

Biological species limits in the Banded Pitta *Pitta guajana*

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The Banded Pitta *Pitta guajana* is widely distributed over the Greater Sunda Islands and Thai-Malay Peninsula. Up to six races have been described, but only three of them are distinct and were formerly considered different species: *guajana* from Java and Bali, *schwaneri* from Borneo, and *irena* from Sumatra and Thai-Malay Peninsula. We here revisit the species status of these three forms with morphometric, plumage and vocal data. We demonstrate pronounced differences in body part measurements and sex-specific coloration amongst all three taxa. Our bioacoustic comparisons also indicate differences in frequency and timing of the two main types of vocalisation among taxa, although further sampling needs to corroborate these findings. We further show that plumage differences—and probably also vocal differences—among Banded Pitta taxa are more pronounced than between sister species in three other *Pitta* complexes. We argue that the three Banded Pitta taxa should be classified as parapatric rather than allopatric, based on their frequent and ongoing contact during glacials when sea-levels drop to create land connections across their Sundaic range. Based on comparisons with other parapatric *Pitta* species, biological species status is recommended for the three Banded Pitta taxa. Ecological and habitat differences in the three Banded Pittas probably evolved to reduce disadvantageous hybridisation during extensive glacial periods of contact.

INTRODUCTION

The Banded Pitta *Pitta guajana* is a Sundaic forest species occurring over a wide area from the Thai-Malay Peninsula through Sumatra, Borneo, Java and a number of offshore islands to Bali (Lambert & Woodcock 1996, Erritzoe 2003). A total of six subspecies have been proposed: nominate *guajana* from east Java and Bali; *affinis* from west Java; *schwaneri* from Borneo; *irena* from Sumatra and peninsular Malaysia; *bangkae* from Bangka Island; and *ripleyi* from peninsular Thailand.

Three of these six subspecies are not universally recognised. The race *bangkae* is widely assumed to be based on a mislabelled specimen from Java (van Marle & Voous 1988). Similarly, *affinis* is considered to be generally indistinguishable from nominate *guajana* in the most recent accounts (e.g. Erritzoe 2003). A third taxon, *ripleyi*, is recognised as a weak subspecies by Erritzoe (2003), but was previously synonymised with *irena* from peninsular Malaysia by Lambert & Woodcock (1996) based on their examination of a series of specimens in the Natural History Museum, Tring (henceforth BMNH). In their synonymisation of *ripleyi*, Lambert & Woodcock (2003) conceded that ‘...there is a tendency for birds from peninsular Thailand to have more orange-red in the supercilium than birds from Sumatra...’. However, they found considerable geographic variation across *ripleyi* and *irena* in the features used by Deignan in describing *ripleyi*, such as the distribution of scarlet in the supercilium, the colour of the central abdomen in males and the mantle coloration. Our own examination of these traits in a range of BMNH specimens of both *ripleyi* and *irena* has only shown potential weak geographical trends in some plumage characters (data not shown), but none that would definitively separate them. Therefore, we support Lambert & Woodcock’s (2003) synonymisation of *ripleyi*. Since the three weak subspecies *bangkae*, *affinis* and *ripleyi* are now widely synonymised under *guajana* and *irena*, respectively, they are not further considered in this contribution.

The three remaining taxa that make up the Banded Pitta are very distinct, to the point that they were each originally described as separate species and continued to be treated as such until the late 1930s (Riley 1938). The

taxa *schwaneri* from Borneo, *guajana* (including *affinis*) from Java and Bali as well as *irena* (including *ripleyi*) from Thai-Malay Peninsula and Sumatra are known to differ considerably in coloration, while vocal differences have been reported anecdotally but remain unanalysed. The two most recent treatises of the genus have both acknowledged that further analysis may demonstrate that the three taxon groups within *P. guajana* may need to be elevated to species rank (Lambert & Woodcock 1996, Erritzoe 2003).

To shed light on the taxonomic status of the three widely recognised subspecies of Banded Pitta, we examined the series of *P. guajana* housed at BMNH. We carried out plumage examinations on subsets of the BMNH series. We also measured various body parts in the same BMNH subsets and present the first statistical comparison of mensural data in Banded Pittas. Furthermore, we collected sound recordings of wild Banded Pittas from throughout their range over the years, and complement this collection with recordings from colleagues. We use this material to investigate the taxonomic classification of the taxa that are currently recognised as members of *P. guajana*.

METHODS

Any taxonomic analysis must be based on a species concept that provides the criteria for assigning species or subspecies rank. We here use Mayr’s (1996) multi-dimensional Biological Species Concept (BSC), which is the most widely followed species concept in ornithology. Biological species rank is accorded to life forms that maintain their taxonomic integrity while in sympatry or parapatry with similar life forms, i.e. the gene pool of a species does not fuse with that of a neighbouring species when the two come into regional contact. Note that the BSC allows for a certain level of hybridisation as long as it is marginal and does not lead to the amalgamation of gene pools of the two taxa in question. BSC rank assignment becomes harder in taxa that do not overlap or abut geographically. In these cases, the BSC has to resort to the yardstick approach (e.g. Mayr & Ashlock 1991, Helbig *et al.* 2002), under which two taxa are assessed as discrete species if

their plumages, vocalisations and/or other characters are at least as different from each other as they are between two unequivocal species of the same genus or family.

We examined various subsets of the BMNH series of *P. guajana*. Only recognisably adult individuals were considered. Measurements of tarsus and upper mandible (as measured from the bill-tip to the point where the upper mandible meets the forehead) were taken with a calliper to the nearest tenth of a millimetre, while wing measurements were taken with a ruler to the nearest millimetre by the same person (FER) to preclude observer bias. Statistical differences between measurements were calculated using a two-tailed Mann Whitney U test as implemented in the program Word Excel. Plumage coloration of birds at BMNH was assessed against natural light. JAE took photos of BMNH specimens using a Sony DSC W90. Sound recordings of birds in the wild were made by JAE using a Sennheiser ME66 and Sony HiMd minidisc. These recordings and additional ones from colleagues and from www.xeno-canto.org (see Acknowledgements) were analysed with respect to various frequency parameters (lowest frequency and two different measures of frequency range) as well as call duration. For all sampled vocalisations, analyses were conducted and sonograms were generated using default settings in the program Syrinx Version 2.6h (by John Burt, downloadable at www.syrinxpc.com). For some recordings, the darkness level of sonogram depiction was adjusted to resemble the other recordings to prevent a measuring bias in call duration based on different levels of loudness in the original recordings.

RESULTS

Morphometrics

Table 1 provides sample sizes and mean measurements of tarsus, upper mandible and wing length for the examined BMNH subset of specimens from all three taxa. Since the size of sexes within each taxon did not differ significantly in any of the three characters, we pooled male and female measurements for the comparison amongst taxa. *P. g. guajana* from Java and Bali is significantly larger in all three characters (tarsus, upper mandible and wing length) than the remaining taxa (Table 1). There are no significant differences between *schwaneri* and *irena* in these measurements.

Our measurements generally fall within the ranges of the same characters given by Lambert & Woodcock (1996), who also worked on the BMNH series. The only exception relates to the bill measurements, which are considerably larger in Lambert & Woodcock (1996) for all taxa because of the different way these authors measured this parameter (i.e. to the base of the gape rather than to the upper base of the upper mandible). However, in agreement with our data, Lambert & Woodcock's (1996) bill measurements are also generally smaller for *P. g. schwaneri* and *P. g. irena* than for the nominate. Unfortunately, the latter authors' data are not directly comparable with ours as no exact sample sizes, means and standard deviations are given.

The inter-taxon size differences in our measurements are in good agreement with weight data provided for the three taxa by Lambert & Woodcock (1996). The weight

Table 1. Taxon-specific mean measurements of tarsus, upper mandible and wing (including sample size and standard deviation); p-values of differences between sexes or taxa refer to two-tailed Mann-Whitney U test; significant p-values are printed **bold**. The taxa *P. g. guajana* and *P. g. irena* as here defined include samples of the proposed taxa *affinis* and *ripleyi*, respectively.

	<i>P. g. irena</i>		<i>P. g. guajana</i>		<i>P. g. schwaneri</i>	
	male	female	male	female	male	female
Tarsus						
n	14	15	7	6	7	7
mean [0.1 × mm]	382	375	422	415	390	384
standard deviation	12.9	14.8	19.3	17	14	12
p-value of sex difference	0.2757		0.5222		0.5687	
p-value of taxon difference vs <i>irena</i>			<0.0001		0.0891	
p-value of taxon difference			<i>guajana</i> vs <i>schwaneri</i> : 0.0005			
Upper mandible						
n	18	16	8	6	7	7
mean [0.1 × mm]	223	221	241	241	218	226
standard deviation	13.1	18.7	11.3	16.8	9.2	6.7
p-value of sex difference	0.8026		0.6527		0.2263	
p-value of taxon difference vs <i>irena</i>			0.0006		0.8808	
p-value of taxon difference			<i>guajana</i> vs <i>schwaneri</i> : 0.0016			
Wing						
n	16	17	8	6	7	7
mean [mm]	101	99	104	105	99	101
standard deviation	4.0	6.8	2.5	3.9	4.1	3.4
p-value of sex difference	0.7718		0.9522		0.5222	
p-value of taxon difference vs <i>irena</i>			0.0183		0.8103	
p-value of taxon difference			<i>guajana</i> vs <i>schwaneri</i> : 0.0178			



Plate 1. Banded Pitta males (lateral view): left to right, *P. g. schwaneri*, *P. g. guajana* and *P. g. irena*. Copyright Natural History Museum, Tring.



Plate 2. Banded Pitta males (ventral view): left to right, *P. g. schwaneri*, *P. g. guajana* and *P. g. irena*. Copyright Natural History Museum, Tring.



Plate 3. Banded Pitta females (lateral view): left to right, *P. g. schwaneri*, *P. g. guajana* and *P. g. irena*. Copyright Natural History Museum, Tring.



Plate 4. Banded Pitta females (ventral view): left to right, *P. g. schwaneri*, *P. g. guajana* and *P. g. irena*. Copyright Natural History Museum, Tring.



Plate 5. Banded Pitta females (dorsal view): left to right, *P. g. schwaneri*, *P. g. guajana* and *P. g. irena*. Copyright Natural History Museum, Tring.

Table 2. Plumage features in males and females of all three taxa.

	Head	Throat	Underparts	Upperparts
male <i>guajana</i>	black crown with long yellow supercilium	white becoming yellow further down	barred dark-blue and yellow (sometimes with a flush of red) with broad blue upper breast-band	medium-brown with white wing-panel
male <i>irena</i>	black crown with fiery red rear-end to supercilium fading to yellow towards front (exact distribution of red can vary individually)	white with yellow wash on sides	uniform deep-blue with red upper flank barring that varies individually in extent and width	rich brown; wing-panel more extensive white than other taxa
male <i>schwaneri</i>	black crown with long bright-yellow supercilium (brighter than <i>guajana</i>)	pale yellow becoming brighter further down	breast dark-blue, almost black, heavily barred bright yellow; belly and undertail-coverts bright blue with barring restricted to lower flanks	rich brown with white wing-panel
female <i>guajana</i>	brown crown with faintly demarcated buff supercilium	white	barred light-brown and dull-yellow to off-white with thin dark-brown upper breast-band	medium-brown with white wing-panel
female <i>irena</i>	faded black crown with supercilium fiery-red fading to buff towards front	white	barred black and buff, sometimes with orange tinge on upper flanks and breast	rich brown, wing-panel more extensive white than other taxa
female <i>schwaneri</i>	dark-brown crown with yellow supercilium becoming paler toward the bill	white with buff wash on sides	upper breast to undertail-coverts barred dark-brown or blackish alternating with dull yellow, lacking blue belly	rich brown with white wing-panel

range given for *guajana* (93–106 g) is above that of *schwaneri* (60–80 g) and *irena* (75–97 g), even though there seems to be a slight overlap between *guajana* and *irena* (Lambert & Woodcock 1996). In contrast, the range of tail lengths given for *guajana* (which includes Lambert & Woodcock's *affinis*) are 62.8–71.5 mm, only slightly—and probably not significantly—higher than that given for *schwaneri* (59–70 mm) or *irena* (59–71 mm). Unfortunately, statistical significance of differences cannot be inferred from Lambert & Woodcock's (1996) data. Nevertheless, the weights add to the conclusion that *P. g. guajana* is a much more massive bird than the Banded Pittas from Borneo, Sumatra and the Malay Peninsula.

Plumage

We closely examined a total of 57 specimens, with a breakdown as follows: *P. g. guajana*, eight males and five females; *P. g. irena*, 14 males and 15 females; *P. g. schwaneri*, seven males and seven females. Table 2 shows the plumage differences we detected between males and females and among all three taxa. Plumage differences given in Table 2 were diagnosed in all individuals examined, unless otherwise stated. Photos of representative individuals for each taxon are presented in Plates 1–5 and confirm the most salient plumage differences. In particular, males of the three taxa differ dramatically in terms of the pattern of barring on the underparts, lack or presence of a breast-band, colour of supercilium and throat pattern (Plates 1–2; Table 2). Females differ especially in their pattern of barring on the underparts, head contrast, colour of supercilium and presence or absence of a breast-band (Plates 3–5; Table 2). The three taxa also show minor differences in back coloration and the extent of white on the wing-panel in both sexes (Plates 1–5; Table 2).

Vocalisations

We obtained recordings of 16 individuals of *P. guajana* representing all three taxa (2 *guajana*, 6 *irena*, 8 *schwaneri*). The vocalisations fell into two different types: (1) the 'territorial call' (Fig. 1), a single inverted-V-shaped note (rarely accompanied by a second minor note: see Fig. 1B)

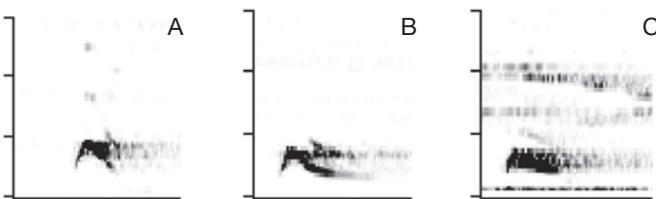


Figure 1. Territorial calls of (A) *P. g. guajana* (Carita, west Java, by R. Hutchinson), (B) *P. g. irena* (Taman Negara, Pahang, peninsular Malaysia by JAE) and (C) *P. g. schwaneri* (Poring, Sabah, Borneo by R. Hutchinson).

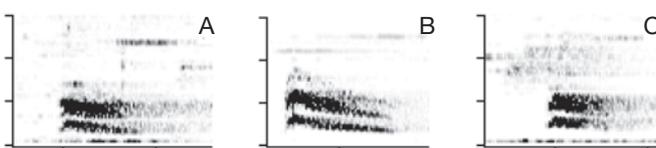


Figure 2. Alarm calls of (A) *P. g. guajana* (Carita, west Java by JAE), (B) *P. g. irena* (= '*ripleyi*') (Khao Nor Chuchi, southern Thailand by A. Meijer) and (C) *P. g. schwaneri* (Poring, Sabah, Borneo by R. Hutchinson).

typically given at 4–10 sec intervals, but sometimes more or less frequently depending on the level of agitation; and (2) the 'alarm call' (Fig. 2), a single note given at similar intervals as the territorial call but usually more drawn-out and consisting of two harmonic notes, the second of which typically covers a much wider frequency range. We refer to these vocalisations as territorial and alarm calls for the sake of simplicity, although it is uncertain whether their behavioural context is as functionally restricted as these terms imply.

We measured the highest and lowest frequency as well as the duration of each territorial call (data not shown). We also measured all alarm calls in terms of duration, lowest frequency, frequency range of first harmonic as well as frequency range of both harmonics combined (data not shown). Even though our sample sizes are too low to allow for statistical analysis, some of the vocal differences detected may not be of an individual or context-dependent nature, but may be taxon-specific. There seem to be pronounced differences in the duration of the territorial call between nominate *P. g. guajana*, which gives a short note, and the other taxa, which utter a much longer note (Fig. 1). Additionally, the territorial call of *P. g. schwaneri* may be characterised by a much narrower frequency range than that of the other taxa (Fig. 1), although more sampling is desirable for confirmation. In terms of the alarm call, *P. g. schwaneri* has a much higher-pitched lowest frequency than the other taxa as well as a much shorter call duration (Fig. 2). Some of these sound differences amongst Banded Pitta subspecies (such as the much shorter territorial call in *P. g. guajana*, or the shorter alarm call and less inflected territorial call in *P. g. schwaneri*) are noticeable in the field and have been corroborated by many unrecorded calling individuals heard by us in the native habitat of these birds. More future vocal sampling is desirable to confirm these differences.

DISCUSSION

The taxonomy of the Banded Pitta *P. guajana* has created much controversy. Some of the proposed subspecies, such as *bangkae*, *affinis* and *ripleyi*, are either based on potentially mislabelled specimens (van Marle & Voous 1988) or are so weak that some authors have chosen to synonymise them (Lambert & Woodcock 1996, Erritzoe 2003), a treatment that we fully concur with based on our own specimen comparisons (data not shown). The remaining three taxa (*schwaneri*, *irena* and nominate *guajana*) were treated as distinct species for a long period in the past. Calls for their re-elevation to species level have been voiced (Lambert & Woodcock 1996, Erritzoe 2003) and need to be examined more closely under the framework of the Biological Species Concept.

Our examination of specimens corroborates previous indications that there are strong and consistent plumage differences in both sexes among all three taxa (Plates 1–5). Moreover, our mensural data indicate that nominate *guajana* is distinctly larger than *irena* and *schwaneri*, although there do not seem to be such size differences between the latter two. Last but not least, we present a selection of vocal data that are indicative of frequency and/or temporal differences between *schwaneri* and the other two in alarm call delivery and amongst all three taxa in territorial call delivery (Figs. 1–2). Although vocal

sample size did not allow for firm conclusions, the bioacoustic results match our experience with these birds in the field, to the extent that an individual in the forest can usually be identified to taxon level (using such traits as call length and vocal quality based on frequency range) if both territorial and alarm calls are given.

The three taxa *irena*, *schwaneri* and *guajana* do not presently come into geographic contact. To assess their taxonomic status under the Biological Species Concept, it is necessary to judge whether their differences equal those between other closely related *Pitta* species (e.g. Mayr & Ashlock 1991, Helbig *et al.* 2002). There are three *Pitta* complexes whose member species are less differentiated in terms of plumage and/or vocalisations than the three Banded *Pitta* taxa. In each of these three complexes, member taxa come into contact with each other in a parapatric or sympatric fashion and behave as good biological species.

(1) The African *P. angolensis* and Green-breasted *P. reichenowi* are a closely related species pair (Irestedt *et al.* 2006) widely replacing each other over their Afrotropical distribution, but breeding and non-breeding populations of both species come into contact both west and east of the Congo Basin with little evidence of intergradation (Erritzoe 2003). Both species are sexually monomorphic and resemble each other closely. The buff breast of *P. angolensis* is replaced in *P. reichenowi* by a dull green that is delimited from the white throat by a narrow black breast patch (Erritzoe 2003). While these underparts differences parallel those among Banded *Pitta* taxa, the two Afrotropical pittas do not exhibit comparable differences in head coloration and can thus be regarded as more uniform than Banded Pittas.

(2) Another closely related species pair, the Blue-naped *P. nipalensis* and Blue-rumped *P. soror* (Irestedt *et al.* 2006), co-occur widely over northern Indochina as good species, although they tend to replace each other altitudinally (Erritzoe 2003). Males in both species are geographically variable but have buff to rufous head and underparts, while the nape, tail, rump and upperparts are an iridescent green to blue. Females in both species closely resemble their respective male counterparts but for the lesser degree of iridescent coloration on the upperparts, nape, rump and tail. Comparing the two species, the main characters that set them apart pertain to differences in distribution and hue of the blue-to-green iridescence on the nape and rump. There are also less marked differences in the hue of their underparts. All in all, the major differences in coloration between these two species are restricted to limited parts of the body and are comparable if not less intense than those among Banded Pittas.

(3) The Mangrove *P. megarhyncha* and Blue-winged *P. moluccensis* were formerly considered conspecific, but are now unanimously treated as different species (e.g. Erritzoe 2003) because of the lack of intergrades in areas of sympatry. *P. megarhyncha* is narrowly confined to mangrove habitat along the eastern Bay of Bengal and Straits of Malacca, but *P. moluccensis* occurs widely in South-East Asia and—although usually replaced by *P. megarhyncha* in mangrove habitat—overlaps widely with the latter in its breeding and non-breeding grounds. Apart from bill size, the only consistent morphological difference between these two sexually monomorphic species is the brown rather than black crown coloration in *P.*

megarhyncha (Erritzoe 2003). In terms of plumage, the two species are therefore much more similar than the three Banded Pittas are to one another. In addition, vocal differences between *P. megarhyncha* and *P. moluccensis* are slight (e.g. description in Erritzoe 2003); in fact, their calls are doubtfully distinguishable in the field (pers. obs.) and consistent differences remain to be documented.

Thus the three strongly differentiated forms of Banded *Pitta* may be accepted as full species since their differences surpass those of the sympatric or parapatric species of *Pitta* enumerated above. However, a further aspect in favour of biological species status for these three forms is the range of ecological differences among them. Bornean *schwaneri* is essentially a hill forest inhabitant, which—although occasionally recorded near sea level—is never found far from areas of topographic relief (Lambert & Woodcock 1996; pers. obs.). In contrast, *irena* from the mainland and Sumatra is characteristic of flat floodplain rainforest, although it does also occur at higher elevations (Lambert & Woodcock 1996; pers. obs.). Among the three taxa, nominate *guajana* is probably the one that is least often recorded at higher elevations. However, in contrast to the other two taxa, it has a broad tolerance for degraded, secondary and floristically poor coastal forest types and even occurs in scrub (Lambert & Woodcock 1996; pers. obs.).

Based on current disjunct distributions, the three Banded *Pitta* taxa are widely regarded as allopatric. However, taking into account the history of land connections in the region, they must be regarded as essentially parapatric, as they have regularly come into prolonged contact during glacial periods. Within the last three million years, Java, Bali, Sumatra, Borneo and the mainland have repeatedly been connected during c.20 glacial epochs that have each lasted c.10,000–50,000 years. These connections arise when glacial periods cause the global sea-level to drop by up to 130 m (Bintanja *et al.* 2005, Caputo 2007) and to expose areas of shallow sea. In fact, the present island distribution of Sundaic rainforests is unrepresentative of the area's biogeographic past, such that the distribution of the three taxa of Banded *Pitta* has probably been connected more often than not during the late Pliocene and Pleistocene (Cannon *et al.* 2009). Since we are now going through the peak of an interglacial, the present allopatry of the three Banded *Pitta* groups is an artefact of timing, while—at most other times in the Pleistocene—they have come into geographic contact or even overlapped regionally. Viewed against this biogeographic background, their ecological and habitat differences may have evolved as isolation mechanisms to avoid the production of hybrid offspring.

If the three Banded Pittas constituted one biological species, we would expect them to vary in a clinal fashion, given ample opportunities for gene flow during much of the late Pliocene and Pleistocene glacial epochs. Such clinality should be particularly noticeable in areas where the different taxa presently come into close geographic proximity, such as south Sumatra and west Java, which are currently only separated by 25 km of shallow shelf. However, pittas on either side of the Sunda Strait exhibit plumages and vocalisations typical of their own taxon, with no intermediacy apparent in any of the museum material inspected. In contrast to the great phenotypic differences between Sumatran and Javan pittas across the

Sunda Strait, populations of *irena* on the Sumatran and Malayan end of the Malacca Strait are identical to each other, even though geographic distance is slightly larger than between Java and Sumatra. The only alternative to species status of the three taxa would be to argue that phenotypic differences between Java, Thai-Malay Peninsula, Sumatra and Borneo have evolved within 10,000 years since the last land connection and are wiped out every time the sea-level drops and creates opportunities for contact. However, such a short time-frame for the evolution of species level differences is untenable even under the most relaxed assumptions of evolutionary speed in birds (e.g. Friesen *et al.* 2007).

Based on their morphological, vocal and ecological differences that equal or exceed those among other *Pitta* species, and based on their taxon integrity despite continual geographic contact throughout much of the past three million years, we propose biological species status for both *P. schwaneri* and *P. irena* as distinct from *P. guajana*. We propose that each of these three species be recognised as monotypic. As English names, we propose Malayan Banded Pitta, Bornean Banded Pitta and Javan Banded Pitta for *P. irena*, *P. schwaneri* and *P. guajana*, respectively. The name Banded Pitta should continue to be applied to the group as a whole. The retention of the word 'Banded' combined with a geographic attribute in the common name ensures that there is no confusion between old treatments and new ones that accept this split. The species resulting from this revision clearly require assessment as to their conservation status. Further research may demonstrate some of them (especially *P. guajana* and *P. irena*) in need of elevation to Vulnerable status.

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