Chameleons (Squamata: Chamaeleonidae) as Bio-Indicators

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Abstract. We examined the suitability of using chameleons as bio-indicators. We want to investigate if chameleons would reliably indicate disturbances in environment, and reflect the responses of other species or the overall biodiversity. While there is no perfect bio-indicator and selecting the most suitable one depends specifically on the main objective of the project: can chameleons be used to assess habitat alteration. The species composition and/or abundances have been shown to change along ecological gradients as well as the level of the disturbance of the habitat. Specialist, such as forest-dependent species decreased with increasing disturbances while generalist, forest edge and open-habitat species increased, and some species might not be affected by moderate disturbances. We conclude that chameleons are useful bio-indicators; but still more studies are needed to determine how well chameleons represent the responses of other taxa.

Key words: bio-indicators, chameleons, forest loss and fragmentation, habitat disturbance, open habitat and forest-depend species

Introduction

A bio-indicator can be defined as a species or species group that reflects the abiotic or biotic state of the environment, represents the impact of the environmental change on a habitat, community or ecosystems, or indicates the diversity of the other species (McGeoch, 1998). In this sense, bio-indicator is generally used to provide rapid information about the complex ecosystems in which it occurs, and as such play key roles in conservation planning and management (Han *et al*., 2015). By using bio-indicators, it is possible to assess the human-induced change on the biota, instead of examining the entire biota. This is a great advantage especially in the tropics, where surveying overall high species diversity is challenging (Rainio & Niemelä, 2003).

While various reasons have been suggested for the selection of biodiversity "indicator" groups (Ejigu *et al*., 2014; Syaripuddin *et al*., 2015), the attributes commonly accepted as essential can be summarized into three key criteria (McGeoch, 1998): (1) environmental, (2) ecological, and (3) biodiversity indicators. Several papers proposed a list of performance criteria for environmental, ecological and biodiversity indicators (Hilty & Merenlender, 2000; Rice, 2003; Niemeijer & de Groot, 2008); but for the context of this study, we use the definitions by McGeoch (1998). As such, "environmental indicator" is a species or species group that responds predictably, in ways that are readily observed and quantified, to environmental disturbance or to a change in environmental state; and "ecological indicator" is a taxon that is sensitive to identified environmental stress factors, that demonstrates the effect of these stress factors on biota, and whose response is representative of the response of other taxa; while "biodiversity indicator" is a taxon or functional group whose diversity (character richness, species richness, level of endemism) reflects the diversity of other taxa. However, the basic division, but not mutually exclusive, is that environmental and ecological indicators are

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used to detect changes in the environment, while biodiversity indicators reflect the diversity of the overall biota (Han *et al*., 2015).

The impacts of the environmental change to the indicators can be seen within the organism (e.g. heavy-metal concentrations and physiological changes), at the species level (species distribution, abundance, social structure, and richness) or at the community level (interactions between species as predator-prey) (Zaghloul *et al*., 2020). Increase or decrease of species number or abundance might be related to change in abiotic and/or biotic factors or simply through restructuring biological assemblage (Ejigu *et al*., 2014). The presence or absence of the species classified as biodiversity indicators indicates the presence or absence of some other species as well as the quality and the integrity of the habitat. Biodiversity indicators can also be classified as: (1) keystone species where their loss or addition may lead to major change in abundance or occurrence of at least one other species, or (2) dominant species which provide a major part of the biomass or number of individuals (Lindenmayer *et al*., 2000).

While many aquatic and terrestrial invertebrates have a long and successful history of use as bio-indicators (Souza *et al*., 2015), attention has focused more recently on the use of some vertebrates groups as fishes, herpetofauna, birds, bats and small mammals as biological indicators (Ejigu *et al*., 2014). Nevertheless, amphibians for a long time around the world have been used as a bio-indicators of the quality and integrity of wetlands (Zaghloul *et al*., 2020).

This study attempts to assess the suitability of chameleons (Squamata: Chamaeleonidae) as bio-indicators. Attention is paid to habitat modification and biodiversity studies in Madagascar and Africa, the geographical areas of the highest chameleon diversity in the world (Tolley & Menegon, 2014; Glaw, 2015), and where, therefore, most of the research has been done in various biotopes (e.g. less disturbed and disturbed forests, forest edge and core). Chameleons are examined because they are mainly forest dwelling species, a suitable group for monitoring programs (Jenkins *et al*., 1999), and sampling methods by the use of a transect is suitable for most of the habitat types where they occur (Jenkins *et al*., 2003; Rabearivony *et al*., 2007; Randrianantoandro *et al*., 2008; 2009; Patrick *et al*., 2011; Lowin, 2012; Shirk *et al*., 2014).

Selecting Suitable Indicators

Different criteria were suggested to define bio-indicator species (Hilty & Merenlender, 2000). However, Ejigu *et al*. (2014), recognized that a good biological indicator should have the following characteristic: well-known taxonomy and ecology; broad geographic distribution area; specialist to particular habitat types (ecological requirement specificity); provide early warning of change (sensibility to change affecting the habitat); be easy and cost-effective to survey; be relatively independent of sample size; its response should reflect the response of other species; easy to detect changes generated by natural phenomena and those induced by human activities; and finally should be of potential economic importance. It is therefore difficult to find species or species groups which meet all of these characteristics, and mostly, the requirement needed depends on the goal of the survey (Rainio & Niemelä, 2003).

For the purpose of having a suitable indicator, studies on distribution and other aspects of its life history should be planned at both spatial and temporal scales. Spatially, species richness or relative abundance depends on the scale of observation, and some species may have more uniform distribution while others can be patchier. Increasing the size of the survey area increases the probability of finding patchily distributed species (Hessa *et al*., 2006). The temporal scale must also be considered as, in many animal species; their activity and abundance vary throughout the year and season. Some species are more abundant in summer, while others peak in the winter (Anu *et al*., 2009). This kind of variation might have a great impact on results, if only a short time period is used for a study. So the knowledge of the biological and

the reproduction cycles of the species are very important for a representative sampling and to get reliable results.

McGeoch (1998) has developed procedural steps, which aim at improving the selection of an appropriate environmental, ecological, and biodiversity indicators. This is a step-by-step procedure beginning with defining the objectives of bio-indicator and ending with the rejection or acceptance of the indicator. During the procedure the relationship between the bio-indicator and environmental data is investigated under two or more different conditions. Below we first examine how well chameleons meet requirements of bio-indicator species mentioned above, and thereafter, test the suitability of this group as bio-indicators by using the method proposed by McGeoch (1998).

Chameleons as Bio-Indicators

Worldwide, chameleons have been studied in several habitat types allowing to assess the species response to changing environmental conditions (Table 1), including forest fragmentation (Lowin, 2012; Shirk *et al*., 2014), edge effect from paths/roads (Andreone *et al*., 2005; Metcalf *et al*., 2005; Patrick *et al*., 2011; Shirk *et al*., 2014), ecological gradient (Lehtinen *et al*., 2003, Rakotondravony, 2004) and different management and agricultural practices (Akani *et al*., 2001; Andreone *et al*., 2005; Rabearivony *et al*., 2007).

Table 1. Examples of chameleons' responses to environmental changes

Goal of survey	Habitat, Location and Country	Comment	Reference
Habitat use, threats	Montane sites, Central Plateau, Madagascar	*Calumma* (three species) were restricted to humid forest with only occasional occurrence (*C. hilleniusi*) in savanna. *Furcifer* (three species) were common in or restricted to tapia (*Uapaca* sp.) forest, agricultural land and savanna/heathland. *F. campani* and *F. minor* are currently listed by the IUCN as Vulnerable.	Randrianantoandro *et al*. (2009)
Density, habitat fragmentation	Three deciduous, unprotected forest fragments, Northern Madagascar	Four species were recorded and their densities vary amongst forest fragments and species	Lowin (2012)
Habitat loss and fragmentation	Vestigial forest patches; East Usambara Mountains, Eastern Arc Mountains, Tanzania	Habitat loss and fragmentation have greatly reduced forest-dependent chameleon population sizes	Shirk *et al*. (2014)
Edge effect from paths	Deciduous forest, North-West Madagascar	Chameleon numbers (*Furcifer oustaleti* and *F. rhinoceratus*) significantly decreased with increasing distance from the path. Understanding of the implications of edge effects from	Metcalf *et al*. (2005)

		paths might be an important aid for management and conservation	
Abundance comparison between forest edge and interior	Sub-montane rainforest; East Usambara Mountains, Tanzania	Seven chameleon species were recorded, of which two were restricted to forest interior (*Kinyongia matschiei*, *Rhampholeon temporalis*) and two were only found on forest edges (*Chamaeleo dilepis*, *Rieppeleon brevicaudatus*) and the other three colonized both forest edge and interior (*Trioceros deremensis*, *Kinyongia tenuis*, *Kinyongia vosseleri*)	Patrick *et al*. (2011)
Impacts of selective logging and forest burning	Selectively logged and riparian forests, secondary regrowth (after burning), Central Plateau of Madagascar	Riparian areas within 50 m from a stream had high abundance compared to both selectively logged forest and secondary regrowth (after burning) located beyond 50 m.	Jenkins *et al*. (2003)
Ecological gradient	Littoral rainforest fragments in South-Eastern of Madagascar	Open-habitat chameleon *Furcifer oustaleti* avoided forest interior beyond of 25 m from edges with other generalist reptile species	Lehtinen *et al*. (2003)
Forest isolation and agricultural land	Lowland rainforest, Eastern Madagascar	Four chameleon species were encountered, of which two (*Furcifer pardalis* and *Calumma parsonii parsonii*) showed the opposite trend. The latter was associated only to the relatively intact forest whilst the first to the abandoned agricultural land. *Brookesia superciliaris* was more common in relatively intact as well as in isolated forests at vicinity to the river. *Calumma nasutum* was more common in relatively intact forest although it was encountered in the abandoned agricultural land.	Rabearivony *et al*. (2007)
Management practices (including logging, forest-plantation mosaics)	Various habitat types in Southern Nigeria	Three forest-dependent species (*Chamaeleo owenii*, *Ch. Cristatus* and *Rampholeon spectrum*) disappeared locally after a period of intensive forest exploitation and were replaced by *Ch. gracillis*, a species with broader habitat requirements.	Akani *et al*. (2001)

Knowledge of Chameleon Taxonomy and Ecology, and Distribution over Geographic Area

According to Glaw (2015), the current taxonomic checklist of chameleons recognized 202 species within 12 genera, of which seven are in Africa (*Bradypodion*, *Chamaeleo*, *Kinyongia*, *Nadzikambia*, *Rhampholeon*, *Rieppeleon* and *Trioceros)*, four are in Madagascar (*Brookesia*, *Calumma*, *Furcifer* and *Palleon*) and one is endemic to the Seychelles (*Archaius)*. Fifty-five percent of known species are found in Africa and 44% in Madagascar, with the remaining few species in Asia and Europe (Tolley & Menegon, 2014). A comparison with the last taxonomic checklist published by Klaver & Böhme (1997), recognizing 132 species within six genera, demonstrates the enormous progress in chameleon taxonomy and systematics over the last twenty years. The discovery of new species continues, increasing the chameleon species richness; and so far, many new species both from Africa and Madagascar still await their scientific description (Tolley & Menegon, 2014).

Classification of chameleons below the family level was controverted until recently when Klaver & Böhme (1986) proposed a new classification based mainly on hemipenis morphology and was more adequate to chameleon biogeography. In this classification, the family Chamaeleonidae was divided into two subfamilies: Brookesiinae including the dwarf chameleons and Chamaeleoninae involving the true chameleons. The typical chameleons from the subfamily Chamaeleoninae are arboreal, usually living in trees or bushes, although a few (notably the Namaqua chameleon, *Chamaeleo namaquensis*) are partially or largely terrestrial. Most species from the subfamily Brookesiinae, which includes the genera *Brookesia*, *Palleon*, *Rieppeleon* and *Rhampholeon*, perch at night on low vegetation and stems, and forage during the day on the forest floor among leaf litter. To date, the most recent taxonomic checklist by Glaw (2015) using this subfamilial division, however, only the genera *Brookesia* and *Palleon* are within the Brookesiinae subfamily, with all other genera being placed in Chamaeleoninae.

Specialization to Habitat Requirements

Chameleon assemblages can be divided according to habitat, with the major division falling between open-canopy habitats (desert in Namibia, savanna, heathland, grassland, and woodland) and closed-canopy habitats (forest). Open-habitat chameleons appear to be most tolerant of disturbance, while forest-dwelling species (about 67% of known taxa) are most often reported as being habitat specialists and thus restricted (Measey *et al*., 2014). Because of high rate of forest-dependent species (Raselimanana & Rakotomalala, 2003; Measey *et al*., 2014) and the high degree of habitat degradation and deforestation in the areas where chameleons occur (e.g. Madagascar, Harper *et al*., 2007), the conservation of this group is becoming a top priority in many tropical countries (Brady & Griffiths, 1999; Measey *et al*., 2014).

Provide Early Warning of Change

Table 1 shows that chameleons illustrate spatial distribution along with ecological gradient from river or forest path and they respond quickly to habitat fragmentation, logging, forest burning, road effects and (abandoned or not) agricultural land. Since chameleons are sensitive to environmental disturbance, the changes in both abiotic and biotic factors as temperature, humidity and vegetation associated to management practices may have rapid impacts to chameleon distribution (Akani *et al*., 2001; Jenkins *et al*., 2003). However, as ecological requirements vary amongst chameleon species, some species are more sensitive to environmental changes than others (Akani *et al*., 2001; Rabearivony *et al*., 2007).

Easiness and Cost-Effectiveness of Survey

There are several methods for surveying chameleon assemblages and densities, but for population monitoring, repeatable line transect survey techniques using distance sampling

methodologies is the most appropriate (Jenkins *et al*., 1999). The mark-recapture method was used for a while, but it may have several shortcomings. It requires intensive effort to define the sampling area and to provide an adequate sample size, however the available manpower is limited (Jenkins *et al*., 1999), and the animal sheds regularly its skin. Another weakness of this method is that, if systematic searching of an area is used to sample the population (Raxworthy, 1988), the assumption of random mixing of individuals required by the current analytical methods will be violated (Jenkins *et al*., 1999), especially for territorial fauna such as chameleons (Karsten *et al*., 2009). Whilst this can be avoided by designing the search strategy to sample an area randomly, by using for instance different observers to search a given area for subsequent sampling dates, this requirement cannot be done satisfactorily for chameleons (Jenkins *et al*., 1999), as it would increase considerably the manpower costs. Pitfall traps is another sampling technique widely used for reptiles (Raxworthy, 1988), but obviously unsuitable for arboreal species like chameleons, even for ground-dwelling species as *Brookesia* and *Palleon* (Jenkins *et al*., 1999). For instance, only two individuals were trapped by Raxworthy & Nussbaum (1994) during 2,244 pitfall-days. Therefore, for long-term monitoring programs, randomly located forest line transect survey techniques based on distance sampling methodologies was recommended. Three main assumptions of this method fit well for chameleon studies. First, all objects at zero distance from the transect line or point are detected. Second, objects are detected at their initial location, before any movement occurs due to disturbance by the observer. Third, perpendicular distances between transect line or point to the object of interest are measured accurately. Since chameleons roost and are immobile at night, and their color becomes pale or brighter under torch light, they are relatively easy to spot during nocturnal surveys (assumption 1), and do not move upon detection (assumption 2). As roosting individuals are approached carefully, accurate measurements of perpendicular distances are possible using decameter or telemeter laser (assumption 3). Furthermore, since distance sampling is function of detectability, it is therefore suited for the spatial and temporal comparison of chameleon population densities. It has proved to be suitable for various habitat types in Madagascar and Africa (Jenkins *et al*., 1999; Karsten *et al*., 2009; Patrick *et al*., 2011; Randrianantoandro *et al*., 2008; Shirk *et al*., 2014), from eastern Malagasy rainforest (Jenkins *et al*., 1999) to dry spiny habitat in south-western (Karsten *et al*., 2009) and western dry deciduous forest (Randrianantoandro *et al*., 2008).

Independence of Sample Size

The altitude, topography (e.g. valleys and rivers) and many other habitat conditions may influence the distribution of chameleons (Jenkins *et al*., 2003; Raselimanana & Rakotomalala, 2003). Therefore, many chameleon species are restricted to small geographical ranges and/or have limited elevational tolerances (Raselimanana & Rakotomalala, 2003; Tolley & Menegon, 2014), and microendemic species are common (Tilbury, 1992; Glaw *et al*., 2012; 2021). Consequently, chameleon surveys are not independent of sample size and the survey results might depend on the number of sites studied. Working on several study sites (replication) may reduce the bias risk, as increasing site number increases the probability to find patchily distributed species, and therefore increases the reliability of the results.

Reflect Response of Other Species

The degree to which changes in chameleon assemblages reflect the response of other species is poorly known. However, some studies showed the resemblance of change in chameleon and other reptile assemblages in response to forest fragmentation (Lehtinen *et al*., 2003). Thus, within fragmented forest, the open-habitat chameleon *Furcifer oustaleti* avoided forest interior beyond 25 m from edges along with other reptile species as *Trachylepis elegans* and *Geckolepis maculata* (Lehtinen *et al*., 2003). These authors revealed that altered

microclimate conditions near the edge influences the distribution of many amphibians and reptiles, and most interior-avoiding or omnipresent species were extinction resistant. Chameleons occupy an intermediate place in the food chain, and any changes affecting their distribution and abundance will have consequential influences on that of other species.

Differentiation of Natural Cycles and Human-Induced Stress

Because of seasonal and year-to-year variations in chameleon population sizes, Brady & Griffiths (1999) and Rabearivony (2013) monitored chameleon communities in Madagascar over summer and winter during two years, 1996-97 and 1999-00. Furthermore, as weather conditions and human impact can cause year-to-year fluctuation, these researchers monitored chameleon populations in Ranomafana National Park, Madagascar, over five years (1993-94, 1996-97, 1997-98, 1998-99 and 1999-00), using relatively intact forest in Vatoharanana as a control site to separate the natural and human-induced effects.

Economic Importance

While the use of (only few) economically important species as indicators for monitoring ecosystem functions and biological diversity could be misleading (Landres *et al*., 1988), Pearson (1994) argued that economic importance of indicator species is significant when convincing politicians of the importance of monitoring efforts, especially in developing countries. Chameleons can be considered economically important, because they are subject to the pet trade industry and exported worldwide (Carpenter *et al*., 2004; Jenkins *et al*., 2014).

Test of Chameleons as Bio-Indicators

Following the procedural steps for selecting indicator species (McGeoch, 1998), chameleons were tested against three broad bio-indicator classifications: environmental, ecological and biodiversity indicators (Table 2). To avoid bias, two to six studies per type of indicator, using different approaches, were selected to test the suitability of chameleons as bio-indicators. Three hypotheses were tested: (1) does the conversion of forest habitat to agricultural land affect the assemblages and abundances of chameleons (environmental indicator)?, (2) do responses of chameleons to ecotonal forest resemble those of other species groups (as vegetation types) (ecological indicator)?, and (3) does chameleon diversity reflect the diversity of other species groups (of reptiles) (biodiversity indicator)?.

Table 2. Procedural steps for testing suitability of chameleons as bio-indicator (modified from McGeoch, 1998)

Step	**Bio-indicator classification**		
Step 1: Broad objective	Environmental indicator	Ecological indicator	Biodiversity indicator
Step 2: Objectives and endpoints	To detect the nature of disturbance (forest conversion to agricultural land) using an indicator (Randrianantoandro et al. 2009)	To detect the impact of habitat changes as ecotonal forest (river edge, path/road) on vegetation types (tree and ground ferns, Bamboo, *Pandanus* palms) using chameleons (Jenkins et al. 2003)	To assess the biodiversity (number of species) of biota using an indicator (Ramanamanjato et al. 2002)
Step 3: Potential indicator	Chameleons	Chameleons	Chameleons

Step 4: Accumulate data on indicator	Density and abundance of six species recorded were surveyed (Randrianantoandro et al. 2009)	Abundance of six recorded chameleon species (and of vegetation types) were surveyed (Jenkins et al. 2003)	Survey in seven sites in southeastern Madagascar yielded four chameleon species and the most diverse site (Malahelo forest) had all of these species (Ramanamanjato et al. 2002)
Step 5: Collect quantitative relational data	Transects of 150 m in length (n = 4-30) were surveyed in four habitat types: Agricultural land, savanna/heathland, humid and tapia forests (Randrianantoandro et al. 2009).	Three 5 x 5 m quadrats were randomly placed on either side of each 50-m transect line at 5, 20, and 35 m interval to describe the basic differences in habitat features (number of tree and ground ferns, Bamboo, *Pandanus* palms) amongst forests: secondary regrowth (after burning), selective logged forest and riparian forest in selective logged (Jenkins et al. 2003).	41 other reptile species belong to eight families were surveyed (Ramanamanjato et al. 2002)
Step 6: Relationship between the indicator and the relational data	Density and abundance of six species vary so that two species were common in agricultural land and tapia forest, three preferred, if not restricted to, the humid forest and one was restricted to savanna/heathland (Randrianantoandro et al. 2009)	There were more chameleons, ground ferns and bamboo in river edge whilst less chameleons, Bamboo, *Pandanu*s palms and Ground ferns in secondary regrowth (Jenkins et al. 2003).	The most diverse Malahelo forest was also the most diverse as regards the total reptile species diversity (Ramanamanjato et al. 2002).
Step 7: Accept or reject an indicator	There was a correlation between agricultural land and species abundance in some, but not in all species (Randrianantoandro et al. 2009)	There was a correlation between ecotonal forest (as river edge), chameleons abundance, and number of Bamboo, *Pandanus* palms and Ground ferns (Jenkins et al. 2003).	There was a correlation between the number of chameleon species and the total number of reptile species (Ramanamanjato et al. 2002)

Step 8: Robustness of the indicator and testing appropriate hypothesis under different conditions	Testing the indicator in other surveys (Rabearivony et al. 2007) proved that chameleons respond to agricultural land.	Testing the indicator in other surveys showed the affinity of chameleons on ecotonal forests as river edge (Rabearivony et al. 2007, 2015) and path/road (Jenkins et al. 1999; Andreone et al. 2005; Metcalf et al. 2005) and proved the change in abundance of ground ferns (Rabearivony et al. 2015), and other vegetation types along ecological gradient (Andreone et al. 2005; Rabearivony et al. 2015).	Testing the indicator in Nosy Komba, North-Western Madagascar, proved that the three most diverse sites in chameleons (5-6 species) were also the most diverse (24-33 species) regarding the total reptile species diversity (Blumgart et al. 2017); but many other surveys did not corroborate to this or showed dissimilar distribution patterns (e.g. Andreone et al. 2003; Rakotoarison et al. 2015)
Step 9: If the null hypothesis is rejected, make specific recommendations, based on the original objectives, for the use of the indicator	Chameleons proved to be suitable indicators and the null hypothesis is rejected. Chameleons can be used as bio-indicators in agricultural land as some species were associated to this human induced habitat.	There are some correlation between chameleons and vegetation types, but there is inconclusive evidence that chameleons would reflect the response of other taxa (as flora)	There is no clear correlation between species richness of chameleons and other reptile species groups and the null hypothesis cannot be rejected. It is better to use chameleons together with some other taxonomic groups to assess biodiversity.

Two studies (Rabearivony *et al*., 2007; Randrianantoandro *et al*., 2009) indicated that chameleons are suitable for environmental indicators (Table 2). Most chameleon species are forest-dependent (Raselimanana & Rakotomalala, 2003; Shrik *et al*., 2014), and conversion of relatively intact forest to agricultural land can affect species composition and/or abundance (Rabearivony *et al*., 2007).

Both chameleons and other species groups (as vegetation types) respond to habitat changes as ecotonal forest (ecological indicator). Jenkins *et al*. (2003) showed that there were more chameleons, ground ferns and bamboo in river edge whilst fewer chameleons, bamboo, *Pandanu*s palms and ground ferns in other habitat as secondary regrowth. Many other studies in ecotonal zones (river edge or path/road) revealed existence of correlation between chameleon diversity and abundance and heterogeneity of vegetation types (Andreone *et al*., 2005; Rabearivony *et al*., 2007; 2015). Further investigations, however, are still needed to get more conclusive evidence that chameleons would reflect the response of other taxa (as flora) since they need plant to perch at night.

Regarding biodiversity indicator, many herpetofaunal surveys showed controversial results. Some studies (e.g. Ramanamanjato *et al*., 2002; Blumgart *et al*., 2017) revealed that

the richest sites in chameleons were also the most diverse in total reptile species diversity. Many other studies, however, proved contrasting results (e.g. Andreone *et al*., 2003; Rakotoarison *et al*., 2015), leading to consider that there is no clear correlation between species richness of chameleons and other reptile species groups.

In the light of these tests, the following conclusions could be raised: (1) Chameleons can be acceptable as environmental indicators, at least when human-caused disturbances as conversion of forests to agricultural lands are concerned and (2) There is some evidence, but not conclusive, supporting the suitability of chameleons as ecological and biodiversity indicators.

Below, some additional studies on the use of chameleons as indicators of habitat changes and their use as biodiversity indicators were reviewed.

Chameleons as Indicators of Habitat Changes

Chameleons as Indicators of Forest Fragmentation and Loss

Chameleons, an understudied taxon are facing many threats; and the most severe of them are the habitat loss and fragmentation (Akani *et al*., 2001). Like in many animal populations (Prugha *et al*., 2009), the poor predictive power of fragment area and isolation for explaining chameleons' responses to fragmentation demonstrates the importance of considering other factors of fragmentation such as edge and matrix effects and vegetation characteristics (Shirk, 2012). Chameleons within fragmented habitat responded consistently more to edge effects and vegetative characteristics associated with fragmentation than to area or isolation effects. Edge-tolerant species and those with higher abundance are less impacted by fragmentation. Ecotones (often unnatural) might be attractive to chameleons for a number of reasons, including increases in prey diversity and abundance, basking opportunities, visibility for intraspecific communication, and vegetation structure (as roosting site) (Measey *et al*., 2014). They may benefit the most from edge effects such as warmer temperature and lower humidity as well as favorable condition for reproduction (e.g. nesting), and can tolerate the conditions in the matrix where many reptile species are susceptible because of their poor dispersal ability. Habitat specialists that respond sensitively to vegetation characteristics and susceptible to the microclimatic variations within habitat edges are more likely to respond negatively to climate change than those that tolerate a wider variety of vegetation and the less stable micro-climate. Therefore, chameleons within fragmented landscape can be categorized as forest-dependent, edge specialists and savanna species. In East Usambara Mountains, Tanzania, for instance, forest-dependent species include *Rhampholeon spinosus*, *Rh. temporalis*, and *Trioceros deremensis* (Shirk *et al*., 2014), and edge specialists include *Kinyongia matschiei*, *K. tenuis*, and *K. vosseleri* while savanna species include *Chamaeleo dilepis* and *Rieppeleon brevicaudatus* (Shirk, 2012). However, the extent of these categories is ambiguous and may depend on the study design and objectives and data analysis. For instance, while Shirk (2012) considered *Ch. dilepis* and *R. brevicaudatus* as savanna species and *K. matschiei* as edge specialist, but Patrick *et al*., (2011) classified the first two species as edge-dwellers and the third (*K. matschiei*) as forest-dependent. The common point, however, is that chameleons can be used as indicators of forest fragmentation and loss but the responses to these changes vary amongst taxa, making up three categories of species: forest-dependent, edge specialists and savanna species.

Chameleons as Indicators of Natural Forest Disturbance

Natural habitat degradation is largely due to forest burning, agricultural practices and exploitation of biological resources such as timber harvesting (Hance, 2014), although mining exploitation is also of special concern (Jenkins *et al*., 2014; Jones *et al*., 2019). Diversity and

abundance of chameleon forest-dependent species decrease in highly disturbed areas as where intense clearing and burning have produced degraded secondary forest, forest mosaic, or plantations (Jenkins *et al*., 2003). In Madagascar, for instance, chameleons were more abundant in rainforest subject to low-disturbance (e.g. selective timber extraction) than in patches of high-disturbance forest that was recovering from burning. Five chameleon species (*C. gastrotaenia*, *C. nasutum*, *C. globifer*, *C. brevicorne* and *B. thieli*) were present in all habitats, but *B. minima* was not recorded in the high-disturbance forest (Jenkins *et al*., 2003). More specialized species tend to disappear with habitat loss, whereas moderately common species (habitat generalist) would increase in abundance, concluded Akani *et al*. (2001) and Gonwouo *et al*. (2006). In Nigeria, accordingly, *Chamaeleo owenii*, *C. cristatus* and *Rhampholeon spectrum* may be dramatically affected by habitat loss and forest fragmentation, whereas *C. gracilis* might even benefit from this situation, possibly because of less inter–specific competition with the other chameleon species (Akani *et al*., 2001). In Madagascar, *Furcifer pardalis* is known as degraded-forest dweller while most of the Malagasy chameleons are forest-dependent species (Andreone *et al*., 2005; Rabearivony *et al*., 2007). Brief, in response to natural forest disturbance, species typical of pristine forest (specialist species) were replaced by species adapted to secondary habitats (generalist species).

Chameleons in Agricultural and Open-Habitat Area

While most of the world chameleons are forest-specialist; few species are associated with agricultural lands (Andreone *et al*., 2005; Rabearivony *et al*., 2007; Randrianantoandro *et al*., 2010) and open-habitat areas (Raselimanana & Rakotomalala 2003; Randrianantoandro *et al*., 2010). In a low-altitude site in Madagascar, *Furcifer pardalis* was found laying eggs in open and sandy areas and newly hatched individuals were found in abandoned manioc (cassava) fields (Rabearivony *et al*., 2007). In the highest peaks of Madagascar, *Furcifer minor* and *F. lateralis* were common in both tapia (*Uapaca* spp.) forest and agricultural and grassland while *F. campani* was restricted to savanna and heathland (Randrianantoandro *et al*., 2010). In the nature of habitat generalists, *F. verrucosus* in Madagascar and *Chamaeleo dilepis*, *Bradypodion melanocephalum* and *B. pumilum* in South Africa are found in reed beds (Tolley *et al*., 2004; Gardner, 2013). To conclude, while specialist species required specific habitat, generalist species can colonize a wide range of habitats where the former cannot survive.

Chameleons as Biodiversity Indicators

Knowing that biodiversity indicator is a taxon or a functional group, the diversity of which (abundance, species richness, level of endemism) reflects diversity of other taxa (McGeoch, 1998), finding reliable indicators is difficult, and indeed impossible, because of the lack of time and resources to investigate species diversity of whole communities (Raven & Wilson, 1992; Duelli & Obrist, 2003).

Some reptile (*Geckolepis maculata*, *Trachylepis elegans*) and amphibian (*Ptychadena mascareniensis*) species in fragmented forest habitat of Madagascar avoid the forest interior and are consistently found at the edges with chameleon *Furcifer oustaleti* (Lehtinen *et al*., 2003; Lehtinen & Ramanamanjato, 2006). However, the presence of *F. oustaleti* at the edges may not predict the presence of those species but may indicate the increasing deforestation rate and the increase in size of open areas around forest fragments. In riparian edges (0-25 m from forest river edges), the Malagasy terrestrial chameleon *Palleon nasus* is associated with vegetation types such as ground ferns and monocotyledons while in forest core areas (25-50 m) with dicotyledons, liana/vine and epiphytes/moss (Rabearivony *et al*., 2015). Again, no study demonstrated that the presence of *P. nasus* predicts the presence of those vegetation types. Generally, however, the presence of terrestrial *Brookesia* and *Palleon* may correlate to

the presence of seedlings and young plants in the undergrowth (Brygoo *et al*., 1972; Randrianantoandro *et al*., 2008) as a roosting site (Razafimahatratra *et al*., 2008).

Sometimes there are correlations between pairs of species (or species groups) but results cannot be generalized. In open habitat, *F. oustaleti* is an edge-associated species, whereas another open habitat chameleon, *F. lateralis* is omnipresent across the ecological gradient in the forest fragment and can be found either at the edges and forest core (Lehtinen *et al*., 2003). Of 13 lizards recorded in the Brazilian Atlantic rain forest, only one species (*Tropidurus torquatus*) responded positively to forest edges and is more abundant in edges than forest interior (Dixo & Martins 2008), despite the expectation that reptiles might respond to edges because of their physiological needs, as basking (Lehtinen *et al*., 2003). In the riparian habitat of Ranomafana National Park, Madagascar, the terrestrial dwarf chameleon *B. superciliaris* is omnipresent along riparian ecological gradient while the ground-dweller *P. nasus* is restricted to riparian edges (0-25 m from river edges) (Rabearivony *et al*., 2015). If so, how can we know in advance whether or not there are significant correlations between species groups? There are no clear answers, but ecological requirements of the species and the scale of observation can provide some guidance.

Therefore, correlation can be expected between species which depend on the same ecological requirements as temperature, forest moisture, canopy covert, vegetation types, abundance and diversity of insect prey and level of tolerance to disturbance (Akani *et al*., 2001; Lehtinen *et al*., 2003). Species richness may also depend on the scale of observation (Rainio & Niemelä, 2003). As most species are ecologically specialized, heterogeneity of the habitat and landscape may directly influence diversity. In the area where they occur, most chameleon species have very limited distribution whereas very few are widespread (Raselimanana & Rakotomalala 2003; Measey *et al*., 2014). In Madagascar, local endemism is very common and each forest block may have its own specific species (Glaw *et al*., 2012; 2021; Prötzel *et al*., 2020). This situation is also common in many other Africa countries (Menegon *et al*., 2009; Stipala *et al*., 2011). In this case, therefore, increasing the sampling unit increases the species numbers at different rates (Weaver, 1995).

The endemism rate for biodiversity in many tropical countries is very high. As far as chameleons, the endemism rate in Madagascar is 100 % and most of the worlds' chameleon species are found only in Madagascar and Africa (Tolley *et al*., 2013). Since a good indicator should also reflect the level of endemism and amount of rare or endangered species (Rainio & Niemelä, 2003), chameleons can be a good indicator as 36 % of world species are threatened by extinction (Hance, 2014). Therefore, species richness might not only indicate the conservation value of an area, as areas of high biodiversity and amount of rare species may not coincide (Prendergast *et al*., 1993). Nevertheless, protecting every hotspot for just one taxon, such as chameleons (Hance, 2014), might protect many target species and species in other groups (Prendergast *et al*., 1993).

Nevertheless, some studies on chameleon abundance and diversity showed in certain circumstances they correlate with other herpetofauna or insect communities (Akani *et al*., 2001; Lehtinen *et al*., 2003). However, since it is rarely only one species or species group which would adequately predict the whole diversity of the biota (Rainio & Niemelä, 2003), it is better to use several species groups with different ecological requirements to indicate biodiversity (Niemelä & Baur, 1998).

Conclusions

Selecting the most optimal indicator is somewhat problematic and depends on the goal of the survey and the characteristics of the indicator. The choice might be compromised between advantages and disadvantages but using chameleon species assemblage provides some advantages in the present context as: (1) most chameleon species are habitat specialized, but

they are sympatric in many cases; (2) community shows well-established vertical and horizontal structure in space; (3) they are sensitive to environmental and ecological changes and use all extent habitat types above and under the soil, respectively for foraging and nesting; (4) they are one of the easier detectable animals in nature; and (5) they occupy intermediate place in the food chain and thus any changes in their distribution and abundance may have an influence on other taxa. So, all other specialist or generalist species would be represented or fall into one or another of these different aspects when they occur in the site where a chameleon assemblage is known.

Moreover, based on cost-effective data and sensitivity to environmental changes, chameleons can also be considered as good candidates for bio-indicators. Their seasonal variation, patchy distribution, presence of some generalist species in the communities and difficulty to predict species richness are the main disadvantages of selecting chameleons as bio-indicators. However, these weaknesses are common to most groups of organisms and have already been addressed for most chameleon communities. Several studies that covered different seasons (e.g. summer and winter) and were undertaken in patchy areas have already been done to address respectively the seasonal and patchily distribution effects. Furthermore, in Africa and Madagascar, simple and repeatable line transect survey techniques based on distance sampling methodologies is applicable for both generalist and specialist species. Nevertheless, compared to other bio-indicators such as carabids (ground beetles), e.g. Rainio & Niemelä, 2003, chameleon populations contain very few generalist species which are mostly forest-dependent. These generalist species might indicate disturbances in the environment and can be used for habitat classification like agricultural lands (e.g. *Furcifer pardalis*) and forest edges (*F. oustaleti*).

Since very few studies have compared chameleon responses to those of other taxonomic groups, it seems difficult to have conclusive results even some herpetofauna species showed similar responses to the same circumstances. The open-habitat chameleon *F. oustaleti* and other herpetofauna taxa are edge-associated because of their physiological needs, as basking without a functional relationship.

To conclude, after forest disturbance, habitat loss and fragmentation, (1) the composition and abundance of chameleons change with, (2) decreasing in abundance of forest-dependent species which will be replaced by more generalist species. In terms of conservation, these species with more specific habitat requirements are the first to suffer from forest degradation or habitat fragmentation and, therefore, are more appropriate focus for conservation. However, still more studies are needed to clarify how well chameleons represent the responses of other species groups. Otherwise, knowledge of community changes following disturbance and the environmental sensitivity of chameleons renders them suitable bio-indicators in studies on habitat degradation and disturbance.

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