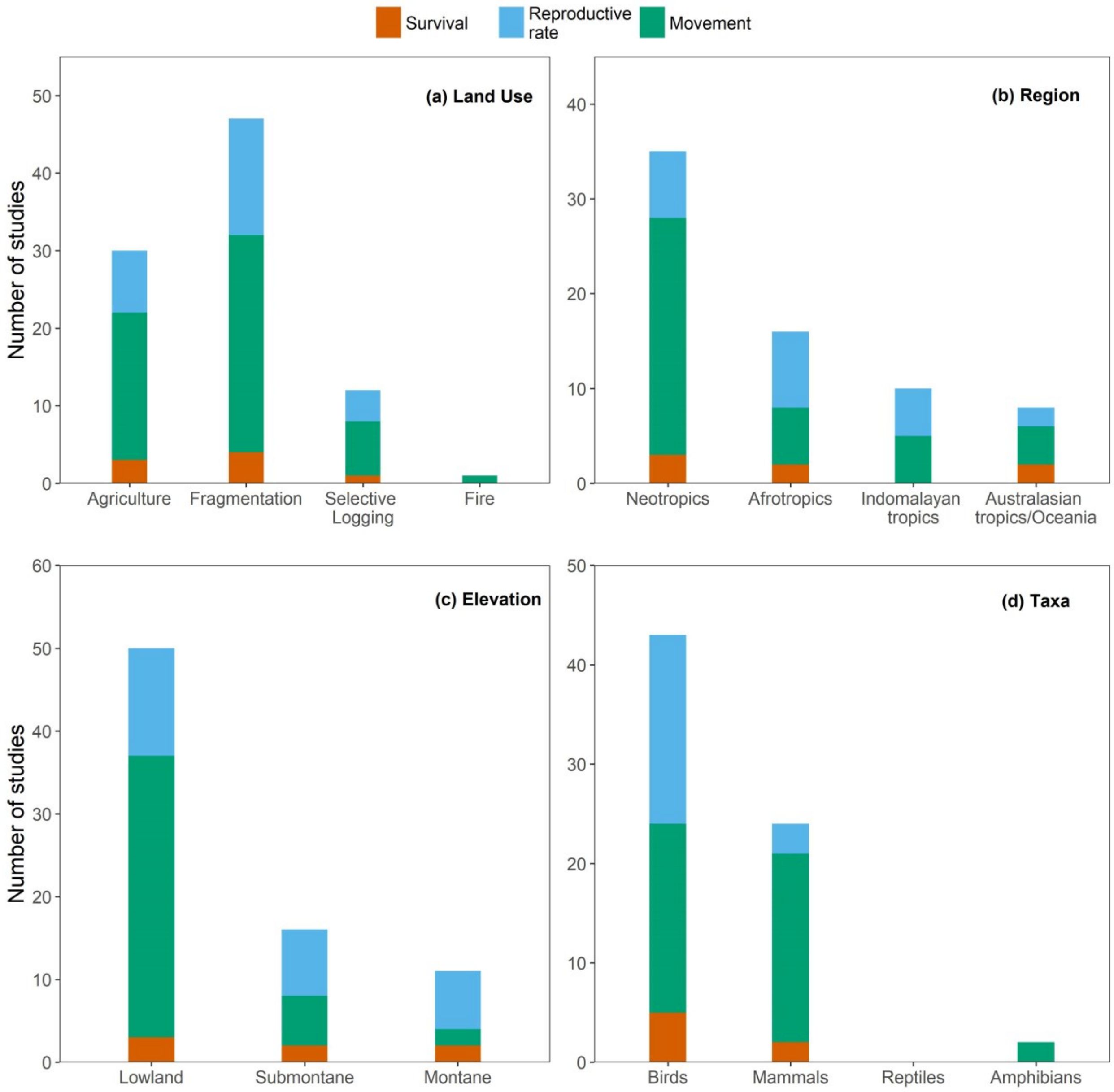

FIG 2. Number of studies assessing animal vital rates grouped by land-use type (a), region (b), elevation (c) and taxa (d). In each grouping, studies are classified into vital rate category: survival, reproductive rates or movement.