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Large-culmed Bamboos in Madagascar: Distribution and Field Identification of the Primary Food Sources of the Critically Endangered Greater Bamboo Lemur *Prolemur simus*

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Abstract: The greater bamboo lemur *Prolemur simus* is a Critically Endangered lemur endemic to eastern Madagascar. Wild *P. simus* populations have diets dominated by bamboo (Poaceae: Bambusoideae), particularly large-culmed species of two endemic genera, *Cathariostachys* and *Valiha*, but also of an endemic *Arundinaria* and the pantropical *Bambusa vulgaris*. A good understanding of the distribution and biology of large-culmed bamboos would, therefore, be a major help in understanding the factors influencing the distribution and conservation requirements of *P. simus*. During four years of research within the context of a collaborative programme aimed at conserving *P. simus*, we undertook surveys at 47 low-, mid- and high-elevation sites in eastern Madagascar between November 2008 and September 2012, covering a distance of over 1000 km from Makira in the north to Midongy in the south. We provide and illustrate characteristics helpful in the field identification, at least to generic level, of the large-culmed woody bamboos we encountered. The most frequently encountered non-endemic large-culmed bamboo was *Bambusa vulgaris*, with both the green and the yellow forms commonly planted in or near rivers, towns and villages. We made 1,343 georeferenced records of endemic, large-culmed bamboos, recording *Cathariostachys* from Makira to Midongy, *Valiha diffusa* from Makira to the southern parts of the COFAV, and *Arundinaria* from Zahamena to the COFAV. *Valiha diffusa* was recorded only at low elevations (9–576 m), and *Arundinaria* only at high elevations (1018–1667 m), while *Cathariostachys* was distributed across a wide range of elevations, from 53 to 1471 m, although most records were between 600 and 1,260 m. *Valiha diffusa* had the most variable culm diameters, ranging from 1.7 to 9.5 cm. *Cathariostachys* had the largest mean culm diameter of the endemic large-culmed bamboos (6.1 cm), and *Arundinaria* the smallest (4.0 cm). Culm diameters of *Bambusa vulgaris* were larger than those of the endemic bamboos, with a mean of 9.58. *Cathariostachys* had thinner mean culms at lowland compared to higher elevation sites. The revised distribution map we provide for *Cathariostachys* appears to correspond well to the potential current distribution of *P. simus* based on recent direct sightings, indirect feeding signs and unconfirmed local knowledge. *Cathariostachys* does not, however, currently occur throughout the historic range of *P. simus*. *Valiha* does occur at one *P. simus* subfossil site outside the current range, and therefore may have been the primary food source for the species there. Further research into the historical distribution of large-culmed bamboos in Madagascar would be very helpful in establishing how eventual changes in bamboo distributions over time may have affected changes in *P. simus* distribution.

Key words: Ankeniheny-Zahamena Corridor, Nosivolo, *Arundinaria*, *Cathariostachys capitata*, *Cathariostachys madagascariensis*, *Valiha diffusa*, *Yushania*

Introduction

Listed as Critically Endangered by IUCN (2012), the greater bamboo lemur (*Prolemur simus*) is considered to be one of the most endangered primates in the world (Wright *et al.* 2009). It is also listed in the top 50 most evolutionarily distinct and globally endangered mammal species (Collen *et al.* 2011). Endemic to Madagascar, sub-fossil records show it was historically one of the most widespread and abundant of the lemurs (Mahé 1976; Vuillaume-Randriamanantena *et al.* 1985; Godfrey and Vuillaume-Randriamanantena 1986; Godfrey *et al.* 2004). In recent years, however, the species was thought to have a much reduced range, in and near the south-eastern rainforests of the island (Mutschler and Tan 2003). Recent range extensions based on confirmed sightings have shown that the present-day range is not as diminished as previously thought (Dolch *et al.* 2008; King and Chamberlan 2010; Ravaloharimanitra *et al.* 2011; Rakotonirina *et al.* 2011), and indirect evidence suggests the species may still be widely distributed through much of eastern Madagascar (Dolch *et al.* 2010; Rakotonirina *et al.* 2011, 2013). Confirmed sightings in recent years have been made in the remaining mid- to high-elevation rainforest corridors from Didy to Andasibe (Dolch *et al.* 2008; Ravaloharimanitra *et al.* 2011; Randrianarimanana *et al.* 2012; Olson *et al.* 2012), and from the Ranomafana National Park to the Andringitra National Park (Petter *et al.* 1977; Wright *et al.* 2008; Delmore *et al.* 2009). They have also been made in lowland, often degraded, landscapes in the Brickaville District (Ravaloharimanitra *et al.* 2011; Bonaventure *et al.* 2012; Lan-tovololona *et al.* 2012; Mihaminekena *et al.* 2012), the Vatoman-dry District (Rakotonirina *et al.* 2011), at the confluence of the Mangoro and Nosivolo rivers in the Mahanoro District (Rakotonirina *et al.* 2011; Andrianandrasana *et al.* in press), around Kianjavato in the Mananjary District (Meier and Rump-ler 1987; Andriaholinirina *et al.* 2003; Wright *et al.* 2008; McGuire *et al.* 2009), and near Karianga in the Vondrozo Dis-trict (Wright *et al.* 2008, 2009). The elevation range for con-firmed sightings is 20 m (Bonaventure *et al.* 2012) to 1,600 m (Goodman *et al.* 2001).

Recent authors consider *Prolemur simus* to represent a monospecific genus (Mittermeier *et al.* 2008 and references therein), although it has previously been considered conge-neric with the other bamboo lemurs *Hapalemur* spp. (Tatter-sall 1982). Most wild *Prolemur* and *Hapalemur* populations have diets dominated by bamboos (Poaceae: Bambusoideae; Mutschler and Tan 2003; Tan 2007), exceptions being some *Hapalemur* populations which occur in sites with little or no bamboo, and which feed primarily on other monocotyledon plants, particularly members of the grass (Poaceae) and sedge (Cyperaceae) families (for example, *H. alaotrensis* in wet-lands at Lac Alaotra, Mutschler 1999, and *H. meridionalis* in littoral forest at Mandena, Eppley *et al.* 2011).

Two lemurs, *Prolemur simus* and the golden bamboo lemur *Hapalemur aureus*, appear to be particularly dependent on bamboo (Tan 1999). Both species must have specializa-tions allowing them to feed on bamboo parts rich in cyanide,

although the exact mechanisms by which they avoid cyanide poisoning have not been identified (Tan 2007; Ballhorn *et al.* 2009; Yamashita *et al.* 2010). *Prolemur simus* has specializa-tions allowing it to exploit the toughest and most mechani-cally-challenging parts of woody bamboos avoided by *Hapal-emur*, such as the mature culm pith and mature leaf-blades of the large-culmed *Cathariostachys madagascariensis* (see Vinyard *et al.* 2008; Yamashita *et al.* 2009), and all known wild *P. simus* populations occur in sites containing large-culmed woody bamboos (Tan 2007; Rakotonirina *et al.* 2011; Ravaloharimanitra *et al.* 2011).

Madagascar is home to a large diversity of woody bam-boos. Dransfield (2000, 2003) lists 32 named species endemic to Madagascar (Table 1). The taxonomy of a number of them is undergoing revision. Two are now considered conspe-cific (*Schizostachyum bosseri* and *S. parvifolium* synonyms of *Sirochloa parvifolium*, Dransfield 2002), several are cur-rently placed in incorrect genera (in, for example *Arundinaria* and *Cephalostachyum*, Dransfield 2000, 2003), and at least three species remain to be described (Dransfield 2003). A fur-ther five named species are either pantropical or introduced (Dransfield 2003; Table 1).

Prolemur simus appears to be particularly associated with large-culmed species of two endemic genera, *Cathariostachys* and *Valiha*, especially *C. madagascariensis* in mid- to high-elevation rainforest, and *V. diffusa* in lowland secondary habi-tats (Tan 2007; Rakotonirina *et al.* 2011; Ravaloharimanitra *et al.* 2011). In addition to these two genera, *P. simus* feeds on other large-culmed bamboos, such as an endemic *Arun-dinaria* species (Randrianarimanana *et al.* 2012, as “volot-sanganana”) and the pantropical *Bambusa vulgaris* (Ravalo-harimanitra *et al.* 2011; Mihaminekena *et al.* 2012), the latter species possibly introduced, being found mainly along rivers or near villages (Dransfield 2003). Various studies indicate that these large-culmed bamboos make up over 90% of the diet of *P. simus* in the wild (Tan 1999; Mihaminekena *et al.* 2012; Randrianarimanana *et al.* 2012).

This close association between *Prolemur simus* and large-culmed bamboos implies that a good understanding of the distribution and biology of large-culmed bamboos would be a major help in understanding the factors influencing the distribution, abundance, biology and conservation require-ments of this Critically Endangered lemur. However, very little is known about any of the woody bamboos of Mada-gascar (Dransfield 2003). We therefore present in this paper a summary of what we have learnt about large-culmed bam-boos in Madagascar during four years of surveys and research in the context of a collaborative programme aimed at conserv-ing *P. simus* (King and Chamberlan 2010; Rakotonirina *et al.* 2011). We update our knowledge on the distribution, eleva-tion ranges, and culm diameter of large-culmed bamboos occurring in the range of *P. simus*, and provide and illustrate characteristics helpful in their field identification, at least to generic level. We hope that this analysis will facilitate further work on various aspects of the endemic bamboos of Mada-gascar, as suggested by Dransfield (2003).

Table 1. Woody bamboo species recorded from Madagascar, based on 1: Clayton *et al.* (2010); 2: Dransfield (1994); 3: Dransfield (1997); 4: Dransfield (1998); 5: Dransfield (2000); 6: Dransfield (2002); 7: Dransfield (2003); 8: *The Plant List* (2010).

Species (1, 6, 7)	Culm diameter (cm)	Elevation (m)	Notes
Introduced/pantropical			
<i>Phyllostachys aurea</i>	0.2–0.3 (1)		Naturalized everywhere around Antananarivo (7)
<i>Bambusa vulgaris</i>	4–10 (1,7)		Occurs nears villages or along rivers (7)
<i>Bambusa multiplex</i>	1–3 (1)		Usually planted as hedges (7)
<i>Dendrocalamus giganteus</i>	20–30 (1)		Planted at various places along the east coast (7)
<i>Gigantochloa</i> aff. <i>pseudoarundinacea</i>	5–10 (1)		Planted near Maroantsetra (7); synonym of <i>Gigantochloa</i> aff. <i>verticillata</i> (8)
Native, erect culms			
<i>Cathariostachys capitata</i>	4–5 (4)	5–700 (3)	Lowland to hill primary forest, and also disturbed forest, mainly east coast (5,7)
<i>Cathariostachys madagascariensis</i>	5–8(–12) (4)	900–1000 (7)	Lower montane forest, Andasibe to Ranomafana (7)
<i>Valiha diffusa</i>	(1.5–)7–10 (4)	50–700 (7)	Primary forest and open hills, from Nosy Be throughout eastern slopes to Ifanadiana (7)
<i>Valiha perrieri</i>			Forest, Andrafiarana, south of Anstiranana (4,5,7)
<i>Valiha</i> sp.			Dry forest, Morondava (7)
<i>Arundinaria ibityensis</i>	2 (1)	1800–2250 (5,7)	Rocky ridges, Mt Ibity, Antsirabe (5,7); synonym of <i>Thamnocalamus tessellates</i> (8)
<i>Arundinaria ambositrensis</i>		1300–1400 (5,7)	Forest, Ranomena (Ambositra) and Ranomafana (5,7); synonym of <i>Yushania humbertii</i> (8)
<i>Arundinaria humbertii</i>		2000 (5,7)	Forest, Andringitra (5,7); synonym of <i>Yushania humbertii</i> (8)
<i>Arundinaria perrieri</i>	5–8 (1)	1000 (5,7)	Forest, Manongarivo (5,7); synonym of <i>Yushania perrieri</i> (8)
<i>Arundinaria madagascariensis</i>		2000 and 2800 (5,7)	Mossy forest, Tsaratanana (5,7); synonym of <i>Yushania madagascariensis</i> (8)
<i>Arundinaria marojejyensis</i>		2000 (5,7)	Mossy forest, Marojejy (5,7); synonym of <i>Yushania madagascariensis</i> (8)
<i>Schizostachyum perrieri</i>		2000 (5,7)	Forest, Tsaratanana (5,7); maybe conspecific with <i>Arundinaria madagascariensis</i> (7)
<i>Decaryochloa diadelpha</i>	2–2.5 (3,5)	800–1000 (3); 900 (7)	Montane forest, common at Andasibe, but died in 1994 following flowering (3,7)
<i>Nastus elongatus</i>	3 (1)	1000 (5,7)	Montane or mossy forest, Andringitra and Ranomafana (5,7)
<i>Hickelia madagascariensis</i>	1–1.8 (1,2)	1000–1600 (7)	Relatively common in montane forests of Central Highlands (7)
<i>Hickelia alaotrensis</i>		1500 (5,7)	Forest at Lac Alaotra (7)
<i>Hickelia perrieri</i>		2400 (5,7)	Tsaratanana (7)
<i>Sirochloa parvifolium</i> (6)	≤ 0.7 (6)	0–70 (6,7)	Very common on white sands, Nosy Be and coastal regions of east (7); occasionally found a long way from the shore at up to 70 m a.s.l. (6); synonym of <i>Sirochloa parvifolia</i> (8)
<i>Perrierbambus madagascariensis</i>	2–3 (1)	Lowlands (5,7)	Dry lowland forest at Locky, near Mahajanga (5,7)
<i>Perrierbambus tsarasaotrensis</i>	2–3 (1)		Tsarasaotra (5,7)
Native, climbing culms			
<i>Cephalostachyum chapelieri</i>			Lower montane forest, Analamazaotra, Andasibe (7)
<i>Cephalostachyum viguieri</i>	1.5–3 (1)	50–1200 (5,7)	Widespread, from Masoala to Andasibe and maybe Ranomafana (5,7)
<i>Cephalostachyum perrieri</i>		c.900 m (5,7)	Mananara Nord and maybe Ranomafana (7)
<i>Cephalostachyum</i> spp.		c.50 m (7)	Two undescribed species in forest, Masoala (7)
<i>Hitchcockella baronii</i>	0.1–0.15 (1)		Montane forest on Manongarivo Massif (7)
<i>Nastus aristatus</i>		900–1200 (5,7)	Montane forest, Manongarivo to Andasibe (5,7)
<i>Nastus emirnensis</i>	0.1–0.2 (1)	1000 (5,7)	Montane forest, Analamazaotra, Andasibe (5,7)
<i>Nastus humbertianus</i>			Andohahela (5,7)
<i>Nastus lokohoensis</i>			Forest, Lokoho (5,7)
<i>Nastus madagascariensis</i>	1 (1)		Forest, Central plains (5,7)
<i>Nastus manongarivensis</i>		500–1600 (5,7)	Forest, Manongarivo (5,7)
<i>Nastus perrieri</i>		1700 (5,7)	Mossy forest, Tsaratanana (5,7)
<i>Nastus tsaratananensis</i>		2000 (5,7)	Mossy forest, Tsaratanana (5,7)

Methods

We carried out surveys at 47 low-, mid- and high-elevation sites in seven major survey regions of eastern Madagascar between November 2008 and September 2012, covering a distance of over 1000 km, from Makira in the north to Midongy in the south (Table 2). Each site falls in the “humid forest” or adjacent “degraded humid forest” vegetation classifications described by Moat and Smith (2007). The primary purpose of the surveys was to discover, and subsequently conserve, new populations of *Prolemur simus* (see King and Chamberlan 2010), and we have published elsewhere more detailed habitat descriptions for most of the sites, along with many of our primary results (Rajaonson *et al.* 2010; Ravaloharimanitra *et al.* 2011; Rakotonirina *et al.* 2011, 2013; Bonaventure *et al.* 2012; Lantovololona *et al.* 2012; Mihaminekena *et al.* 2012; Randrianarimanana *et al.* 2012; Andrianandrasana *et al.* in press; Rajaonson and King in press).

We recorded thousands of GPS points during these surveys. In this paper, we analyse a subset of these GPS points referring to the location of large-culmed bamboos. We mapped them using MapInfo GIS software, to illustrate their distribution across Madagascar, and calculated summary statistics and created scatter graphs to illustrate elevation ranges for each genus.

We measured culm diameters at breast height (dbh) of large-culmed bamboos at ten sites in six of the survey regions, and we present summary statistics for dbh of each genus at each of these sites. We used the *z* test for unmatched samples (Chalmers and Parker 1989) to test for differences in mean culm diameter at different sites, or under different

canopy openness at some sites, for samples with at least 25 measurements.

We photographed bamboos at each survey region, and sent photos to Soejatmi Dransfield to help with initial identifications. One of us (TK) verified that photos of each taxon identified at a survey area were available for that area. We also referred to the detailed botanical descriptions of *Valiha diffusa* and *Cathariostachys* spp. given by Dransfield (1998), and of *Bambusa vulgaris* and *Dendrocalamus giganteus* given by Clayton *et al.* (2010). We follow Dransfield (2003) for bamboo nomenclature, although we also refer to synonyms for some species following *The Plant List* (2010). Notably, *The Plant List* (2010) does not use the genus *Arundinaria* for any Malagasy bamboos, placing several in *Yushania* and one in *Thamnocalamus* (Table 1). We follow Mittermeier *et al.* (2010) for lemur nomenclature.

Results

Field identification of large-culmed bamboos

With care, identification of large-culmed woody bamboos within our survey regions was relatively simple, at least to genus. Of the large-culmed clumping bamboos (Fig. 1), the most frequently encountered was *Bambusa vulgaris*, with both the green and the yellow forms commonly planted in or near rivers, towns and villages, and we recorded it in the Makira, CAZ, Nosivolo and COFAV survey regions. The larger *Dendrocalamus giganteus* was less frequently observed. Of the non-clumping species, *Valiha diffusa* was easily recognizable within its range by its characteristic drooping culm tips, long lateral branches, stiff culm sheaths readily shed, and a thin



Figure 1. The pantropical bamboo *Bambusa vulgaris* (left: green form; centre: yellow form) and the introduced *Dendrocalamus giganteus* (right). Photographs by Tony King and Maherisoa Ratolojanahary.

whitish ring above the internodes following the shedding of the culm sheath (Fig. 2). *Cathariostachys* spp. often lacked major lateral branches, had persistent culm sheaths that were not readily shed, and often showed a pale ring under the internodes (Figs. 3–6). *Arundinaria* spp. had slimmer culms, with delicate culm sheaths often appearing torn or shredded, and a distinctive pattern of leaf growth (Figs. 7–10). The young emerging culm shoots of each genus were also highly distinctive (Figs. 1–10).

Local names for bamboos were very variable. *Valiha diffusa* was usually referred to as Vologasy or Volojatsy, although both names were used for other species in some places. *Cathariostachys* bamboos were usually called either Voloahosy, Volo lagnana or Volobe, but in lowland areas Volobe was more often used for the green form of *Bambusa vulgaris*. The yellow form of *B. vulgaris* was usually called Volovanga or Volovazaha. *Arundinaria* bamboos were almost always called Volotsanganana, and we only rarely heard this name used for other bamboos. The use of local names varied from region to region, but also between local people in the same region—sometimes simply due to misidentification of bamboos to

the appropriate local name by less-experienced local guides. Names used for various smaller-culmed bamboos included Voloahando, Voloahoto, Voloandotra, Volomadinika, Volotami-hana, Volosodina, Volokitrana, Volovahy and Tsimbolovolo.

Distribution and elevation ranges of Valiha diffusa, Cathariostachys and Arundinaria

We made 1,343 georeferenced records of endemic large-culmed bamboos (*Valiha diffusa*, *Cathariostachys* and *Arundinaria*) across the seven survey regions. The majority of our observations (74%, $n = 994$) were made in and around the Ankeniheny-Zahamena forest corridor (CAZ), where we have long-term monitoring of *Prolemur simus* populations. One region had only one observation (Anjozorobe), the remaining five had between 43 and 129 observations each. *Cathariostachys* bamboos were recorded from Makira in the north to Midongy in the south, *Valiha diffusa* from Makira to the southern parts of the COFAV, and *Arundinaria* bamboos from Zahamena to the COFAV (Table 2; Figs. 11–14).

Valiha diffusa was only recorded at low elevations (9–576 m), and *Arundinaria* only at high elevations



Figure 2. The Malagasy endemic bamboo *Valiha diffusa* in lowland deforested landscapes of eastern Madagascar. Photographs by Lucien Randrianarimanana and Hery Randriaingo.

Table 2. Geographic coordinates of the 47 survey sites, within seven survey regions, with elevation ranges at each site for endemic large-culmed bamboos *Valiha diffusa*, *Cathariostachys* spp. and *Arundinaria* spp.

Region	Survey site	Latitude (°S)	Longitude (°E)	GPS points	Elevation range (m)		
					<i>Valiha diffusa</i>	<i>Cathariostachys</i> spp.	<i>Arundinaria</i> spp.
Makira	Antohaka Lava	14.73 to 14.79	49.71 to 49.75	18		454–1030	
	Mahevaratra	14.83 to 14.90	49.73 to 49.80	35	403–552	340–725	
Zahamena	Andringitra	17.64 to 17.66	48.66 to 48.67	15			1171–1164
	Volotsanganana	17.69 to 17.73	48.74 to 48.79	28		845–955	
Anjozorobe	Saha Forest Camp	18.41	47.94	1			1322
CAZ	CAZ: Didy	18.12 to 18.17	48.64 to 48.73	11		868–1007	
	CAZ: Ranomainty	18.30 to 18.39	48.44 to 48.50	352		1042–1471	1084–1467
	CAZ: Fierenana	18.42 to 18.45	48.44 to 48.59	17		992–1334	1048–1268
	CAZ: Morarano	18.66 to 18.76	48.35 to 48.43	285		893–1256	
	CAZ: Ankerana	18.47	48.82 to 48.83	2		496–516	
	Ambohimanana	18.46 to 18.53	48.72 to 48.79	8	172–370	464–678	
	Maroseranana	18.58	48.89	4	127–303		
	Vohimientana	18.59	48.76	1	145		
	Andriantantely NE	18.63 to 18.68	48.79 to 48.82	59	68–332		
	Andriantantely SE	18.71 to 18.74	48.79 to 48.83	86	103–229		
	Sahavola	18.69	48.97 to 48.98	100	26–148		
	Vohiposa	18.75 to 18.79	48.93 to 48.95	26	46–191		
	Ambalafary	18.8	48.81	35	67–124		
	Andekaleka	18.81	48.58	2	391–407		
	Ranomafana Est	18.95	48.8	1	63		
	Mahatsara	18.98	48.92 to 48.93	2	16–22		
Mahalina	19.07	48.85 to 48.88	3	64–82			
Nosivolo	Antanambao Manampotsy	19.42 to 19.45	48.56 to 48.57	2	196–217		
	Tsinjoarivo	19.67 to 19.72	47.77 to 47.83	57			1294–1667
	Ambohimiadana	19.89 to 19.90	47.87 to 47.92	23		1022–1072	1348–1422
	Ambohimalaza	19.97 to 19.98	47.89	6		887–999	
	Vohibe & Vohitrambo	19.92 to 19.96	48.46 to 48.50	37	98–576	236–536	
	Andranambolava	20.21	48.15	2		668–680	
	Beranomintina	20.25	48.13	2		784–791	
COFAV	Mananjary	21.09 to 21.18	48.18 to 48.22	17	21–68		
	Ranomafana NP	21.25	47.36 to 47.42	9		951–972	1122–1158
	Ambindrabe & Ambendrana	21.37 to 21.40	47.34 to 47.40	8			1032–1227
	Antarehimamy & Ambodiara	21.89 to 21.91	47.33 to 47.35	4	824		1018–1075
	Antaranjaha	21.97 to 22.01	47.43 to 47.44	5	324–367	302–316	
	Sahalanona	22.05 to 22.10	47.59 to 47.63	22	129–213		
	Andringitra: Manambolo	22.07	46.99	1			1238
	Sahamadio	22.52	47.58	1	27		
	Mahazoarivo: Ifasy	22.65	47.25	1	203		
	Mahazoarivo: Mitimbato	22.66	47.32	1	147		
	Mahafasa	22.67	47.68	1	41		
Iandraina	22.77	47.69	1		53		

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Table 2. continued

Region	Survey site	Latitude (°S)	Longitude (°E)	GPS points	Elevation range (m)		
					<i>Valiha diffusa</i>	<i>Cathariostachys</i> spp.	<i>Arundinaria</i> spp.
Midongy	Ambalavero	23.14 to 23.16	47.18 to 47.21	16		480–610	
	Ambadikala	23.29 to 23.30	47.30 to 47.36	2		172–187	
	Marovovo	23.38	47.12	3		649–751	
	Marovato	23.47	47.06 to 47.08	3		687–770	
	Halampo	23.63 to 23.67	46.91 to 46.95	9		718–890	
	Ampasy	23.73 to 23.78	47.02 to 47.03	19		708–961	
Total	47 sites	14.73 to 23.78	46.91 to 49.80	1343	9–576	53–1471	1018–1667
					n=396	n=710	n=237

Figure 3. *Cathariostachys* sp. near Makira in north-eastern Madagascar. Photographs by Lucien Randrianarimanana.

(1018–1667 m), while *Cathariostachys* bamboos were distributed across a wide range of elevations, from 53 to 1471 m (Table 2, Fig. 11). Low-elevation records of *Cathariostachys* were rare (Fig. 11), with only five of 710 records (0.7%) below 300 m, 12 (1.7%) below 400 m, and 65 (9.2%) below 600 m. Very high elevation records of *Cathariostachys* were also rare, with only three records (0.4%) over 1,300 m. Most records of *Cathariostachys* could therefore be considered mid-elevation, with 90.4% ($n = 642$) between 600 and 1,260 m.

At the most northerly region surveyed, Makira (c. 14.8°S), there appeared to be a continuum of elevation records for *Cathariostachys*, from 340 to 1040 m (Fig. 11). At our more central survey regions, from 17 to 22°S (Zahamena, CAZ, Nosivolo, COFAV), there appeared to be two groups of elevation records, below 600 and above 800 m, with very few records between 600 and 800 m (Fig. 11). At the most southerly region, Midongy (23 to 24°S), most records were between 400 and 1000 m, with two below 200 m and none between 200 and 400 m (Fig. 11).

Culm diameters

Valiha diffusa had the most variable culm diameters at our sites, ranging from 1.7 to 9.5 cm (Table 3). *Cathariostachys* had the largest mean culm diameter of the endemic large-culmed bamboos (6.1 cm), and *Arundinaria* the smallest (4.0 cm). Culm diameters of the green form of the pantropical *Bambusa vulgaris* (measured at the Ambalafary site to the east of the CAZ) were larger than those of the endemic bamboos, ranging from 3.2 to 13.4 cm, with a mean of 9.58 cm (SD 2.04, $n = 248$).

There were some inter-site differences in culm diameters of the endemic bamboos (Table 3). For example, the *Cathariostachys* species at the lowland sites of Maherivaratra (Makira region) and Vohibe (Nosivolo region) had mean culm diameters one to 2.5 cm smaller than at the other, higher elevation, sites (Table 3). This is a statistically significant difference, when comparing each with the site with the next lowest mean *Cathariostachys* culm dbh measured by the same researcher (Maherivaratra with Ranomainty: $z = 14.08$, $p < 0.001$; Vohibe with Zahamena: $z = 8.80$, $p < 0.001$).



Figure 4. *Cathariostachys madagascariensis* in the western Ankeniheny-Zahamena Corridor in eastern Madagascar. Photographs by Lucien Randrianarimanana and Tony King.

Table 3. Summary statistics for culm dbh measurements for endemic large-culmed bamboos at some of the survey sites.

Survey region	Elevation	<i>Valiha diffusa</i>			<i>Cathariostachys</i> spp.			<i>Arundinaria</i> spp.		
		DBH Range	Mean (SD)	n	DBH Range	Mean (SD)	n	DBH Range	Mean (SD)	n
Makira: Maherivaratra	340–725 m	3.7–6.5	5.48 (0.71)	26	3.6–5.5	4.52 (0.60)	25			
Zahamena	863–1298 m				5.1–8.3	6.24 (0.85)	85	3.5–5.7	4.69 (0.49)	135
Anjozorobe	1322 m							3.0–4.8	3.83 (0.61)	20
CAZ: Ranomainty	1025–1471 m				5.0–8.4	6.84 (0.72)	42	2.3–4.8	3.58 (0.54)	59
CAZ: Sakalava	893–1256 m				3.2–8.9	7.08 (1.07)	478			
CAZ: Ambalafary	48–124 m	2.9–7.3	5.39 (0.93)	231						
CAZ: Sahavola	26–148 m	2.9–9.2	6.15 (1.49)	103						
CAZ: Vohiposa	46–191 m	3.5–7.0	5.33 (1.05)	12						
Nosivolo: Vohibe	167–576 m	1.7–9.5	4.42 (1.43)	76	2.4–7.2	5.18 (0.88)	127			
Midongy	687–961 m				5.5–8.5	6.82 (0.90)	17			
Total		1.7–9.5	5.4	448	2.4–8.9	6.1	774	2.3–5.7	4.0	214

**Figure 5.** *Cathariostachys* sp. in and around the Midongy du Sud National Park in south-eastern Madagascar. Photographs by Laingo Rakotonirina.

The mean culm diameter of *Valiha diffusa* was 0.6 cm lower in open areas than in areas of closed or semi-closed canopy cover at both lowland sites where this was measured, a statistically significant difference at both sites (Table 4).

Table 4. Comparison of mean culm diameters (dbh) of *Valiha diffusa* under differing levels of canopy cover at two lowland sites in the CAZ survey region, using the *z* test for unmatched samples.

		Mean DBH	SD	N	<i>z</i>	<i>p</i>
Amabalafary						
	Open canopy	5.27	0.91	181	4.31	<0.001
	Closed canopy	5.85	0.83	50		
Sahavola						
	Open canopy	5.83	1.57	48	2.05	<0.05
	Semi-closed canopy	6.43	1.37	55		

Discussion

Distribution of large-culmed bamboos in Madagascar

By comparing the distribution of our field observations with georeferenced published herbarium specimen locations (Table 5), our study has resulted in a southern extension of the published range of *Valiha diffusa* (Fig. 12), and southern and northern range extensions for species of *Cathariostachys* (Fig. 13). We have also shown that *Arundinaria* occurs in remaining high elevation forests in the Zahamena National Park, the Ankeniheny-Zahamena Corridor, the Anjozorobe Corridor, and around the high-reaches of the Nosivolo River (Fig. 14). We recommend the collection of herbarium specimens from these sites to help resolve the taxonomic uncertainties surrounding the Malagasy bamboos currently included in *Arundinaria* (Dransfield 2000, 2003; or alternatively in *Yushania* and *Thamnocalamus* by *The Plant List* 2010).

Herbarium specimens are also needed to help determine species' distributions within *Cathariostachys*, as we were unable to differentiate the two recognized *Cathariostachys* species in the field, and also found no consistent pattern that



Figure 6. *Cathariostachys* sp. (probably *C. capitata*) in the lowland forest fragment of Vohibe in eastern Madagascar. Photographs by Anjara Bonaventure, Anselmo Andrianandrasana and Tiana Ratolojanahary.

might separate them based on elevation. It may be that there is only one, highly variable, *Cathariostachys* species, as suggested by Dransfield (1998), although the thinner mean culm diameter of *Cathariostachys* at our lowland sites of Maherivaratra and Vohibe compared to our higher elevation sites is consistent with the descriptions of the two species given by Dransfield (1998). The species identity of *Valiha* in the Ankarana National Park in the far north of Madagascar also requires further study (Dransfield 2003). Although close to the type locality of *Valiha perrieri*, the large-culmed bamboos of Ankarana appear very similar to *Valiha diffusa* (L. Rakotonirina and T. King, unpubl. data), and probably are indeed the latter (S. Dransfield, in litt. 2012).

Bamboo distribution is often affected by disturbance (Griscom and Ashton 2006; Gagnon *et al.* 2007; Olson *et al.* 2013). However, disturbance may affect different bamboo species differently. *Cathariostachys madagascariensis* appears to be found at higher densities in disturbed forests than in non-disturbed forests, perhaps indicating an evolutionary

adaptation to regular cyclonic disturbance in the eastern rainforests (Olson *et al.* 2013), but does not appear to tolerate excessive disturbance, and does not persist in deforested areas far from the forest edge (Fig. 13; see also Olson *et al.* 2013). *Valiha diffusa*, conversely, appears to thrive in many deforested landscapes of lowland eastern Madagascar (Figs. 2 and 12; Dransfield 1998), and is probably more abundant now than when lowland forest cover was more extensive. However, although apparently more tolerant to major disturbance than *Cathariostachys*, *V. diffusa* probably also has a limit to its tolerance of disturbance, with culm diameters reduced in heavily-disturbed areas where it is cut or burnt regularly (Dransfield 1998); a phenomenon common to several bamboo species (Franklin *et al.* 2010). We also found that *V. diffusa* culm diameters were lower in more open habitats, possibly due to higher rates of culm production in open areas (Gagnon *et al.* 2007), or perhaps due to environmental stress related to extreme micro-habitat variables such as moisture or light levels (Reid *et al.* 1991).

Table 5. Herbarium specimen locations for *Valiha* spp., *Cathariostachys* spp., and *Arundinaria* spp., given by Dransfield (1998, 2003), georeferenced for this study.

Species	Location	Elevation (m)	Longitude (°E)	Latitude (°S)
<i>Cathariostachys madagascariensis</i>	Analamazoatra	800, 900, 1000	48.43	18.93
	East of Moramanga		48.30	18.95
	Ranomafana National Park	900, 950	47.42	21.26
<i>Cathariostachys capitata</i>	Masoala Peninsula, Antalavia, near Ambanizana	5 and 200	49.97	15.65
	Mananara	700	49.68	16.18
	Antananambe Biosphere Reserve, Ambolokely	235	49.76	16.43
	Soanierana-Ambedra	200	49.56	16.88
	Fandrangato			
	(Farafangana), Vondrozo	500	47.32	22.82
	Varahina			
<i>Valiha diffusa</i>	Nosy-be	Low	48.25	13.33
	Nossi Camba (Komba)	Low	48.34	13.47
	Sambirano		48.44	13.77
	Massif of Manongarivo		48.42	13.93
	Marojejy	200 to 500	49.63	14.54
	Mananara	300	49.76	16.21
	Toamasina (Tamatave)	30	49.37	18.15
	Ampasimanolotra (Brickaville)	50	49.06	18.82
	Fianarantsoa, Ifanadiana, below Mt. Vatovavy	150	47.94	21.40
	Fianarantsoa, 10 km east of Ifanadiana	Low	47.74	21.33
<i>Valiha perrieri</i>	Andrafianamena	Low	49.41	12.81
<i>Arundinaria ambositrensis</i>	Ranomafana (Ambositra)	1300 to 1400	47.48	20.54
	Ranomafana	1300 to 1400	47.37	21.24
<i>Arundinaria humbertii</i>	Andringitra	2000	46.90	22.24
<i>Arundinaria ibityensis</i>	Mt. Ibity, Antsirabe	1800 to 2250	47.01	20.13
<i>Arundinaria madagascariensis</i>	Tsaratanana	2000 and 2800	48.87	14.03
<i>Arundinaria marojejyensis</i>	Marojejy	2000	49.72	14.42
<i>Arundinaria perrieri</i>	Manongarivo	1000	48.38	13.99

Large-culmed bamboos and *Prolemur simus*

At least 29 species have been recorded as food plants of *Prolemur simus*, of which nine are woody bamboos, ten are other monocotyledons, and ten are dicotyledons (Table 6). The Poaceae family (including bamboos) makes up 45% of recorded food plants. At sites where quantitative studies have been undertaken, over 90% of the feeding time of *P. simus* is devoted to one or two of the large-culmed bamboo species *Cathariostachys madagascariensis*, *Valiha diffusa*, *Bambusa vulgaris* and *Arundinaria* sp. (Tan 1999; Mihaminekena *et al.* 2012; Randrianarimanana *et al.* 2012). *Bambusa vulgaris* may or may not be native to Madagascar (Dransfield 2003), and does not occur in natural forest in the country (this study). The native large-culmed bamboos of *Cathariostachys*, *Valiha* and *Arundinaria* are, therefore, likely to be the primary natural food plants of *P. simus*. Of these, *Arundinaria* species are restricted to high elevation forest, and appear to be less frequently consumed by *P. simus* than the more widespread *Cathariostachys* species and *Valiha*.

If *Cathariostachys* and *Valiha* can therefore be considered the principle food plants of *P. simus*, their distribution should be one of the major factors influencing the range of

P. simus itself. The distribution map we provide for *Cathariostachys* (Fig. 13) does appear to correspond well to the potential current distribution of *P. simus* (Fig. 15) based on recent direct sightings and indirect feeding signs (as given by Rakotonirina *et al.* 2011) and unconfirmed local knowledge (as given by Dolch *et al.* 2010), with perhaps the notable exception of the Masoala peninsula in the north-east of the country from where there is currently no indication of the presence of *P. simus*.

Sub-fossil records of *Prolemur simus* are more widely distributed (Godfrey *et al.* 2004), occurring in areas where *Cathariostachys* species do not occur, at least in recent times (Fig. 15). However, *Valiha* does occur in at least one of these sub-fossil sites (Ankarana), and therefore may have been the primary food plant of the species in that area, and conceivably could still be so (L. Rakotonirina and T. King, unpubl. data). There is also an unidentified bamboo resembling *Valiha* in western dry forest near Morondava (Dransfield 2003), which may have been the food plant of *P. simus* when it existed in that part of the country. Further research into the historical distribution of large-culmed bamboos in Madagascar would be very helpful in establishing how eventual changes in



Figure 7. *Arundinaria* sp. in high elevation forest at Anjozorobe in eastern Madagascar. Photographs by Tony King.

Table 6. Recorded foodplants of *Prolemur simus* at five sites in eastern Madagascar, based on 1: Petter *et al.* 1977; 2: Meier & Rumpler 1987; 3: Tan 1999; 4: Tan 2007; 5: McGuire *et al.* 2009; 6: Ravaloharimanitra *et al.* 2011; 7: Rakotonirina *et al.* 2011; 8: Bonaventure *et al.* 2012; 9: Mihaminekena *et al.* 2012; 10: Lantovolo-lona *et al.* 2012; 11: Randrianarimanana *et al.* 2012; 12: L. Randrianarimanana, unpubl. report 2011; 13: Andrianandrasana *et al.* in press.

Family	Species	English name / description	Ranomafana NP	CAZ west	Brickaville District	Vohibe	Kianjavato
			Mid to high elevation		Low elevation, degraded habitats		
Large-culmed bamboos							
Poaceae	<i>Cathariostachys madagascariensis</i>	Erect bamboo	3	11			5 (in error?)
Poaceae	<i>Cathariostachys</i> cf. <i>capitata</i>	Erect bamboo				13	
Poaceae	<i>Valiha diffusa</i>	Erect bamboo			6,8,9,10	7,13	2 ^a ,4
Poaceae	<i>Arundinaria</i> sp.	Erect bamboo		11 ^b			
Poaceae	<i>Bambusa vulgaris</i>	Erect bamboo			6, 9		
Other bamboos							
Poaceae	<i>Nastus elongatus</i>	Erect bamboo	3				
Poaceae	<i>Cephalostachyum</i> cf. <i>perrieri</i>	Viny bamboo	3				
Poaceae	<i>Cephalostachyum</i> sp.	Viny bamboo	3,4	12		13	
Poaceae	<i>Nastus</i> sp.	Viny bamboo		11 ^c			
Poaceae	?	Viny bamboo					2
Other monocots							
Arecaceae	<i>Dypsis</i> sp.	Palm		11		13	1,2
Bromeliaceae	<i>Ananas comosus</i>	Pineapple					5
Cyperaceae	<i>Scleria</i> sp.	Sedge	3				
Musaceae	<i>Musa</i> sp.	Banana			6		
Poaceae	<i>Saccharum</i> sp.	Sugar cane			6		
Poaceae	<i>Pennisetum clandestinum</i>	Kikuyugrass					2
Poaceae	<i>Oryza</i> sp.	Rice					2
Poaceae	<i>Poecilostachys festucaceus</i>	Forest grass	3				
Strelitziaceae	<i>Ravenala madagascariensis</i>	Traveller's palm		12	6	7,13	1,2
Zingiberaceae	<i>Aframomum</i> sp.	Wild ginger			6,9,10	13	2
Dicots							
Anacardiaceae	<i>Mangifera indica</i>	Mango					2
Annonaceae	<i>Annona squamosa</i>	Custard apple			6		
Lauraceae	<i>Cryptocarya</i> sp.	Forest tree		12			
Moraceae	<i>Streblus dimepate</i>	Woody shrub	3				
Moraceae	<i>Artocarpus heterophilus</i>	Jackfruit			6,9		2
Moraceae	<i>Artocarpus altilis</i>	Breadfruit			6		
Moraceae	<i>Ficus</i> sp.	Figs					2
Rosaceae	<i>Rubus moluccanus</i>	Weedy shrub			6		
Rubiaceae	<i>Coffea</i> spp.	Coffee			6		
Sapindaceae	<i>Litchi sinensis</i>	Lychee			6,9		
14 families	29 or 30 species	Total per site :	7	7	12	6	11 or 12

Notes: 2^a: as voloajatsy; 11^b: as volotsanganana; 11^c: as volohoto



Figure 8. *Arundinaria* sp. in high elevation forest of the western Ankeniheny-Zahamena Corridor in eastern Madagascar. Photographs by Lucien Randrianarimanana.

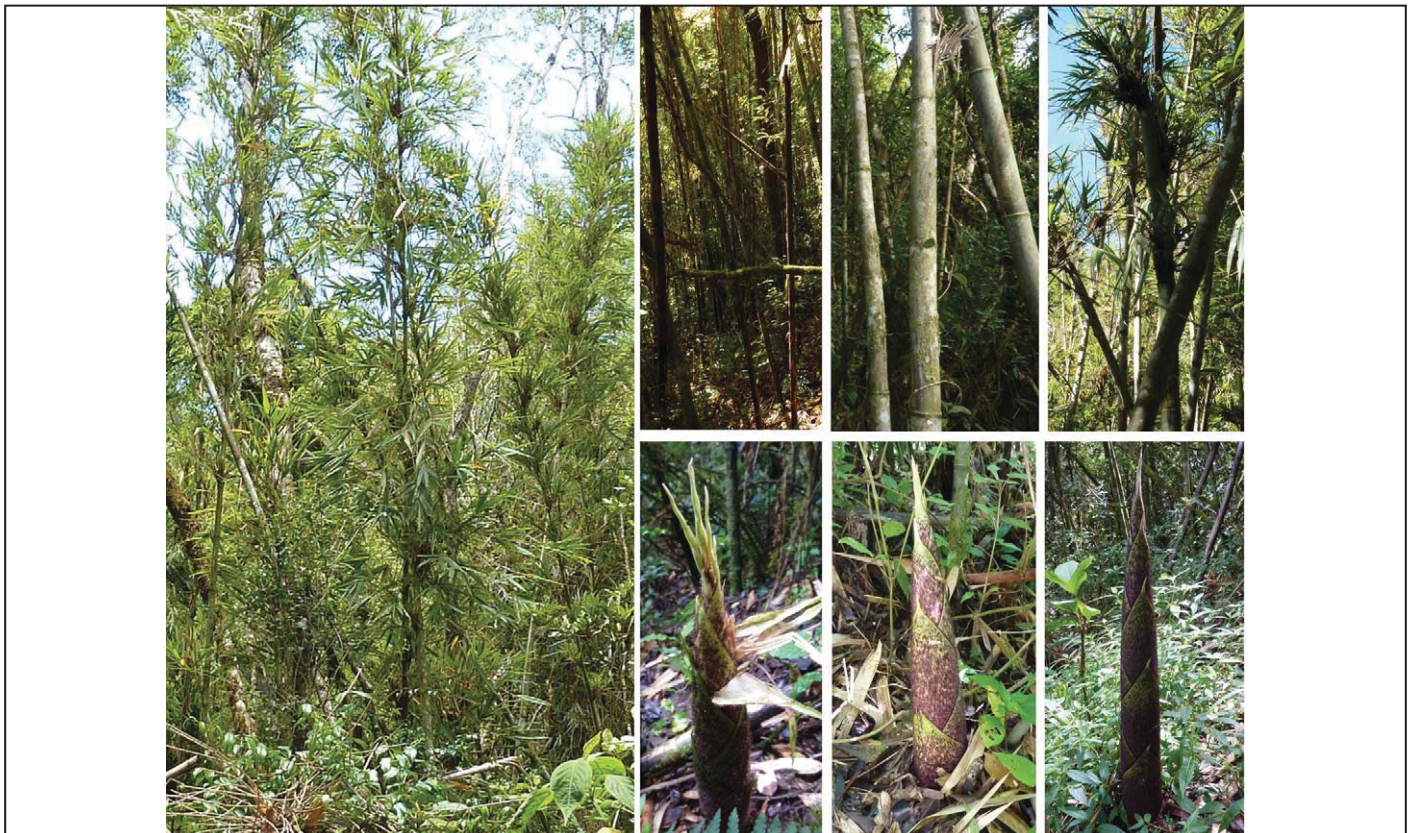


Figure 9. *Arundinaria* sp. in high elevation forest at Tsinjoarivo in eastern Madagascar. Photographs by Laingo Rakotonirina.



Figure 10. *Arundinaria* cf. *ambohitrensis* in high elevation forest at Ranomafana National Park in south-eastern Madagascar. Photographs by Tony King.

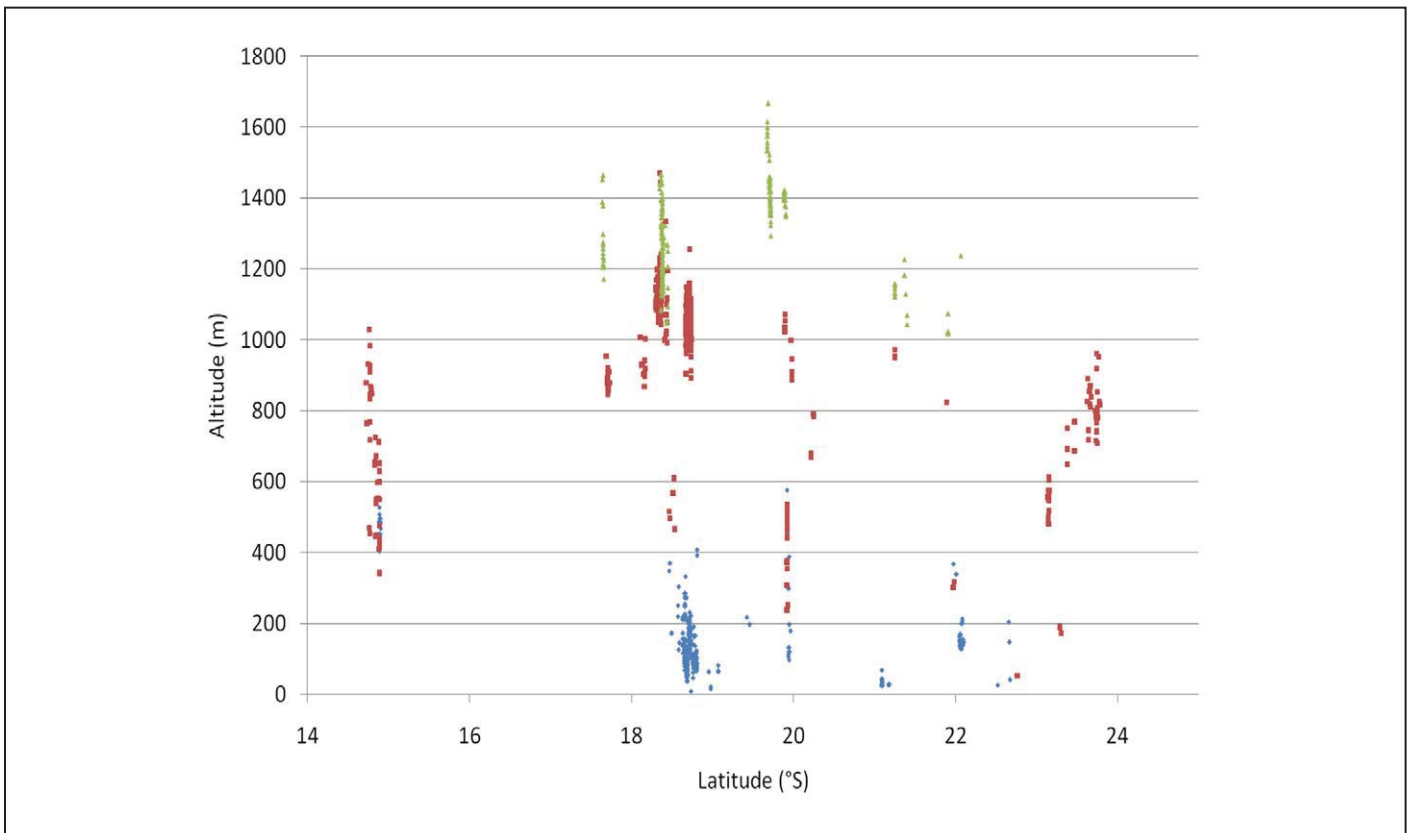


Figure 11. Scatter graph of GPS points taken for *Valiha diffusa* (blue), *Cathariostachys* spp. (red) and *Arundinaria* spp. (green), by elevation and latitude.

bamboo distributions over time may have affected changes in *P. simus* distribution.

Prolemur simus is known to have a very seasonal diet (Tan 1999), feeding primarily on young large-culmed bamboo shoots when they are available (Figs. 16–18), and switching to other bamboo parts when they are not. In Ranomafana National Park, *P. simus* feeds primarily on the young ground shoots of *Cathariostachys madagascariensis* during the early wet season months of November to February, then supplements its diet with bamboo leaves and branch shoots as the number of ground-emerging shoots declines, whilst during the drier months of June to October it feeds principally on the mature culm pith, still of *C. madagascariensis* (Tan 1999). At our study sites, the seasonality of the emergence of ground shoots of *Cathariostachys madagascariensis* was generally similar to that described by Tan (1999), as was that of *Valiha diffusa*, with the latter perhaps a month later than

C. madagascariensis. Other large-culmed bamboo species, however, did not follow the same seasonality, especially those in the genus *Arundinaria* and the yellow variety of *Bambusa vulgaris*. The presence of these bamboos may therefore influence the seasonality of *P. simus* feeding behaviour if ground shoots emerge when those of other species are not available. This is particularly apparent at the lowland Ambalafary site, where the *P. simus* group spends a lot of time feeding on the ground shoots of yellow *Bambusa vulgaris* during the dry, austral winter months from June onwards (T. H. Mihaminekena, unpubl. data; Fig. 19). Similarly, at the high-elevation Ranomainty site, ground shoots of *Arundinaria* appear to be sometimes eaten during the austral winter dry season, especially in drier years when *Cathariostachys* ground shoots are rarer (H.L.L. Randrianarimanana, unpubl. data).

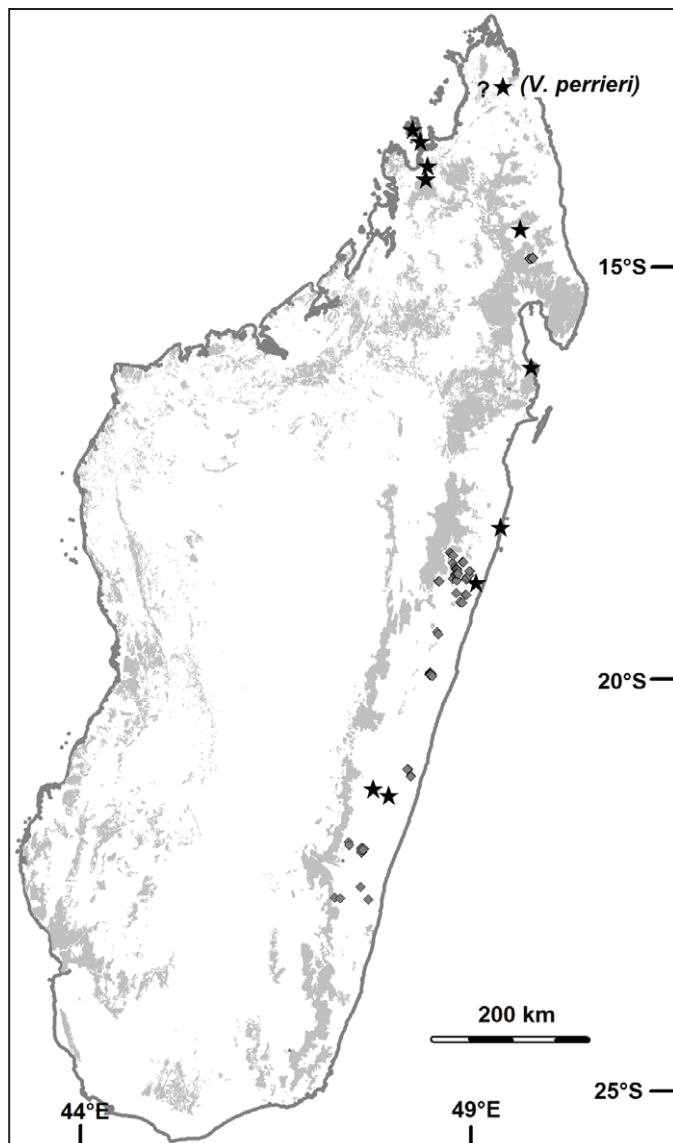


Figure 12. Distribution of herbarium specimens (black stars) and our field observations (gray diamonds) of *Valiha diffusa*, with approximate forest cover given in gray.

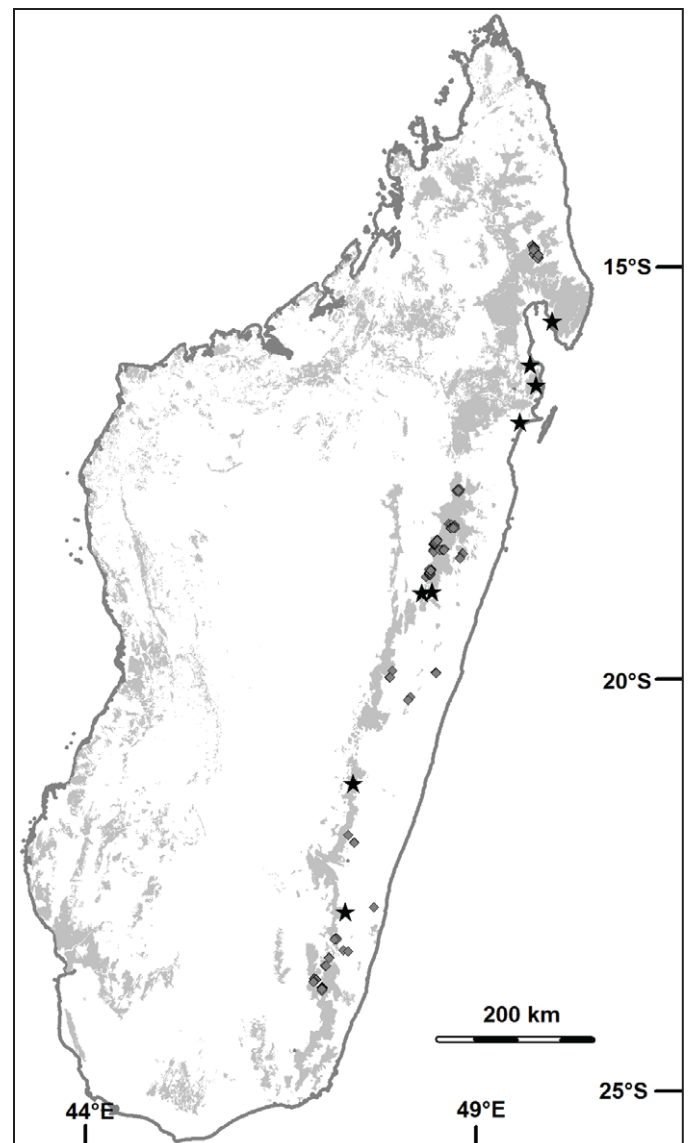


Figure 13. Distribution of herbarium specimens (black stars) and our field observations (gray diamonds) of *Cathariostachys* spp., with approximate forest cover given in gray.

Conclusions

The woody bamboos of Madagascar are in need of research and conservation activities in their own right (Dransfield 2003). A better understanding of their taxonomy, distribution and ecology will be key also to a better understanding of the factors influencing the distribution and conservation needs of bamboo lemurs in general, and of the Critically Endangered greater bamboo lemur in particular. It was this latter motivation that led us to write this paper, but in doing so we have hopefully contributed to the former. Our presentation of photos of various large-culmed bamboos in Madagascar, and preliminary distribution maps and elevation ranges, should facilitate other researchers to take on the otherwise daunting task of trying to identify bamboos, at least to genus.

This should lead to improved understanding of distribution and other aspects concerning them, and consequently to the potential distribution of associated fauna such as bamboo lemurs. The recent discoveries of previously unknown populations of the greater bamboo lemur indicate that there is still much to be learnt about the remarkable endemic biodiversity of Madagascar, not least of bamboos and bamboo lemurs.

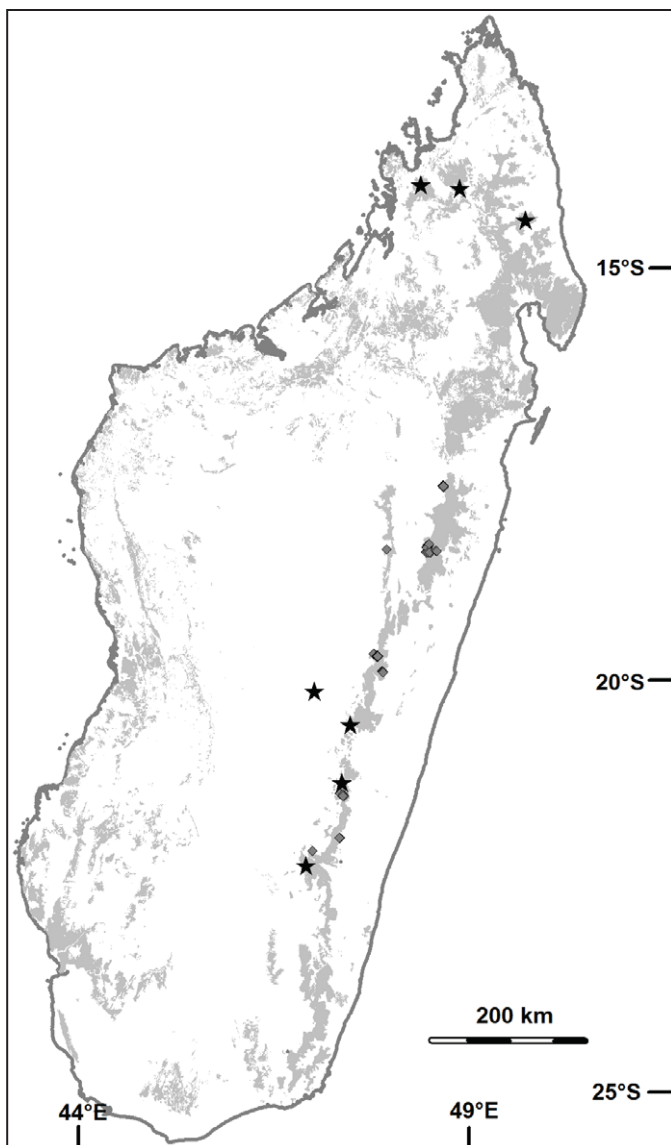


Figure 14. Distribution of herbarium specimens (black stars) and our field observations (gray diamonds) of *Arundinaria* spp., with approximate forest cover given in gray.

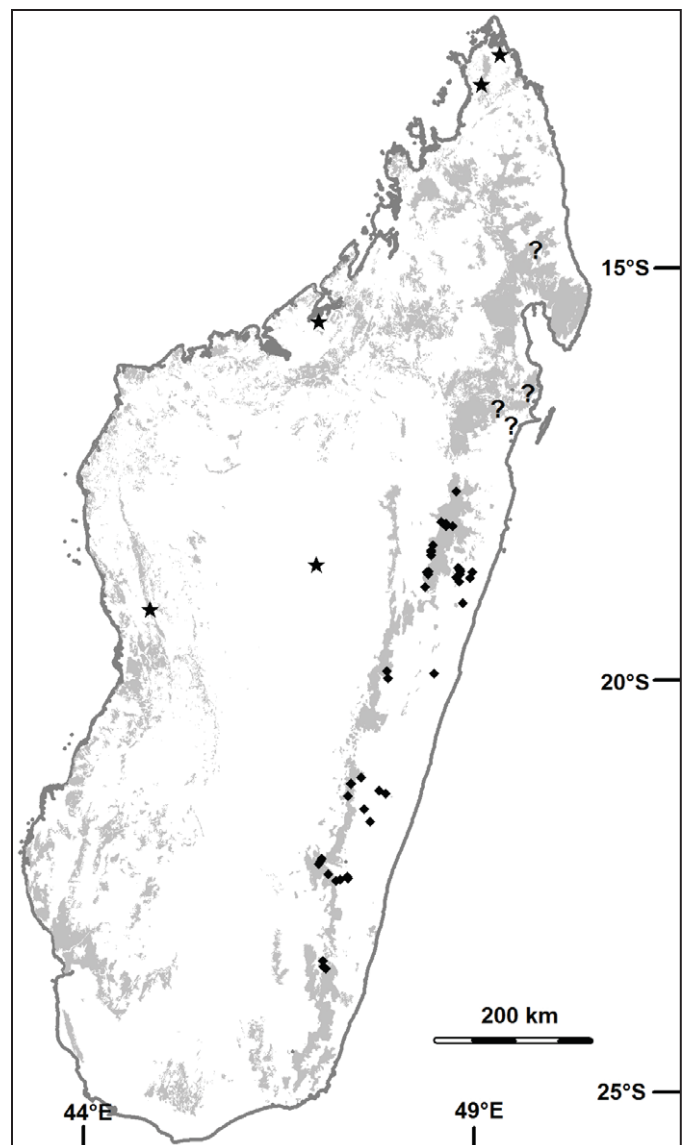


Figure 15. Distribution of sites of recent direct or indirect observations of *Prolemur simus* (diamonds; from Rakotonirina *et al.* 2011), unconfirmed local knowledge suggesting possible recent presence of *P. simus* (question marks; from Dolch *et al.* 2010), sites where *P. simus* historically existed based on sub-fossil remains (stars; from Godfrey *et al.* 2004), and approximate current forest cover (gray areas).



Figure 16. *Prolemur simus* feeding on young ground shoots of *Cathariostachys madagascariensis* in Ranomafana National Park, February 2012. Photograph by Tony King.

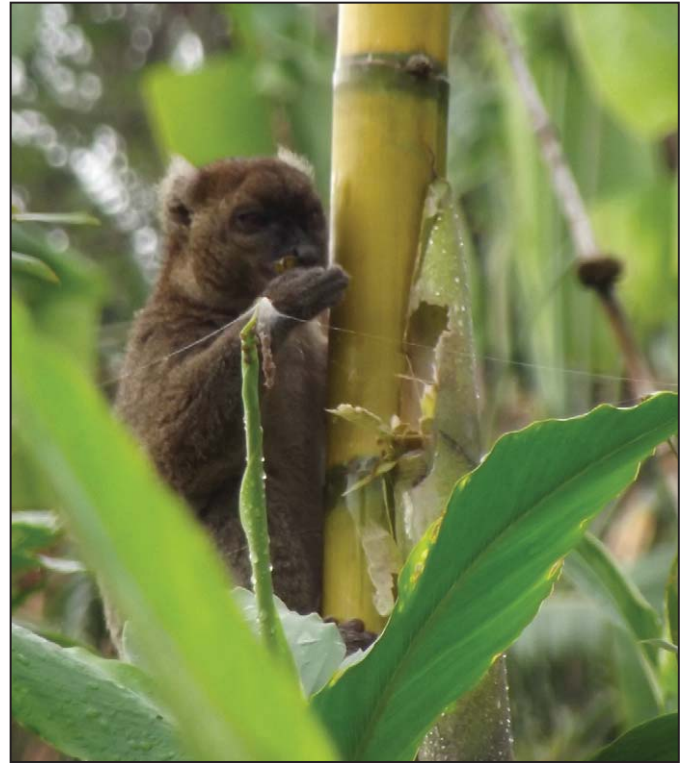


Figure 17. *Prolemur simus* feeding on a young culm shoot of *Valiha diffusa* at the Vohiposa lowland site, Brickaville District, March 2012. Photograph by Hery Randriaingano.



Figure 18. Feeding remains left by *Prolemur simus* on young ground shoots of *Valiha diffusa* surrounding Andriantantely lowland forest, Brickaville District, January 2012. Photograph by Hery Randriaingano.



Figure 19. Feeding remains left by *Prolemur simus* on young ground shoots of the yellow variety of *Bambusa vulgaris* at the Ambalafary lowland site, Brickaville District, August 2011. Photograph by Hasimija Mihaminekena.

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