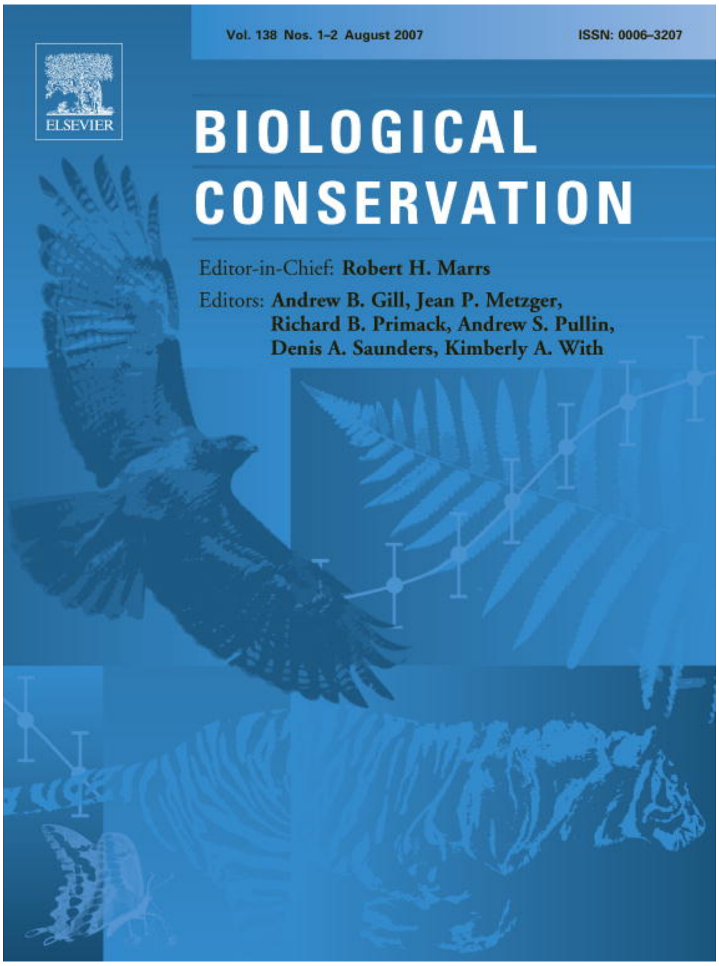
Vol. 138 Nos. 1–2 August 2007
ISSN: 0006-3207
ELSEVIER
BIOLOGICAL CONSERVATION
Editor-in-Chief: Robert H. Marrs
Editors: Andrew B. Gill, Jean P. Metzger,
Richard B. Primack, Andrew S. Pullin,
Denis A. Saunders, Kimberly A. With

BIOLOGICAL CONSERVATION 138 (2007) 166–179

available at www.sciencedirect.com

ScienceDirect

journal homepage: www.elsevier.com/locate/biocon

Paradox, presumption and pitfalls in conservation biology: The importance of habitat change for amphibians and reptiles

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ARTICLE INFO

Article history:
Received 3 June 2006
Received in revised form
28 January 2007
Accepted 9 April 2007
Available online 30 May 2007

Keywords:
Habitat change
Population declines
Research bias
Herpetology
Sampling

ABSTRACT

The recent shift in research attention by amphibian biologists towards the causes of "enigmatic" population declines appears paradoxical given the almost unanimous recognition that habitat change is the primary cause of population declines worldwide. Justification for this shift is given by the growing concern associated with more novel stressors, as well as a general presumption that we have a good understanding of the ecological mechanisms that underlie the effects of habitat change. We tested the validity of this presumption by conducting a global scale review of the state of research regarding the consequences of structural habitat change (fragmentation, logging, fire, native regeneration and plantations) for amphibians and reptiles. We reveal a number of serious deficiencies, namely that existing research efforts are characterised by distinct geographic and study biases (e.g. most studies are confined to North America and focus on amphibians), a lack of clear consensus regarding the consequences of many forms of habitat change with many studies reporting seemingly contradictory results, and a number of common limitations in sampling design. The recent shift in research agenda towards the study of more novel stressors, and away from a focus on structural habitat change, cannot therefore be easily explained by differences in our understanding of the threats currently facing amphibians and reptiles. If research priorities are to be dictated by differences in scientific uncertainty then our results suggest that the study of habitat change is deserving of considerably more attention.

1. Introduction

Amphibians and reptiles have the highest threat status of all terrestrial vertebrates, with significantly more species at risk than either birds or mammals (IUCN, 2006). Particular concern has been raised about many amphibian species following a rising number of enigmatic population declines in areas of relatively pristine habitat (Stuart et al., 2004; Beebee and Griffiths, 2005). The recent Global Amphibian Assessment (Stuart et al., 2004; Young et al., 2004) identified only 35% of all neotropical and nearctic amphibian species (which together comprise 53% of the global fauna) in the Least Concern category, defined as widespread, common, and holding a good chance of survival under prevailing conditions. Reptiles, although poorly studied, are likely to be equally or more threatened than amphibians (IUCN, 2006), and are often vulnerable to the same types of threat (Gibbons et al., 2000).

A number of recent reviews have identified an array of threats to account for declining amphibian and reptile populations (Alford and Richards, 1999; Gibbons et al., 2000; Semlitsch, 2000, 2003; Blaustein and Kiesecker, 2002; Collins and Storfer, 2003; Beebee and Griffiths, 2005). Collins and Storfer (2003) recently summarized these threats into two classes of hypotheses, defined as (i) direct factors including habitat change, over-exploitation and the introduction of exotic species (termed Class I hypotheses); and (ii) more indirect factors

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0006-3207/$ - see front matter
doi:10.1016/j.biocon.2007.04.017

such as global climate change, acidification, pollution and infectious diseases (Class II hypotheses). For the purposes of our study we simplify this categorisation further to distinguish threats concerned with structural habitat change (i.e. changes in habitat and/or landscape vegetation structure and/or hydrological regime), versus all other "non-structural" threats (although we note that many conservation biologists relate to certain types of "Class II" hypothesis as forms of habitat degradation).

Habitat change is unanimously accepted amongst conservation biologists as being the primary cause of biodiversity loss worldwide (Sala et al., 2000), and the situation for amphibians and reptiles is no exception (Alford and Richards, 1999; Gibbons et al., 2000; Collins and Storfer, 2003; Crump, 2003; Dodd and Smith, 2003; Hazell, 2003; Cushman, 2006). For example the Global Amphibian Assessment recently identified habitat loss as affecting 89% of all threatened species in the New World, rendering it approximately three times more prevalent than any other threat (Young et al., 2004). Understanding the consequences of habitat change for biodiversity is important because the current protected area network is insufficient to safeguard the majority of the world's species (e.g. Rodrigues et al., 2004), and the persistence of many species depends upon the effectiveness of strategies for conserving biodiversity in human-dominated landscapes (Daily, 2001; Lindenmayer and Franklin, 2002; Semlitsch and Rothermel, 2003; Vandermeer and Perfecto, 2007). It is therefore paradoxical that the last two decades have witnessed a shift in the research attention of studies concerned with amphibian declines away from the consequences of habitat loss and towards a focus on non-structural threats ("Class II" hypotheses) (Collins and Storfer, 2003; Beebee and Griffiths, 2005).

There are two main reasons for this change. First, particular concern has been raised by the enigmatic declines of many amphibian populations (Stuart et al., 2004), with recent declines in different populations frequently occurring simultaneously, and in areas isolated from direct human influence (Collins and Storfer, 2003). Especially worrying are the losses that have been attributed to disease outbreaks (Daszak et al., 2003; Lips et al., 2006), and the likely interaction between disease epidemics and climate change (Pounds et al., 2006; Cunningham et al., 2006), because such threats cannot be easily dealt with by direct policy action. Second, there is a general presumption that we have a good understanding of the basic ecological mechanisms that underlie population declines associated with structural habitat change (Alford and Richards, 1999; Gibbons et al., 2000; Collins and Storfer, 2003; Semlitsch, 2003; Storfer, 2003), whereas Class II type hypotheses are argued to be intrinsically complex and involve the subtle interaction of multiple factors that are more difficult to understand (Collins and Storfer, 2003).

Is the current shift towards a research agenda focussed on Class II hypotheses a fair reflection of differences in scientific uncertainty associated with different stressors currently facing amphibians and reptiles? Understanding this balance is important because given the desperately limited resources available to conservation (Balmford and Whitten, 2003), it is essential that we are strategic in directing research efforts towards the highest priorities. One way to answer this question, and test whether the presumption that we have a good understanding of the consequences of habitat change for herpetofauna is justified, is to review the evidence from existing studies that have focussed on different forms of structural habitat change. If this presumption is correct, then we would expect that (i) there is a substantial amount of data available from all areas of the world that describe the responses of herpetofaunal assemblages to multiple gradients of habitat change; and (ii) the majority of these studies provide a clear consensus regarding the effects of different forms of habitat change on amphibians and reptiles, with conclusions faithfully mirroring *a priori* predictions based on our understanding of the underlying ecological mechanisms.

The main aim of this paper is to test whether these expectations are supported by the available evidence. Existing reviews of the consequences of habitat loss for amphibians and reptiles have largely been limited to studies on temperate amphibians, especially in North America (Demaynadier and Hunter, 1995; Cushman, 2006; but see Gibbons et al., 2000 for an account of reptiles) and the Australian sub-tropics (Hazell, 2003), or have been limited to the consequences of fragmentation (Cushman, 2006). To address this knowledge gap we conducted a global assessment of the current status of research, and any biases in research focus and effort, on the consequences of structural habitat change on amphibian and reptile communities. We considered the main forms of structural habitat change (habitat fragmentation, logging, fire, secondary forest regeneration, and plantations), and address three main questions. First, what is the extent and focus of existing research? – including the existence of any biases that relate to the choice of study taxon, geographic region, type of habitat change studied, and the type of data that were collected and analysed. To assess whether amphibians and reptiles have suffered from particular neglect compared to studies of other vertebrates, we also reviewed the extent of similar research available for birds and mammals. Second, what are the major conclusions of research that has been conducted with respect to different forms of habitat change regarding patterns of species richness? Finally, are there any biases in the sampling design and effort that can assist in interpreting the conclusions of these studies? We use these findings to evaluate the global status of research on the consequences of habitat change for herpetofauna, and discuss the implications of our findings for amphibian and reptile conservation.

2. Materials and methods

2.1. Data collection

To review published studies reporting the consequences of habitat change for amphibian and reptile assemblages we made a series of comprehensive searches using Thompson ISI Web of Knowledge (1945–2006). All studies returned by the database in response to key terms relating to different forms of structural habitat change were checked for relevance, namely: "amphibians" or "reptiles" or "herpetofauna" together with one of, "habitat fragmentation", "logging", "secondary forest", "plantations", "fire", "habitat loss", as well as "disturbance" and "conservation". References cited within these papers were also checked. Because we were primarily interested in studies of structural habitat change we ignored studies concerned with temporal change at a single site, and all studies concerned with non-structural stressors. We also ignored studies on road-kills or those located wholly within an urban environment. We were interested primarily in studies reporting changes in community or assemblage parameters (richness, abundance and community structure), and therefore ignored studies addressing either a single species, genetic diversity, or biogeographic patterns based on independently derived species range distributions.

2.2. Extent and focus of existing research

Using the selected studies we compiled a database detailing: (i) the focal group investigated (amphibians, lizards, reptiles, or the entire herpetofauna); (ii) the type of disturbance (habitat fragmentation – including edge effects, logging – including both selective and clear-fell logging, fire, natural forest regrowth, and plantation forestry); (iii) the geographic location of study; (iv) the biome (tropical, sub-tropical, temperate); and (v) the dominant habitat type (forest or dry woodland/savannah). To provide a coarse-scale comparison of the extent and focus of research that has been conducted on the consequences of structural habitat change for birds and mammals, we compared the number of publications returned by a single search on Thompson ISI Web of Knowledge (1990–2006, to account for the fact that international concern surrounding amphibian declines only arose 16 years ago) for each taxon name together with each form of habitat change. While this approach is not as thorough as that conducted for amphibians and reptiles alone (e.g. not all publications selected will be empirical studies), it provides an adequate measure of any gross differences in research volume that may exist between different vertebrate classes. To further assess the variability in research focus of different studies we recorded the type of data that was collected as well as the type of analyses that were used.

2.3. Research conclusions

Differences in design and sampling methods of different studies, as well as a failure to report basic statistics by many studies, prevented us from conducting a formal meta-analysis, or from considering any effects other than species richness. However, for the purposes of our study a qualitative review of the reported results regarding species richness – the most commonly employed diversity metric in conservation – provides a useful assessment of any similarities and differences in overall conclusions.

2.4. Bias in sample design and effort

Significant variability in the level of sample design information reported by different studies confounded our attempts to make comparisons of the plot sizes used to represent different habitat change treatments. However, most studies reported summary information on the existence and quality (extent of historical disturbance) of control sites, and for those studies that had a control we scored whether the area was greater than 100 ha or greater than 1000 ha.

Comparisons of sampling effort among studies are even more problematic than comparisons of sampling design. A wide range of sampling methods are frequently employed in herpetological studies (e.g. Heyer et al., 1994), many of which differ substantially in their effectiveness at sampling either different habitats or different species groups. Moreover, depending on their sampling protocol, different researchers have used a wide range of definitions of what constitutes an independent replicate sample. Unfortunately, these differences prevented us from comparing different levels of replication, and the extent to which different studies are beset by pseudoreplication, both of which may restrict a researcher's ability to capture any true variability in the distribution of herpetofauna.

Despite these limitations, our ability to understand the relationship between species occurrences and/or abundances and habitat quality increases with the number of individuals caught per species of interest. One of the greatest potential perils in policy-relevant conservation science is our failure to identify an effect of human activity on natural systems when one exists (Type II errors); either because of small sample sizes, poor sampling design or an inappropriate significance (probability) value or effect size. If a study reports either a significant or non-significant difference in species richness between treatments, we can be more confident that either conclusion is valid if all species were well represented in the overall sample, thereby reducing the risk of both Type I and Type II errors. Consequently we used the number of individuals captured/encountered per species captured/encountered as a useful index of "sampling intensity" which partially accounts for differences in habitat and method between studies (see Coddington et al., 1996). Although this index is crude because it will be strongly influenced by differences in species-abundance relationships between sites, it does provide a useful and valid comparison of sampling effort among biomes. Most importantly, given that tropical and subtropical sites are usually more species-rich (and contain comparatively more rare species) than temperate sites, we would expect that larger levels of sampling intensity would be required to achieve levels of statistical power comparable to that found in temperate areas for surveys of similar quality. We tested for differences in sampling intensity using non-parametric Kruskall–Wallis and Mann–Whitney comparisons.

3. Results

3.1. Extent and focus of existing research

We found a total of 112 suitable studies worldwide reporting the consequences of structural habitat change for amphibians and reptiles that matched our selection criteria (see Appendix A). The distribution of these studies between species groups and among biomes was non-random (Table 1, and Fig. 1). For example, nearly half of all studies included only amphibians (48%), whilst only 16% included only lizards and 6% included other reptiles in addition to lizards. The remaining 30% of all studies recorded patterns of land-use change for both amphibians and reptiles. Of these, one third (8% of the total) did not consider amphibians and reptiles

Table 1 – The total number of herpetological studies that have evaluated the consequences of different forms of habitat change across the world

Biome	Location	Fire	Selective logging	Fragmentation[b]	Plantation forestry[c]	Second growth[d]	Clear cuts	Other land-use change[e]	Totals
Temperate	Europe			1				1	2 (3)
	North America	5	10	18	6	13	7	2	61 (97)
	Total	5	10	19	6	13	7	3	63 (40)
Sub-tropical	Australia	5	3	4	2	2	1	2	19 (36)
	Africa							2	2 (4)
	Central America/Caribbean			5	5	4	1	3	18 (35)
	India				1	1			2 (4)
	North America	2	2	1		3	1		9 (17)
	South America					1		1	2 (4)
	Total	7	5	10	8	11	3	8	52 (33)
Tropical	Africa		1		2	1		1	5 (6)
	Australia	1							1 (1)
	India			1	2			1	4 (5)
	Madagascar[a]	1	1	2	1	1	1		7 (10)
	Pacific			1					1 (2)
	South East Asia		1		2	2	1	1	7 (17)
	South America	1	5	5	2	3		1	17 (40)
	Total	3	8	9	9	7	2	4	42 (27)
Totals		15 (10)	23 (15)	38 (24)	23 (15)	31 (20)	12 (8)	15 (10)	157

Some studies included more than one form of habitat change. Percentages for each category are given in brackets.
a Madagascar is considered separately from continental Africa.
b Fragmentation studies include all those concerned with area, isolation and edge effects.
c Plantation forestry includes monocultures and agroforestry systems.
d Second growth includes regeneration from degraded land as well as abandoned plantations.
e Other land-use categories are mostly arable and pastoral systems but also include mining and bush encroachment.

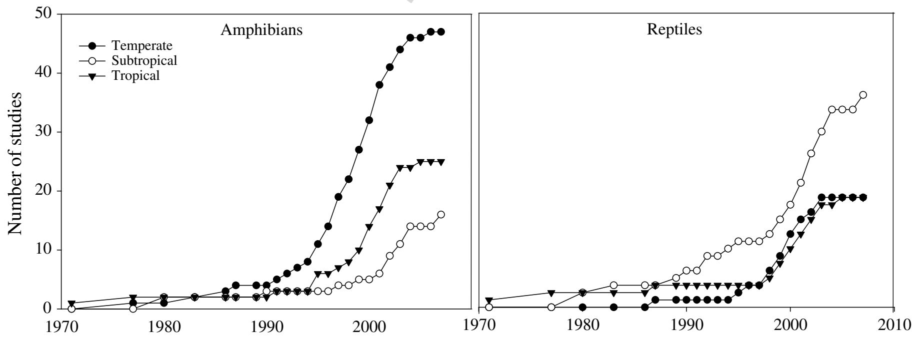

Fig. 1 – Number of studies reporting the effects of habitat change on amphibian and reptile assemblages over the last three decades. Studies that sampled the entire herpetofauna contributed towards both panels.

separately but examined patterns of diversity/abundance for the entire herpetofaunal assemblage. The volume of research concerned with the consequences of habitat change for amphibians and reptiles is much less than that for either birds or mammals (Fig. 2).

In terms of geographic representation, most studies were from the New World (67%), with 45% from North America and only 13% and 9% from South and Central America respectively. Australia held the same number of studies as South America. Comparing between major biomes, the number of studies was relatively similar with slightly more in temperate biomes (43%) than in the subtropics (28.5%) or the tropics (28.5%). The distribution of studies focusing on amphibians or reptiles was uneven between major regions, with proportionately more amphibian studies in temperate biomes, and more reptile studies in the sub-tropics (Fig. 1). Over three quarters of all studies were from currently or historically forested areas (77%), with the remainder from either wetlands (10% – all in the North America), dry woodlands and savannahs (12% – mostly in Africa), or grasslands (1% – North America).

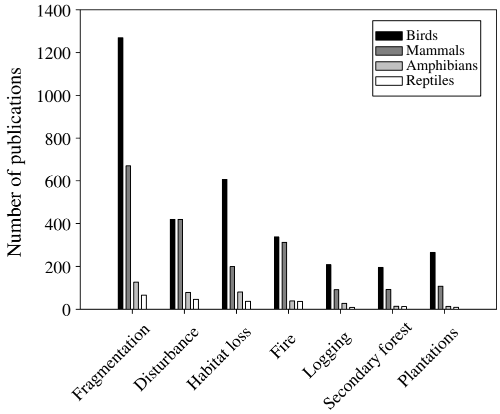

Fig. 2 – Number of publications found by searches on Thompson ISI Web of Knowledge, that include a focus on the consequences of different forms of structural habitat change for amphibians, reptiles, birds and terrestrial mammals.

All studies combined provided a total of 157 separate land-use/habitat change comparisons (45 studies addressed more than one type of change), with a relatively even split between studies concerned with different forms of habitat change (although the objectives were not evenly balanced among different geographical zones – Table 1).

Different studies reported different types of effect and analysed data in different ways, although the majority evaluated patterns of assemblage richness and abundance, while also incorporating some explanatory environmental or habitat data (Table 2). Nearly half of all studies evaluated patterns of individual species abundance, while comparisons of species occupancy (presence/absence) were particularly popular in the temperate biome (Table 2). Relatively few studies attempted to define differences in the response of individual guilds, analyse patterns of community structure, or assign a measure of conservation value to each species (defined as endemicity, range size, threat status or habitat specialization) (Table 2).

Table 2 – The choice of community and species parameters (effect sizes) used in herpetological studies of habitat change across major geographic regions

Biome	Temperate	Sub-tropical	Tropical	All studies
Parameter		Percent of studies		
Species richness	67	88	56	70
Assemblage abundance	69	59	56	63
Guild abundance	8	22	34	20
Individual species abundances	44	59	44	48
Species presence/absence	25	6	3	13
Diversity indices	23	34	19	25
Community structure/turnover	13	38	41	28
Species value	0	9	9	5
Environmental relationships	75	88	59	74

3.2. *Research conclusions*

3.2.1. *Fragmentation and edge effects*

Most habitat fragmentation studies on both amphibians and reptiles supported the positive species–area relationship for both temperate (Findlay and Houlahan, 1997), and sub-tropical and tropical systems (Vallan, 2000; Alcala et al., 2004; Driscoll, 2004; Krishnamurthy, 2003; Pineda and Halffter, 2004), although few studies found an effect of isolation (e.g. Lehtinen et al., 1999). In contrast, habitat fragment size had no effect on lizard richness in Tasmania, where local differences in habitat and vegetation structure were more important (Jellinek et al., 2004). Lima and Gascon (1999) found no differences in frog species richness or abundance in linear forest remnants compared to continuous forest in the central Brazilian Amazon. At the same site, Tocher et al. (1997) found more frog species in forest fragments than in continuous forest, which was attributed to the invasion of open-habitat species from the surrounding secondary forest matrix. Only one study examined the consequences of fragmentation at an appropriate landscape (rather than patch, see Fahrig, 2003) scale (Driscoll, 2004).

There was no strong support for the importance of edge effects for either amphibians or reptiles, with a number of studies finding either no effect (Gascon, 1993; Biek et al., 2002; Toral et al., 2002), a weak effect (Demaynadier and Hunter, 1995), or a species-specific effect with no overall change in richness (Schlaepfer and Gavin, 2001; Lehtinen et al., 2003).

3.2.2. *Selective logging*

Only one study reported a significant loss in species richness in selectively logged areas (salamanders: Vesely and McComb, 2002), whilst many others in both temperate and tropical forests found either no difference for both amphibians (Pearman, 1997; Fredericksen and Fredericksen, 2004; Vallan et al., 2004) and reptiles (Greenberg et al., 1994; Goldingay et al., 1996), or a higher species richness in logged areas for both amphibians (e.g. Lemckert, 1999) and the entire herpetofauna (Vonesh, 2001; Fredericksen and Fredericksen, 2002). Only two studies, however, reported both pre- and post-harvest species data (Renken et al., 2004; Vallan et al., 2004).

3.2.3. *Secondary forests*

All studies in regenerating forests/woodlands (15–35 years old) found consistently fewer amphibian and reptile species than in neighbouring primary forest, although one half to two-thirds of primary forest species in a given landscape were recorded in secondary forest (Crump, 1971; Lieberman, 1986; Bowman et al., 1990; Heinen, 1992; Petranka et al., 1993; Tocher et al., 2002; Vallan, 2002; Ashton et al., 2006; Gardner et al., 2007b). Marked differences in local habitat conditions and disturbance history confound comparisons among sites (Chazdon, 2003), although studies encompassing different age-classes of secondary forest indicate that amphibian and reptile species richness generally increases with stand age in both tropical (Bowman et al., 1990; Heinen, 1992; Pawar et al., 2004) and temperate systems (Petranka et al., 1993; Herbeck and Larsen, 1999), although a woodland restoration project in the Argentinan Chaco resulted in no change in the number of lizard species after 25 years (Leynaud and Bucher, 2005). Dunn (2004) predicted that the species richness of regenerating forest can resemble mature forest within 20–40 years, although there are very few studies with sufficiently long-term time series to support this prediction for amphibians and reptiles, and it is likely that much longer time scales are required (Petranka et al., 1993, 1994; Pawar et al., 2004).

3.2.4. *Plantation forestry*

Most studies in different types of plantation forest found fewer amphibian and reptile species than in neighbouring primary forest, both for temperate (Hanlin et al., 2000) and sub-tropical systems (Glor et al., 2001; Parris and Lindenmayer, 2004; Pawar et al., 2004; Pineda and Halffter, 2004; Pineda et al., 2005; Kanowski et al., 2006; Gardner et al., 2007b). Nevertheless, a number of studies found either no difference in the number of species (Ryan et al., 2002; Germano et al., 2003) or a greater number of species in plantation sites compared to adjacent controls (Vonesh, 2001; Loehle et al., 2005).

3.3. *Bias in sample design and effort*

Temperate biomes had fewer studies with undisturbed control sites than either the subtropics or the tropics (Fig. 3), with only 14% of all temperate studies reporting access to a control site. Most studies did not have, or failed to report, access to a control site larger than 1000 ha (Fig. 3). Sampling effort as defined by our metric of sampling intensity was significantly different among major geographic regions for amphibians ($\chi^2 = 6.9$, $p = 0.032$; Fig. 4a), with a higher level of effort in temperate than tropical studies ($U = 77.5$, $p = 0.008$). However, there was no significant difference between tropical and sub-tropical ($U = 60$, $p = 0.59$) or sub-tropical and temperate studies ($U = 80$, $p = 0.18$). There was no difference in sampling effort among geographic regions for reptile studies ($\chi^2 = 0.7$, $p = 0.69$, Fig. 4b). Amphibian samples were significantly larger than reptile samples in temperate biomes ($U = 24$, $p = 0.004$), but similar in subtropical and tropical biomes ($p > 0.54$).

4. Discussions and conclusions

4.1. *Extent and focus of research on the consequences of habitat change for amphibians and reptiles*

Our review uncovered many high quality studies that have significantly improved our understanding of the consequences of structural habitat change for both amphibians and reptiles. This body of work has made an effective contribution towards developing landscape management strategies for conservation, particularly with regard to aquatic breeding amphibians in North America (Semlitsch, 2000; but see also

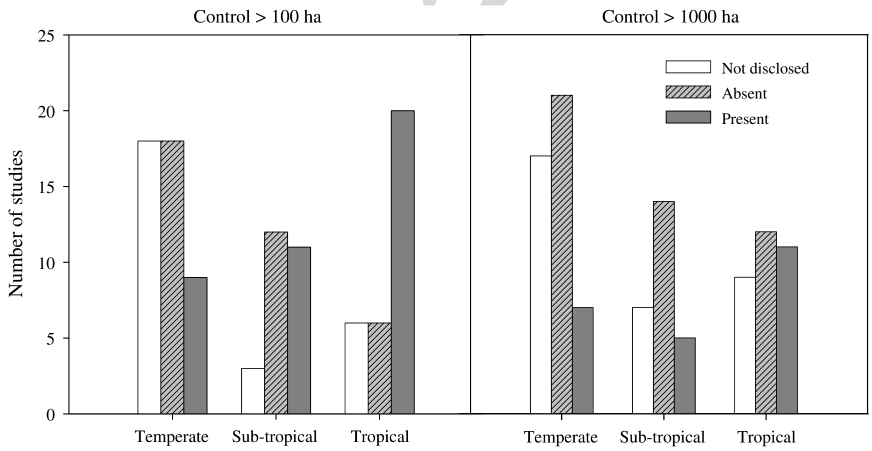

Fig. 3 – Availability and disclosure of control sites in studies of habitat change on herpetofaunal assemblages.

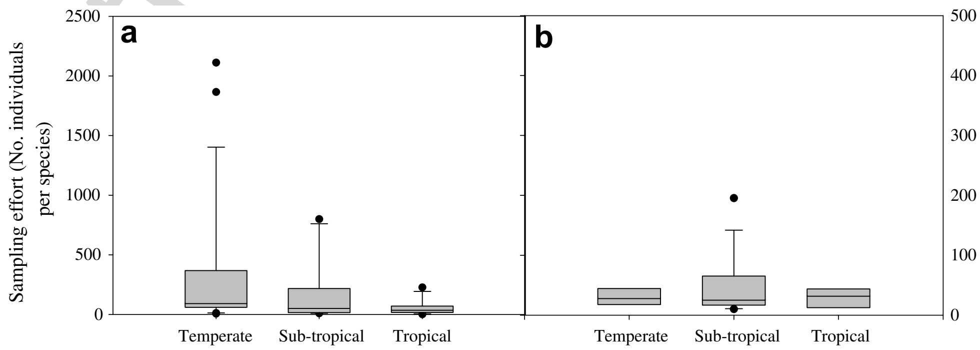

Fig. 4 – Differences in sampling effort in studies of habitat change on (a) amphibian, and (b) reptile assemblages across major geographic regions. Boxplots illustrate median, lower and upper quartiles as boxes, 10% and 90% quartiles as whiskers, and outliers as black dots. Note the difference in the scale of the y axis for each panel.

Calhoun and Hunter, 2003; Semlitsch and Rothermel, 2003). Despite these developments we feel that our failure to find more than 112 internationally published herpetological studies on the consequences of structural habitat change is cause for concern, suggesting that the level of threat associated with habitat change is not balanced by a proportional level of research effort. This apparently paradoxical lack of researcher attention regarding the consequences of habitat change is not restricted to herpetofauna, but is symptomatic of conservation field research in general. For example, in a survey of all 527 conservation biology papers published in three leading international journals in 2001, only 2% were concerned with the loss of native habitat, whereas 54% were conducted exclusively in undisturbed areas (Fazey et al., 2005a) Furthermore, our review indicates that almost an order of magnitude more research has been conducted on the consequences of each form of structural habitat change for birds and mammals than for amphibians and reptiles (Fig. 1, and see Fazey et al., 2005a), despite the fact that both birds and mammals are less threatened (IUCN, 2006).

Given the heightened concern surrounding amphibian populations in recent years, it is unsurprising that studies of amphibians are more abundant than those of reptiles. Furthermore, reptiles often lead predominantly secretive and solitary lives, without the breeding aggregation behaviour characteristic of so many frogs. These habits make them exceptionally difficult to study, and their plight is more difficult to discern than that of any other class of terrestrial vertebrates (Gibbons et al., 2000). The increase over time in the number of both amphibian and reptile studies is encouraging, but is greatly outpaced by habitat degradation and the corresponding rise in the number of threatened species (IUCN, 2006).

Nearly half of all studies were from North America which supports a strong cadre of professional herpetologists, with comparatively fewer studies from elsewhere in the New World despite the significantly greater number of endangered amphibians (Young et al., 2004). This pattern of researcher effort is unsurprising, as the United States of America consistently contributes more than one third of the global scientific output as measured by the total number of publications (May, 1997; Fazey et al., 2005b). Australia contributed the second highest number of studies to the database, yet our understanding of the consequences of habitat change on native amphibians and reptiles in this biologically unique continent remains critically poor (Hazell, 2003; Kanowski et al., 2006). However, of greatest concern is the near absence of studies from many parts of the world that are currently experiencing unprecedented rates of habitat destruction and degradation, including the Caribbean, South-East Asia, Oceania and continental Africa.

Some important patterns emerged regarding the different metrics used to evaluate the consequences of habitat change for amphibians and reptiles. Species richness is the most popular metric of conservation importance among field biologists, policy makers and the public alike (Gaston, 1996), and this fact is reflected in our review (Table 2), although there were proportionally fewer tropical studies comparing patterns of species richness than either temperate or sub-tropical studies. Cushman (2006) identified the importance of investigating species level implications of habitat loss and fragmentation, and we were encouraged by the fact that nearly half of all studies included some consideration of individual species patterns (not including additional single-species studies outside this review).

Few studies made any attempt to classify species into ecologically meaningful functional groups or guilds, despite the fact that measures of body size, reproductive mode, microhabitat association or taxonomic family are all useful proxies of ecological function, and can easily be identified for many assemblages (Stebbins and Cohen, 1995; Vitt and Pianka, 2003). Furthermore, most studies failed to assign any measure of species value in evaluating responses to habitat change. Conservation biologists are increasingly recognizing that not all species are equally “important”, and that interpreting patterns of biodiversity value between different land-use options can be improved using an independent and objective measure of value such as sensitivity to disturbance (e.g. Tocher et al., 2002; Vallan et al., 2004), threat status, or endemicity (e.g. Gillespie et al., 2005).

4.2. *Examining the biodiversity consequences of habitat change for amphibians and reptiles: challenges and pitfalls*

In general, we identified a gradient of increasing severity of impact on species richness with decreasing structural and habitat complexity, and increasing management intensity from selective logging through habitat fragmentation, to secondary forests and plantations. However, we also identified a notable lack of consensus among studies, both within and between biomes. More specifically, many studies revealed either no impact or a positive impact of habitat change on species richness, especially in relation to habitat fragmentation and selective logging. In order to gain a broader insight into our understanding of the ecological mechanisms that underpin this complexity of response patterns, it is necessary to consider the results of different studies in light of potential biases in sampling design and effort. A number of factors should be considered in the planning, execution and interpretation of effective biodiversity studies, and these can be grouped into three main classes: (i) the type of effect size (i.e. change in dependent variable, Table 2) or subject (i.e. assemblage definition) under consideration; (ii) variability in sampling design; and (iii) variability in sampling effort. Next we consider each of these factors.

4.2.1. *Variability in effect size*

Differences in the choice of effect size can have a marked impact on the interpretation of a particular study. The most common limitation results from a restriction of analyses to simple patterns of species richness, diversity and abundance that fail to account for patterns of species identity or assemblage turnover. Direct measures of individual species responses have shown that different species frequently respond to the same process of habitat change in highly idiosyncratic ways (e.g. Marsh and Pearman, 1997; Schlaepfer and Gavin, 2001; Toral et al., 2002; Lehtinen et al., 2003; Fischer et al., 2004). Furthermore, analyses of guild or assemblage structure can often reveal contradictory species responses. For example, both Pearman (1997) and Lemckert (1999) found an increase in the number of amphibian species in selectively logged areas due to the occurrence of generalist tree-frogs. However, closer inspection of the data revealed that logged areas had significantly *fewer* disturbance-sensitive primary forest species (e.g. *Eleutherodactylus* spp., Pearman, 1997). Other amphibian studies that found no differences in species richness between logged and un-logged forest sites also revealed marked differences in species composition when comparing between the same habitats (Greenberg et al., 1994; Vallan et al., 2004). These results emphasise that species richness alone is often a poor indicator of conservation value, and that patterns of richness can mask contrasting species or guild-specific disturbance response trajectories.

Regarding a similar problem, a number of herpetological studies that have focused on the consequences of habitat change have combined amphibians and lizards into a single "ecologically coherent" assemblage (Lieberman, 1986; Heinen, 1992; Vonesh, 2001; Fredericksen and Fredericksen, 2002; Gillespie et al., 2005). Results of some of these studies showed either no effect (Fredericksen and Fredericksen, 2002) or a positive effect (Vonesh, 2001; Gillespie et al., 2005) of structural habitat change on assemblage diversity. Given the often contrasting disturbance responses of these two taxa (e.g. Bell and Donnelly, 2006; Gardner et al., 2007b), we question whether researchers are justified in grouping leaf-litter amphibians and lizards together, and suggest that this traditional practice may generate dangerously misleading implications regarding the consequences of habitat change for biodiversity conservation (Gibbons et al., 2000).

4.2.2. Sampling design and spatial scale

Differences in sampling design can have a profound influence on the conclusions of studies on the consequences of habitat change for biodiversity. First, logistical and/or financial constraints usually restrict the spatial scale and level of replication of herpetofaunal samples, so that very few studies are conducted at large sub-regional scales (>20 km^2) (see Doan and Arriaga, 2002). However, species are rarely, if ever, distributed randomly in their environment, and a poor understanding of the relationship between patchiness and scale (Marsh and Trenham, 2001) can frequently mean that an evaluation of treatment effects at the plot scale (commonly <5 km^2) may not accurately reflect responses at the landscape scale (Fahrig, 2003; Renken et al., 2004; Loehle et al., 2005). In particular, between-patch turnover in species composition (beta-diversity) can often make a significant contribution to the regional diversity of any given habitat type (Pineda and Halffter, 2004; Gardner et al., 2007b), meaning that a limited number of closely spaced (pseudoreplicated) samples can provide a weak, if not biased, assemblage description. Furthermore, it is possible that patterns of species turnover among primary habitat sites are likely to be more influenced by geographic distance (e.g. topography, edaphic features) than turnover among converted habitat sites, which are more likely influenced by local habitat factors and disturbance history (see Ernst and Rodel, 2005). The consequence of this bias is that spatially restricted studies are more likely to result in idiosyncratic or unrealistically small experimental effects when comparing patterns of diversity across gradients of habitat change (Gardner et al., 2007a).

Allied to the problem of securing access to independent sampling sites is the need to secure sites that are located in sufficiently large habitat patches; thereby providing a reliable reflection of local habitat quality or suitability based on patterns of species abundance or occupancy. In particular, samples from habitat fragments (of either native remnants or converted patches) that are surrounded by a contrasting landscape matrix can produce counterintuitive results due to confounding spill-over and edge effects (Cook et al., 2002). For example, Vallan (2002) found that 46% of all amphibian species occurring in a rainforest landscape in Madagascar were found in *Eucalyptus* plantations, but acknowledges that many of these species are likely to be transient visitors that can only breed in neighbouring primary forest. Similarly, Tocher et al. (1997) found more frog species in fragments than in continuous forest in central Amazonia, which was attributed to the colonization of fragments by open-habitat species. Neither of these studies can provide a clear picture of the long-term ability of a given habitat type to support the species assemblage that is revealed by short-term sampling. Although patterns of abundance can often provide a misleading picture of habitat quality (van Horn, 1983), it is possible to improve the reliability of abundance data by locating samples within large habitat patches (Gardner et al., 2007b). Because of their highly philopatric nature, patterns of amphibian abundance and occupancy can provide more reliable indicators of habitat quality than those of several other vertebrate taxa (Waldman and Tocher, 1998). However, our failure to find more than a few studies reporting the size of either treatment or control sites obscures the interpretation of the ecological significance of many results.

Perhaps the most important factor in the design of studies addressing patterns of biodiversity in human-dominated landscapes is access to a large, undisturbed area of native habitat that can operate as an experimental control. One of the most alarming results from our review is that most studies did not have access to a control site >1000 ha. Furthermore, most North American studies, which form the backbone of many discussions regarding the consequences of habitat change for amphibians and reptiles (e.g. Alford and Richards, 1999; Gibbons et al., 2000; Dodd and Smith, 2003), did not have access to any control site at all. As native habitat is inexorably cleared, eroded and fragmented, we are forced to evaluate the biodiversity consequences of habitat change against a shifting baseline. For many parts of the world the chance to evaluate patterns of diversity against areas of continuous, undisturbed habitat (our nearest estimate of "wild nature" Balmford and Bond, 2005) is already gone (Lenart et al., 1997; Germano et al., 2003; Pineda et al., 2005; Scott et al., 2006; and see Gardner et al., 2007a), and elsewhere we are faced with a rapidly closing window of opportunity. In order to properly understand the consequences of habitat change for biodiversity, it is vital that we deploy many more studies in regions that still retain large areas of relatively pristine habitat.

4.2.3. Sampling effort

It is well established among herpetologists that differences in sampling effort can make a significant contribution to our understanding of the consequences of habitat change for patterns of diversity, abundance and community structure

(Gibbons et al., 1997). We found significantly higher levels of sampling effort (defined here as individuals, Gotelli and Colwell, 2001) in temperate than tropical studies for amphibians. However, species richness and rarity are much higher in the tropics (Mittermeier et al., 2005), and tropical and subtropical studies will therefore usually require a greater level of sampling effort than temperate studies in order to obtain comparisons of diversity across alternative land-use options with comparable statistical power. Similarly, it is also reasonable to expect that within a given landscape, higher levels of sampling effort are required in areas of native compared to disturbed habitat. This is because differences in sample heterogeneity, species richness, rarity and patterns of species abundance between different habitat types can mean that even-effort standardisation (samples or individuals) often fails to provide an unbiased comparison of diversity (Cao et al., 2002).

We also found that sample sizes of reptile assemblages are usually much smaller than those of amphibian assemblages. This is partly explained by natural differences in population densities, as well as behavioural differences that render reptiles significantly more difficult to sample than amphibians (Gibbons et al., 2000). Problems of small sample sizes have often been cited as justification for pooling amphibian and reptile samples into a single analysis of the consequences of habitat change for the entire herpetofauna (e.g. Vonesh, 2001; Fredericksen and Fredericksen, 2002).

Differences in study duration and temporal replication can also have an important effect on perceived patterns of diversity across different land-use options, and many researchers have found that their results can be highly dependent on seasonality and the temporal scale of sampling (Pechmann et al., 1991; Gibbons et al., 1997; Schlaepfer and Gavin, 2001; Lehtinen et al., 2003; Goldstein et al., 2005). Finally, differences in sampling techniques can produce contrasting results (Pearman et al., 1995; Doan, 2003), as different methods are associated with different detection biases for different species (Heyer et al., 1994; and see Schmidt, 2003). Studies of longer duration that include a suite of complementary sampling methods are likely to provide more robust conclusions regarding the consequences of land-use change than intensive studies using a single technique (Gardner et al., 2007b).

4.3. *How good is our understanding of the consequences of habitat change for amphibians and reptiles?*

While it is clear that a lot of progress has been made in our understanding of the consequences of some forms of habitat change for amphibians and reptiles during the last 15 years (e.g. Cushman, 2006), a number of serious deficiencies remain. Existing research efforts are characterised by distinct geographic and study biases, a lack of clear consensus regarding the consequences of many forms of habitat change with many studies reporting seemingly contradictory results, and almost ubiquitous limitations in sampling design.

It appears therefore that the recent shift towards studies of "Class II" hypotheses, and away from a focus on structural habitat change (Collins and Storfer, 2003; Beebee and Griffiths, 2005), cannot be easily explained by differences in our understanding of the different stressors currently facing amphibians and reptiles. Contrary to expectation, our results indicate that we still lack a robust understanding of the consequences of many forms of structural habitat change for amphibians and reptiles in much of the world. Furthermore, our ability to understand the nature of the ecological mechanisms that underlie any observed patterns is limited both by the relative paucity of studies, but also by the challenges that face field biologists attempting to implement effective biodiversity surveys in degraded landscapes.

These problems are not particular to herpetofauna. For example recent reviews of both butterflies (Hamer and Hill, 2000), birds (Hill and Hamer, 2004; Barlow et al., 2007), and terrestrial vertebrates (Gardner et al., 2007a) have revealed a marked lack of consensus regarding the consequences of structural habitat change on species diversity. Furthermore, all of these studies have identified common methodological shortcomings resulting in systematic biases that often serve to underestimate the value of primary habitat for biodiversity conservation (see Gardner et al., 2007a). In a recent synthesis of the consequences of habitat fragmentation for biodiversity, Lindenmayer and Fischer (2006) concluded that the study of landscape change has made "relatively little tangible progress". Instead we have a piece-meal understanding that is largely based on the amalgamation of context-specific and predominantly descriptive studies that are often underpinned by biased anthropocentric perceptions of the biodiversity value of different habitat types (Lindenmayer and Fischer, 2006).

We suggest that part of the explanation for why structural habitat changes have been marginalised by amphibian biologists as being relatively "well understood" compared to Class II hypotheses (e.g. Collins and Storfer, 2003) is due to a confounding of the role of ultimate versus proximate stressors. While it is often trivial to isolate the ultimate cause of population declines (e.g. loss or degradation of habitat) this does not equate to an understanding of the proximate ecological mechanism (e.g. loss of breeding sites, inability to disperse across gaps, changes in microclimatic conditions) that is responsible for the loss of a given species. Our ability to mitigate the negative impacts of human activities, and develop much needed strategies for the conservation of amphibians and reptiles outside protected areas, depends critically on our understanding of such mechanisms (see Dodd and Smith, 2003; Cushman, 2006).

It is clear therefore that understanding the consequences of habitat change for biodiversity continues to represent a formidable challenge for conservation biology. If research priorities in conservation science are to be dictated by differences in the scientific uncertainty associated with different problems, then our results suggest that, despite the considerable efforts of a generation of field herpetologists, the study of habitat change is deserving of considerably more attention. The plight of amphibians and reptiles is particularly marked by the fact that they have received disproportionately little research attention compared to either birds or mammals (Fig. 2). We propose two explanations for this discrepancy.

First, there is a historical taxonomic bias in research of terrestrial vertebrates towards birds and mammals (see Fazey et al., 2005a). Amphibians and reptiles are further disadvantaged because they lack cheap and effective standardised sampling methodologies. The requirement for a higher investment in both time and money can serve to provide a disincentive for study, leading to the polarisation of research towards species that are easier to survey (Pawar, 2003). This polarisation has dangerous implications, because further underinvestment can in turn lead to increasingly poor levels of sample representation in field projects and encourage a culture of "taxonomic chauvinism" (Pawar, 2003).

A second explanation is that the number of studies concerned with the consequences of structural habitat change is diluted because they are less appealing to researchers than studies of novel and enigmatic stressors such as disease and climate effects. Why should this be the case? As we have demonstrated, studies of habitat change are often confounded by serious practical and logistical difficulties. This is especially true for amphibians and reptiles that usually require labour-intensive sampling methods. Furthermore, the results of such field studies are often unsatisfactory and cannot be easily developed into general theory or principles (Lindenmayer and Fischer, 2006). In contrast, the testing of Class II hypotheses often supports a reductionist scientific approach (e.g. microbial ecology, environmental chemistry) that is more amenable to controlled experimentation, and therefore more able to provide stronger inference (Platt, 1964). The promise of more certain conclusions regarding novel and interesting problems, together with an accelerated learning process holds great attraction for many researchers who are often under pressure to generate original findings, and publish in leading scientific journals.

4.4. *Recommendations for future research*

The fact that the number of herpetological studies concerned with habitat change is increasing in recent years is an encouraging sign, but it is important that new studies help to balance existing biases in research effort. We propose the following 10 recommendations for future studies that can help redress this balance:

(1) While the emergence of enigmatic stressors in precipitating declines of amphibians in areas remote from human influence is undeniably cause for great concern, this should not serve to eclipse the importance of understanding the more fundamental (and superficially more elementary) problem of habitat change. We argue that the study of the consequences of habitat change for amphibians and reptiles needs *more* attention relative to Class II hypotheses (not less), and at least as much funding as is currently invested in the study of birds and mammals.

(2) Greater investment is needed in studies of the consequences of habitat change on amphibians and reptiles in tropical and subtropical countries currently experiencing the highest rates of habitat loss. In addition, greater effort is required to assist the publication of many grey literature studies from developing countries which are unavailable to the international audience. Project reports and theses frequently remain unpublished due to a lack of funding, language barriers and differences in attitudes towards research in different countries (Fazey et al., 2005b).

(3) Maximise attempts to secure adequate sample sizes through a combination of extended multi-season field campaigns, the application of complementary sampling methods, and careful analyses of the degree of representation of individual samples. Both established and developing statistical techniques can be used to reduce the contribution of variability in sampling effort to the description of patterns of diversity and richness (Gotelli and Colwell, 2001; Cao et al., 2002; Magurran, 2004).

(4) Studies should attempt to sample at the landscape scale in order to capture natural variability in patterns of abundance and species occurrence which can be difficult to evaluate at the scale of individual habitat patches (Fahrig, 2003; Storfer, 2003; Cushman, 2006).

(5) Wherever possible ensure that samples from different habitat types are located at sufficient distances from patch boundaries to avoid confounding edge and spillover effects.

(6) Wherever possible ensure that comprehensive comparisons are made with available primary habitat by maximising the size and separation distance of control sites.

(7) Optimise the opportunities for data collecting during each field campaign. For example leaf-litter amphibians and lizards can often be sampled using the same techniques at very little extra cost or effort to the researcher (provided the necessary taxonomic expertise is available). In addition, environmental data on patterns of habitat structure and composition can be very cheap to collect yet are often absent from many biodiversity studies.

(8) Improve reporting of basic data to describe the sampling design (size and quality of control sites, size of treatment plots, distance between sites), methods, and effort (individuals caught, trap nights). Such improvements will greatly increase the opportunity for formal meta-analyses of the consequences of different forms of habitat change.

(9) Complex ecological data sets describing the response patterns of individual species to different environmental factors cannot be analysed satisfactorily using traditional statistical approaches that are dominated by hypothesis testing. Instead, better use needs to be made of alternative techniques that deal more effectively with uncertainty and emphasise thoughtful hypothesis formulation and model building as part of the enquiry process (e.g. information-theoretic approaches, Bayesian techniques and meta-analyses; Burnham and Anderson, 2002; Hobbs and Hilborn, 2006). Adopting such approaches will accelerate our understanding of the ecological mechanisms that underlie observed changes in abundance and diversity.

(10) Studies of habitat change are frequently "patch-centric", and focus on habitat fragmentation at the expense of understanding the consequences of habitat loss and patterns of diversity in the surrounding landscape matrix (Fahrig, 2003; Lindenmayer and Fischer, 2006). Consequently, more focussed research is needed to understand the consequences for biodiversity of

alternative land-use options, especially in the tropics (e.g. agricultural systems, Daily, 2001; Vandermeer and Perfecto, 2007; and plantation forestry, Lindenmayer and Hobbs, 2004).

Many of these recommendations pose serious challenges to researchers working in logistically difficult parts of the world, and with little access to minimum levels of financial and technical support. However, despite these difficulties it is vital that we focus efforts to improve our understanding of the consequences of habitat change for amphibians and reptiles, as well as biodiversity in general. If we do not then we will never know what we have lost.

Acknowledgments

We thank James Watling and two anonymous reviewers for comments that helped to greatly improve an earlier version of this manuscript. T.A.G. is supported by a studentship from the Natural Environment Research Council (UK). This is publication number 9 of the Land-Use Change and Amazonian Biodiversity Project.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2007.04.017.

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