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Rainforest frogs of the Australian Wet Tropics: guild classification and the ecological similarity of declining species

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Rainforest frogs are classified into nine ecological guilds based on features of reproduction, habitat use, temporal activity, microhabitat and body size. The largest ecological differences are between the microhylid frogs and the rest of the frog species. Within the non-microhylids, there are two primary groups consisting of (i) regionally endemic rainforest specialists, and (ii) a more ecologically diverse group of species that are less specialized in their habitat requirements.

Most of the regionally endemic rainforest specialists, which includes species in three ecological guilds, have declined or gone missing in recent years. Multivariate analyses of the ecological characteristics of these species show that it is not a single characteristic that isolates those species that have declined from those which have not. The guilds that have undergone significant population declines in the Wet Tropics are all characterized by the combination of low fecundity, a high degree of habitat specialization and reproduction in flowing streams. These results have important implications for the determination of the causal factors in the unexplained global decline of many amphibian species.

Keywords: frogs; biodiversity; functional groups; extinction; declines; rainforest

1. INTRODUCTION

The widespread decline of many amphibian species has caused global concern beyond that caused by many other extinctions. There are several reasons for this: (i) many of the declines have occurred in relatively pristine areas with the causes remaining unknown, and (ii) the possibility that the disappearance of these species is indicative of a global decline in environmental health. The Australian Wet Tropics may be the ideal place to study frog declines because the rainforest is largely protected by World Heritage listing and therefore relatively free of ongoing impacts. In addition, the pre-decline distributions of rainforest frogs have been relatively well documented throughout the region (Covacevich *et al.* 1982; Covacevich & McDonald 1991, 1993; Ingram & Longmore 1991; McDonald 1991, 1992; McDonald *et al.* 1991; Richards *et al.* 1993; Williams *et al.* 1996).

McDonald (1992) presented a comprehensive review of the patterns of distribution and he stated that, at the time of writing, 'the status of the north Queensland rainforest frogs is in a healthy state'. However, in the following years, a dramatic decline of seven frog species that are regionally endemic to the Wet Tropics rainforest was documented by Richards *et al.* (1993). Four species (*Litoria lorica*, *L. nyakalensis*, *Taudactylus rheophilus* and *T. acutirostris*) have not been found for some years despite intensive surveys by the authors and other amphibian biologists (R. Alford, K. McDonald, S. Richards, A. Dennis, personal communication). Three additional species (*Litoria nannotis*, *L. rheocola* and *Nyctimystes dayi*) have severely declined in many upland areas (above 300 m) where they were once common (Richards *et al.* 1993), and there has been a suggestion of a less severe decline in at least one other species (*L. genimaculata*) (K. McDonald, personal communication). There have been similar declines in central Queensland (McDonald 1990), southern Queensland (Czechura & Ingram 1990; Czechura 1991) and globally (Barinaga 1990; Blaustein & Wake 1990; Phillips 1990; Wyman 1990).

Classifying species into ecologically similar groups or guilds has been an extremely useful tool in understanding complex patterns in biogeography, evolution and community structure (Wiens 1989). The use of multivariate techniques to objectively define guilds is widespread (see Wiens (1989) for examples) and is used here to examine the ecological similarity of frog species in the Wet Tropics biogeographic region of Australia. The aim was to determine whether species that have declined over recent years consistently share ecological characteristics that separate them from those species that have not undergone population declines. Additionally, the guild classification can be used to gain a greater understanding of spatial patterns of species richness and assemblage structure (e.g. Williams 1997).

2. METHODS

(a) *Analytical methods*

We have defined rainforest frogs as those species that regularly occur within the rainforest of the Wet Tropics, but which are not

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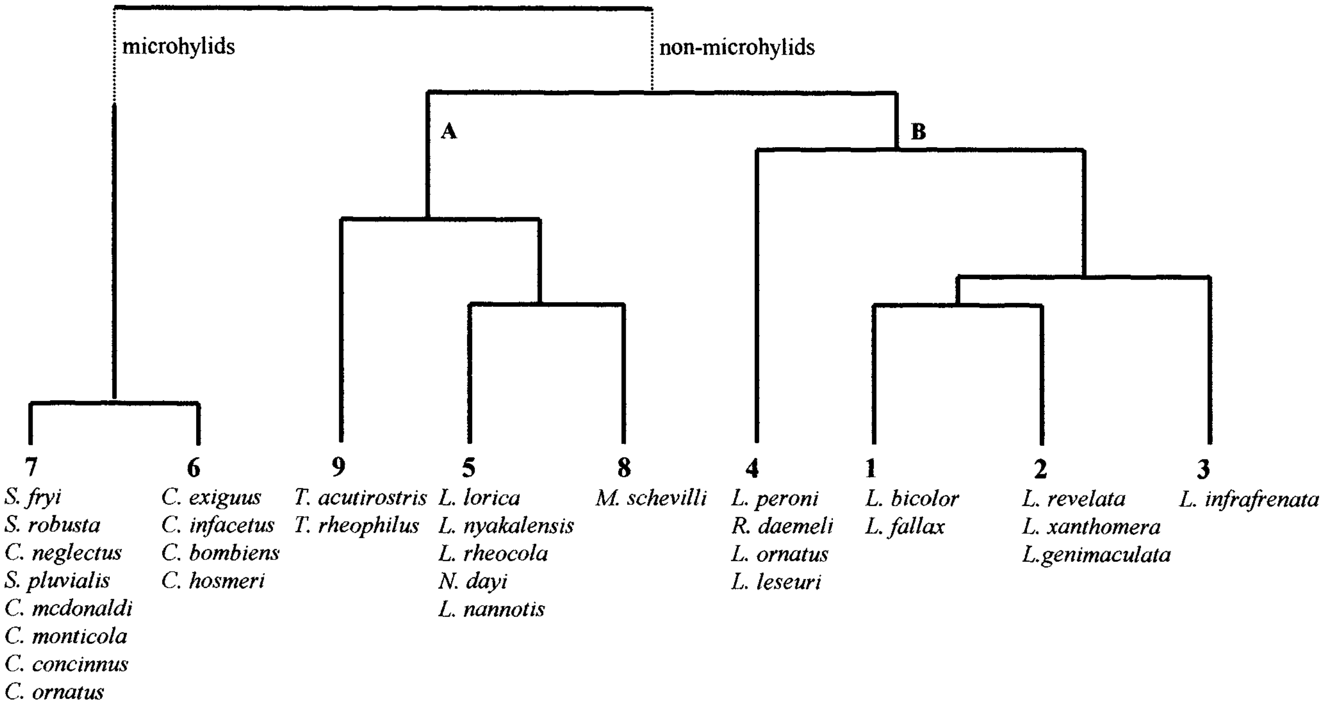

Figure 1. Classification of rainforest frog species into nine ecological guilds on the basis of the ecological variables in Appendix 1. The classification method used was Ward's method, using eculidean distance with all variables standardized between 0 and 1. The dotted line indicates that the ecological distance between microhylids and the other species is much greater than the diagram shows.

necessarily confined to rainforest, and endemic species as those species that only occur in the Wet Tropics biogeographical region (regional endemic) (Williams *et al.* 1996; Williams & Pearson 1997). We classified the rainforest frogs into guilds based on six variables describing the functional ecology of each species: the degree of habitat specialization, fecundity, reproductive habitat, activity period, microhabitat and size (see Appendix 1 for details of each variable and species). Classification of species into ecological guilds was conducted by Ward's method using euclidean distance with all variables standardized between 0 and 1. Diet characteristics are usually an integral part of guild analyses (e.g. Braithwaite *et al.* 1985); however, insufficient diet information was available for most species in these analyses.

Multidimensional scaling (MDS) (euclidean distance, 0–1 standardization) was used to illustrate the similarity of each guild with the other guilds in a continuum, and to identify which ecological variables were responsible for guild differences by correlation of ecological variables with the MDS axes (Spearman-rank correlations as data are ordinal).

3. RESULTS

(a) *Guild classification*

Rainforest frogs were classified into nine guilds (figure 1). The ecological characteristics of each guild are described in table 1. There was a very large difference between microhylids (Microhylidae) and non-microhylids (Hylidae, Myobatrachidae and Ranidae) (figure 1) caused by the differences in many aspects of their biology. Within the non-microhylids the next split essentially separates, on the basis of ecological characteristics only, the frogs that have declined in recent years (group A, figure 1) from those that have not (group B). Two species (*Mixophyes schevilli* and *Litoria genimaculata*) are possible exceptions to this pattern. However, there is some evidence that there may have been declines in some localities in these two species, but they appear to be stable at present (K. McDonald, personal communication).

Using multidimensional scaling, the patterns within the non-microhylids were compressed by the large difference between microhylids and non-microhylids (see the large difference in figure 1); therefore the analysis was re-run with microhylids excluded. This allowed us to examine the patterns in species similarity within the non-microhylids at a finer resolution and to determine which ecological traits were associated with the declining versus the non-declining non-microhylid groups. The ecological similarity of each non-microhylid species is illustrated by the MDS ordination (figure 2) with the guild structure defined in figure 1 superimposed (dotted lines). The ecological variables that were most significantly correlated with the MDS scores for the first two ordination axes are shown on the axes in decreasing order of importance. The first MDS axis explains 76% of the variation between species and is correlated with fecundity ($r=0.899$, $p<0.001$), the degree of rainforest specialization ($r=-0.894$, $p<0.001$), and reproductive habitat ($r=-0.8571$, $p<0.001$). The second axis explained a further 17% of the variation between species and correlated with microhabitat use ($r=-0.941$, $p<0.001$) and temporal activity period ($r=-0.741$, $p<0.001$). The third MDS axis (not shown) only explained a further 5.5% of the variation and correlated with body size.

The declining frogs (guilds 5 and 9) are characterized and distinguished from the non-declining frogs by the combination of low fecundity, a high degree of rainforest specialization and breeding in flowing streams. That is, they are on the left of the ecological gradient represented by the first MDS axis in figure 2. Perhaps just as

Table 1. *Ecological characteristics of the rainforest amphibian guilds (from figure 1) guild species guild description*

guild	species	guild description
1	*Litoria bicolor* *L. fallax*	small (< 30 mm) tree frogs; high fecundity; non-endemic habitat generalists; larval development in swamps and ponds
2	*Litoria genimaculata* *L. revelata* *L. xanthomera*	moderate sized (25–55 mm) tree frogs; high fecundity; non-endemic and endemics; associated with wet forest; larval development in streams, swamps and ponds
3	*Litoria infrafrenata*	largest tree frog in Australia (90–120 mm); high fecundity; non-endemic habitat generalist; larval development in swamps
4	*Limnodynastes ornatus* *L. peronii* *Rana daemeli* *Litoria lesueuri*	small and large (33–70 mm) terrestrial species; high fecundity; non-endemic habitat generalists; larval development in streams, swamps and ponds
5	*Litoria lorica* *L. nannotis* *L. nyakalensis* *L. rheocola* *Nyctimystes dayi*	moderate sized (25–55 mm) tree frogs; low fecundity; endemic rainforest specialists; larval development in streams
6	*Cophixalus* spp.	small (< 20 mm) microhylids; low fecundity; endemic rainforest specialists; terrestrial larval development in the leaf litter
7	*Cophixalus* spp. *Sphenophryne* spp. large	(> 20 mm) microhylids; low fecundity; endemic rainforest specialists; terrestrial larval development in the leaf litter
8	*Mixophyes schevilli*	largest (65–80 mm) terrestrial frog in the wet tropics; high fecundity; endemic rainforest specialist; larval development in streams
9	*Taudactylus acutirostris* *T. rheophilus*	small (25–30 mm) tinker frogs; low fecundity; endemic rainforest specialists; larval development in streams

importantly, the declining frogs are not characterized by their microhabitat use, temporal activity period or size, that is, there is no differentiation between declining and non-declining species along the second or third axes.

4. DISCUSSION

(a) *Ecological guilds*

The guild classification described here is not meant to be a definitive classification of frog guilds in the Australian Wet Tropics: rather, it examines patterns of ecological similarity in order to determine if there are basic ecological differences between declining and non-declining frogs. The lack of knowledge on the basic ecology of most species limited the number of ecological variables available for inclusion in the guild classification analysis. However, even with a limited set of variables, the patterns of ecological similarities were extremely useful in determining the shared characteristics of the declining species (figure 2) and in interpreting biogeographical patterns of species richness (Williams 1997; S. E. Williams & J.-M. Hero, unpublished data). Patterns of ecologically similar groups have previously been very useful in understanding patterns of mammalian diversity in the Wet Tropics (Braithewaite *et al*. 1985; Williams 1997).

(b) *Implications for the 'declining frog problem'*

In recent years, the frogs in guilds 5 and 9 have declined from many high-altitude sites where they were once common (Richards *et al*. 1993; Hero & Fickling 1994; K. McDonald, personal communication). Four species appear to have disappeared entirely, despite intensive searches for them: the two species in guild 9 (*Taudactylus acutirostris* and *T. rheophilus*) and two of the species in guild 5 (*Litoria lorica* and *L. nyakalensis*). The remaining members of guild 5 (*L. rheocola*, *L. nannotis* and *N. dayi*) have disappeared from many high-altitude sites where they were once common. Furthermore, one species in guild 2 (*L. genimaculata*) has suffered declines in some parts of its range (K. McDonald, personal communication). Ongoing work by the authors shows that the distributions of the species in guild 5 (declining species: hylids with low fecundity, high rainforest specialization and streams as their reproductive habitat), and guild 2 (non-declining: rainforest hylids with some rainforest specialization, high fecundity and reproducing in stream-pools and isolated ponds) both had significant relationships with rainforest area and rainforest shape. According to the hypothesis suggested by Williams & Pearson (1997), this suggests that these guilds were more susceptible to extinction during historical contractions in rainforest area. Whereas these guilds may have responded in similar ways to large-scale historical changes in habitat area, they differ clearly in their ecology (figure 2). These ecological differences may make guild 5 more susceptible to environmental perturbations than guild 2.

Rainforest specialization should make species in both guilds 2 and 5 more susceptible to localized extinction due to habitat loss, for example the historical reduction in the area of rainforest as discussed above. However, species with low fecundity (guild 5) have a slower population turnover and may not recover quickly from either

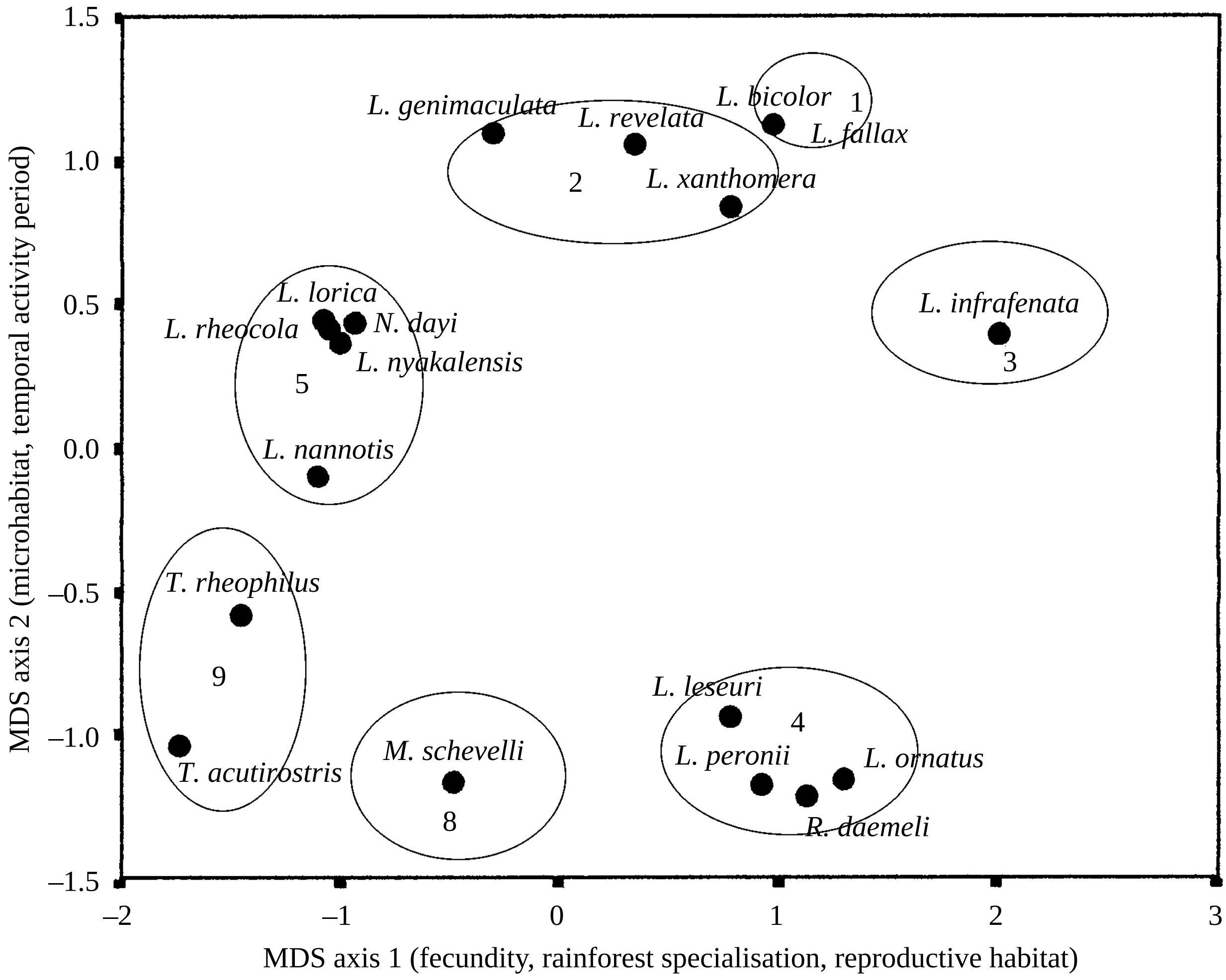

Figure 2. Ecological similarity of each non-microhylid frog species based on the ecological variables describing each species in Appendix 1. Ordination by multidimensional scaling (MDS) using euclidean distance and all variables standardized between 0 and 1. Guild numbers and structure from figure 1. All species in groups 5 and 9 have undergone recent declines.

historical contractions or catastrophic population crashes. In contrast, species with high fecundity (guild 2) may respond quickly to environmental fluctuations and any associated declines in population levels.

The implications of stream habitat specialization are not so obvious. However, it is important as it is this factor that differentiates the declining frogs from the microhylids, which are also characterized by low fecundity and a high degree of rainforest specialization. Both of the guilds of declining species breed in flowing water although the declining hylid frogs (guild 5) have 'torrent-adapted' tadpoles that live in the fast flowing water of mountain streams (Richards 1992), whereas the tadpoles of the declining myobatrachid *Taudactylus* species (guild 9) occur in the stream-pools and are not torrent-adapted. However, the declines cannot be explained by stream specialization alone as a number of stream-dwelling species have not undergone noticeable declines.

In contrast, none of the species in guild 4 (terrestrial, high fecundity, non-endemic habitat generalists) or guilds 6 and 7 (microhylids, low fecundity, endemic rainforest specialists with terrestrial larval development in the leaf litter) appear to have suffered recent population declines (Richards *et al.* 1993; K. McDonald, personal communication). The species in guild 4 are habitat generalists with high fecundity so this result is not surprising for this species group. Although microhylid frogs are habitat specialists with low fecundity, their reproductive mode of laying eggs in moist litter enables them to use the entire area of forest with no dependency on streams. It is likely that the cause of the population declines is associated with the stream habitats where it has affected the most extinction-prone species, that is, those species that have low fecundity and are habitat specialists. There are many possible causal factors that could be stream-borne, ranging from a disease to undetected pulses of high-elevation atmospheric pollution.

The analyses presented here cannot determine the causal factor but they do show that the species that have been affected share common ecological characteristics. The analyses presented here show the value in seeking multivariate patterns of similarity since each of the characteristics that separate declining species from non-declining species has groups of species which form an exception (for example, microhylids have low fecundity and are rainforest specialists, but they do not breed in streams). The important result here is that the frog species that have declined or gone missing are not characterized by any single feature. It is the combination of low fecundity, high habitat specificity and breeding in streams which characterizes the declining frogs of the Wet Tropics. We hypothesize that it is the combination of these ecological characteristics which makes these species particularly extinction-prone and susceptible to whatever factor or factors lie behind their current population declines. The same ecological characteristics have made them susceptible to localized extinction in a historical biogeographical context, which in turn has had a large influence on the spatial patterns of frog biodiversity in the Australian wet tropical rainforests (Williams & Pearson 1997). The decline and possible loss of these species of frogs in the Wet Tropics of Australia represent not only a reduction in species richness but the loss of the very group which causes most of the geographical variation in assemblage structure; a significant loss of regional biodiversity. These results have serious implications for the long-term preservation of biodiversity: these species represent the more sensitive, extinction-prone species, and they may be the indicators of a widespread decline in global environmental quality.

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APPENDIX 1

Rainforest frogs were classified into guilds on the basis of six variables describing the functional ecology of each species:

1. Degree of habitat specialization: 1, generalist (open forest, wet sclerophyll and rainforest); 2, wet forest generalist (wet sclerophyll and rainforest); 3, rainforest specialist (only found in rainforest).
2. Fecundity (mean number of eggs per female per clutch): 1, 0–50 eggs; 2, 50–200; 3, 200–1000; 4, >1000.
3. Reproductive habitat: 1, terrestrial; 2, ephemeral ponds; 3, seasonal ponds; 4, isolated permanent ponds; 5, swamps; 6, stream-side ponds; 7, stream pools; 8, runs; 9, riffles.
4. Adult microhabitat: 1, terrestrial; 2, both terrestrial and arboreal; 3, arboreal.
5. Activity period: 1, diurnal; 2, mostly diurnal; 3, mostly nocturnal; 4, nocturnal.
6. Size: mean male and female snout/vent length (SV) in millimetres. The ecological characteristics of each species of rainforest frog are listed in the table below.

species	endemic species	rainforest specialist	fecundity code	Reproductive habitat	Microhabitat	activity period	male SV	female SV
Hylidae								
Litoria bicolor		1	3	5	3	4	25	27
Litoria fallax		1	3	5	3	3	24	28
Litoria genimaculata		3	3	7	3	4	36	46
Litoria infrafrenata		1	3	5	3	4	90	120
Litoria lesueuri		1	4	7	1	4	40	59
Litoria lorica	*	3	2	9	2	4	31	35
Litoria nannotis	*	3	2	9	2	3	45	55
Litoria nyakalensis	*	3	2	9	2	4	32	40
Litoria revelata		2	3	6	3	4	27	33
Litoria rheocola	*	3	2	8	2	4	31	35
Litoria xanthomera	*	2	3	4	3	4	50	55
Nyctimystes dayi	*	3	2	9	2	4	36	50
Microhylidae								
Cophixalus bombiens	*	3	1	1	1	3	14	15
Cophixalus concinnus	*	3	1	1	1	3	18	22
Cophixalus exiguus	*	3	1	1	1	3	15	18
Cophixalus hosmeri	*	3	1	1	1	3	13	15
Cophixalus infacetus	*	3	1	1	1	3	15	18
Cophixalus mcdonaldi	*	3	1	1	1	3	20	24
Cophixalus monticola	*	3	1	1	1	3	20	24
Cophixalus neglectus	*	3	1	1	1	3	25	29
Cophixalus ornatus	*	2	1	1	1	3	20	25
Sphenophryne fryi	*	3	1	1	1	3	24	30
Sphenophryne pluvialis	*	3	1	1	1	3	24	29
Sphenophryne robusta	*	3	1	1	1	3	24	30
Myobatrachidae								
Limnodynastes ornatus		1	4	3	1	3	33	39
Limnodynastes peronii		1	3	5	1	3	58	60
Mixophyes schevilli	*	3	3	7	1	4	67	80
Taudactylus acutirostris	*	3	1	8	1	2	25	30
Taudactylus rheophilus	*	3	1	6	1	3	25	30
Ranidae								
Rana daemeli		1	4	5	1	3	50	70