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Factors affecting frog density in the Solomon Islands

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Abstract. This paper identifies some important factors affecting the density of frogs in the Solomon Islands. Distance sampling was used to estimate frog density in all major frog habitats across 13 islands. A total of 109 transects, covering five forest types (coastal, freshwater marshes, lowland forest, hill or ridge, and montane forest) were used, with 16 species being sampled. Estimated densities ranged from 2 ha^{-1} to 675 ha^{-1}. Akaike's Information Criterion (AIC) was used to select the most parsimonious model of frog density. Factors identified in the selected model to predict density of *Batrachylodes elegans*, *Batrachylodes vertebralis*, *Ceratobatrachus guentheri*, *Discodeles bufoniformis*, *Discodeles guppyi*, *Discodeles malukuna*, *Litoria thesaurensis*, *Palmatorappia solomonis*, *Platymantis guppyi*, *Platymantis neckeri*, *Platymantis solomonis*, *Platymantis* sp., *Platymantis weberi*, and *Rana kreffti* were island, landform, and forest type. Additional factors such as disturbance, leaf litter, shrub, and understorey were also described by the regression model as predictors of density for *B. vertebralis*, *C. guentheri*, *D. guppyi*, *D. malukuna*, *Pal. solomonis*, *P. guppyi*, and *R. kreffti*. These findings have important management implications for the conservation of frogs in the Solomon Islands. High densities of most species were strongly related with forest type and low disturbance. Preservation of rainforest, in especially high conservation value old-growth forests, is imperative to protecting these species.

Additional keywords: conservation, density, forest type, frogs.

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Introduction

Geographically, the Solomon Islands (including Bougainville and Buka Island) support one of the richest frog faunas in the insular Pacific region, with 25 described species from seven genera (Menzies 2006; Brown and Richards 2008; Pikacha *et al.* 2008*b*). Most species (11 of 25 described) belong to the widespread genus *Platymantis* (Menzies 2006; Brown and Richards 2008; Pikacha *et al.* 2008*b*). Two genera (*Ceratobatrachus* and *Palmatorappia*) are endemic to the Solomon Islands (Goin and Goin 1962; Pikacha *et al.* 2008*b*) and two others (*Batrachylodes* and *Discodeles*) occur outside the archipelago in the Bismarck and Admiralty Islands in Papua New Guinea (Richards and Gamui 2011). Species diversity dramatically reduces eastwards across the Melanesian region, with no naturally occurring frogs in Vanuatu or New Caledonia. Two *Platymantis* species are found in Fiji (Gorham 1968; Morrison 2003; Osborne *et al.* 2008, 2013).

This fauna is rich, with forms adapted to a range of habitats including large stream-associated species, small arboreal frogs, scansorial species, and ground frogs (Menzies 2006; Pikacha *et al.* 2008*b*). Frogs represent some of the most abundant terrestrial vertebrates on larger islands of the archipelago (Filardi 2004; Scoville 2006; Pikacha *et al.* 2008*b*). However, little is known of factors affecting densities of frogs in the Solomon Islands (Morrison *et al.* 2008). Possible declines in Solomon Island frogs appear to be consistent with global patterns of amphibian decline mainly due to the loss of habitat (Menzies 2006; Morrison *et al.* 2008; Pikacha *et al.* 2008*b*). In other regions, frog densities are known to be affected by factors such as forest type (Nájera-Hillman *et al.* 2009; Santos-Barrera and Urbina-Cardona 2011), hydrology (Mazerolle *et al.* 2005; Otto *et al.* 2007), high salinity (Hart *et al.* 1990; Christy and Dickman 2002), the presence of invasive species (Taylor and Edwards 2005; Walker 2010; Wilson *et al.* 2011), and disease (Briggs *et al.* 2005).

The present study aims to determine what factors affect the density of frogs in the Solomon Islands. This knowledge is useful for developing strategies to conserve these frogs, given the rapid and unsustainable logging of old-growth forest across the archipelago (Bennett 2000; Greenpeace 2008; Nguyen and Kereseka 2008; Pauku 2009).

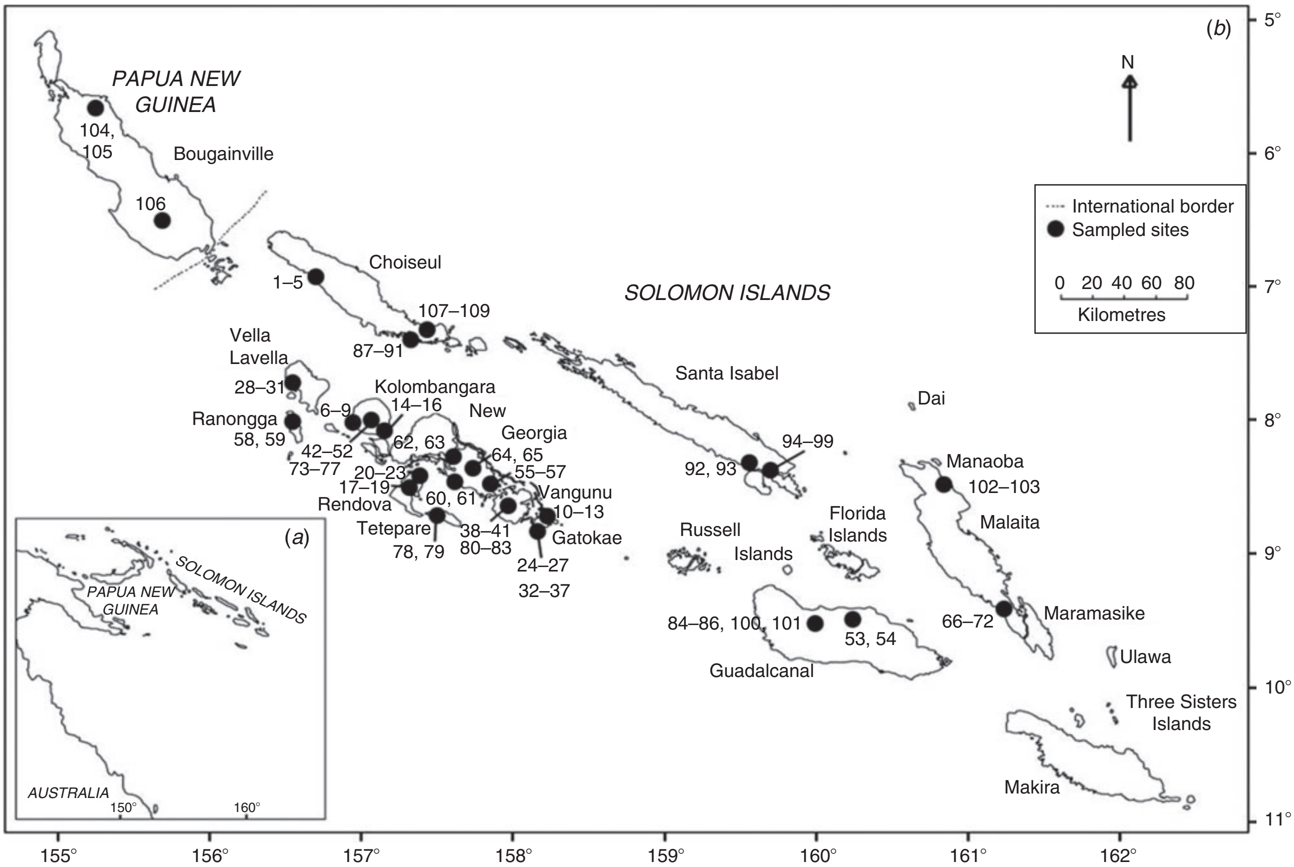

Fig. 1. Location of Solomon Islands (*a*) and survey areas (black dots) in the Solomon Islands archipelago (*b*). The numbers represent transect ID numbers (1–109).

Materials and methods

Site description

The Solomon Islands are located north-east of Australia (Fig. 1*a*). Data were collected from 13 islands in the Solomon Islands (Fig. 1*b*). These included eight islands from the New Georgia Island group (Gatokae, Kolombangara, New Georgia, Ranongga, Rendova, Tetepare, Vella Lavella, and Vangunu), and five other main islands (Bougainville, Choiseul, Guadalcanal, Isabel, and Malaita). The islands range in area from 100 km^2 to 5302 km^2, and are separated by oceanic barriers that vary in distance from 2 km to more than 50 km.

There is little seasonal temperature change in tropical oceanic island rainforests (Brookfield 1969; Castro *et al.* 2007). In the Solomon Islands high rainfall occurs between November and March whilst dry periods occur from April to October (Hiriasia and Tahani 2011), although there is high variability between islands. Average rainfall for New Georgia between 1990 and 2010 was 306 mm per month, with no clear seasonal variation (Hiriasia and Tahani 2011; MECMDM 2011).

Environmental factors

Nine environmental factors (island, landform, forest type, leaf litter, canopy cover, shrub cover, understorey cover, soil moisture content, and forest disturbance) were investigated as they potentially influence frog density. Islands may have biogeographical effects on frog species/density with exceptionally high densities of organisms frequently occurring on some islands (Rodda and Dean-Bradley 2002). Landform characteristics or landscape structure are known to influence habitat quality, providing niche space, breeding sites and in turn affecting populations of frogs (Wilkins and Peterson 2000; Osawa and Katsuno 2001). Landform was assigned to one of the six categories of landforms of Solomon Islands (Hackman 1980): (1) ridges (e.g, occurring mostly in lowland forests on gentle slopes not higher than 400 m above sea level; (2) high ridges (e.g. on the top of steep, often precipitous, slopes occurring above 700 m above sea level); (3) alluvial soils; (4) valleys; (5) streambeds; and (6) karst. Ridges and high ridge landscapes were interpreted by using a Garmin 78 GPS (Garmin International, Inc.1200 East 151st Street, Olathe, KS 66062, USA). Alluvial soils of river flats and terraces, valleys, streambed and karst, were visually defined (de Groot and van den Born 2003).

Frogs are found in different forest types (Wilkins and Peterson 2000). In this study forests were classified into five forest types based on descriptions by Whitmore (1969), (Whitmore 1969; Bennett 2000; Wilkie 2005): (1) coastal forest, (2) freshwater marshes, (3) lowland forest, (4) hill and ridge forest, and (5) montane forest. Coastal forests include

Table 1. Ecological and environmental factors

Factors	Details
Canopy crown cover	Low cover (30–59%), high cover (>60%)
Understorey cover	Low cover (30–59%), high cover (>60%)
Disturbance	Disturbed, undisturbed
Forest type	Coastal, freshwater and marshes, lowland, hill and ridge, montane
Islands	Bougainville, Choiseul, Gatokae, Guadalcanal, Isabel, Kolombangara, Malaita, New Georgia, Ranongga, Rendova, Tetepare, Vangunu, Vella Lavella
Landform pattern	Alluvial soil, high ridge, karst, ridge [low], riparian/streambed, valley
Leaf litter	Thin (1–2 cm), thick (>2 cm)
Shrub	Sparse (0–20% cover), dense (20–40% cover)
Soil moisture	Dry, moist

mangroves and vegetation along beaches and coastal fringes. Typically, they are not as dense as lowland forests (Pikacha 2008). Freshwater marshes, sometimes referred to as swamps, are often inundated and dominated by *Campnosperma brevipetiolata* forests, closed-canopy *Terminalia brassi* forests and sago trees (*Metroxlyon solomonense*), and *Panadanus* spp. (Mueller-Dombois and Fosberg 1998). Lowland forests occur at altitudes of 5–70 m above sea level. They can be exposed to high degrees of disturbance from cyclones, and human activities (Mueller-Dombois and Fosberg 1998; Pikacha 2008; Pikacha *et al.* 2015). Hill and ridge forests usually occur up to an altitude of 600 m, and are a complex of variable tree heights and canopy densities. Due to the Massenerhebung Effect, where tropical forests on smaller islands are compressed, montane forests that appear at 2000 m on large islands like New Guinea, generally appear at 600 m on smaller islands like the Solomon Islands (Grubb 1971; Flenley 1995; Pikacha 2008; Pikacha *et al.* 2015). Montane forests are stunted with lighter canopies, increased epiphytes and lichens (Pikacha 2008; Pikacha *et al.* 2015).

Other factors included characteristics of the vegetation cover. Rainforest leaf litter is an important habitat and breeding ground for many frog species (Siqueira *et al.* 2009). Leaf litter was classified into two categories (thin [1–2 cm] or thick [>2 cm]) based on average measurements collected at each transect. Studies examining forest canopy and frog occupancy and abundance indicate that some species prefer open areas and others closed canopies (Werner and Glennemeier 1999). Canopy and understorey were classified by the crown projection of the tree, and was based on estimated categories of percentage cover. This method of estimation is a common concept in forestry (Rautiainen *et al.* 2005). Shrub cover is known as a positive predictor of the presence of frogs (Vonesh 2001). Shrub cover was categorised as sparse (covering up to 10% of transect area) or dense (covering more than 10% of transect).

Microhabitat factors such as soil moisture have been known to influence frog densities (Regosin *et al.* 2003). Visual and hand feel method is a way of monitoring soil moisture, and has been used in rapid assessments (Leib *et al.* 2002). A selected sample is collected using a probe, squeezed firmly in the hand and observed for soil texture, firmness and water glistening. This method was used to classify soil moisture as either dry or moist. Disturbance was assessed under two categories: disturbed (old gardens and villages, trails and roads) and undisturbed (continuous unbroken habitats). The nine tested ecological and environmental factors are summarised in Table 1. General habitat characteristics such as perch plant species for some frogs were also noted where appropriate.

Line sampling to estimate density

Distance sampling was used to estimate frog density. The first author walked along a transect line between 1700 and 2300 h with the use of a head torch (Petzl Tikkina Led Head Torch, Grenoble, France). Upon detection of frog(s), identification was made using standard morphology and call descriptions (Brown 1952; Menzies 2006; Pikacha *et al.* 2008*b*). A laser distance meter (UK Parts Deal, Hong Kong) was used to measure the perpendicular distance (w) of the frog(s) from the line. Where possible, individual frogs were photographed for further identification. Sampling was conducted both in the dry season (May–June 2009, October 2009, June–August 2010, June–July 2011), and wet season (January 2010, November 2010 – January 2011, November 2011 – January 2012). A total of 109 transects were surveyed across 13 islands.

Density estimates were computed for eight common species using the program DISTANCE 5 (Thomas *et al.* 2010). Low frog counts at some individual transects meant that the detection function at the transect level could not be estimated. A global detection function was therefore used in this study (Reidy *et al.* 2011). Based on the density computed in DISTANCE 5 for eight species the average area covered in the transect surveys was estimated. Based on the estimated area covered in the transect surveys, the density (individuals ha^{-1}) was estimated for the other six species with low abundance counts.

Statistical analysis

Regression was performed to identify the relationship between frog densities and a series of independent factors. Prior to any statistical testing, a model diagnostics analysis of the data was done. Minitab 17 (Minitab, Pennsylvania, USA) was used to construct individual indicator variables that simplified the dataset. To construct a best-fit model, individual variables were employed as factors or predictors and added as best subsets in the model screening (Ryan *et al.* 2005). With density set as the dependent variable, multiple environmental factors were examined simultaneously using subset regression. Some factors

Fig. 2. Photographic identification of species of frogs recorded in the study, including average snout to vent length (SVL). (*a*) *Batrachylodes elegans* (32 mm SVL), (*b*) *Batrachylodes vertebralis* (28 mm SVL), (*c*) *Batrachylodes wolfi* (30 mm SVL), (*d*) *Ceratobatrachus guentheri* (65 mm SVL), (*e*) *Discodeles bufoniformis* (78 mm SVL), (*f*) *Discodeles guppyi* (110 mm SVL), (*g*) *Discodeles malukuna* (72 mm SVL), (*h*) *Litoria lutea* (50 mm SVL), (*i*) *Litoria thesaurensis* (55 mm SVL) (*j*) *Palmatorappia solomonis* (28 mm SVL), (*k*) *Platymantis guppyi* (75 mm SVL), (*l*) *Platymantis neckeri* (45 mm SVL), (*m*) *Platymantis solomonis* (56 mm SVL) (*n*) *Platymantis* sp. (32 mm SVL), (*o*) *Platymantis weberi* (35 mm SVL), (*p*) *Rana kreffti* (52 mm SVL). All photographs by P. Pikacha.

that presented similar effects on density were combined in order to obtain a best-fit model.

To select the best regression model (e.g. subset of predictors) Akaike's Information Criterion (AIC) was used (Burnham and Anderson 2002). This method weighs each model by the amount of variance explained and the complexity of the model (e.g. the number of explanatory variables, *K*). To determine the best support for an AIC value, ΔAIC (e.g. $AIC_i - AIC_{min}$) and Akaike weights (Burnham and Anderson 2001) were used. Models with ΔAIC values between 0 and 2 give comparable support. Akaike weight (w_{AIC}) determines the relative likelihood of the model, provided the dataset. The best of three models (the most parsimonious model with the highest AIC value) is reported.

Results

A total of 16 species of native frogs (Fig. 2) were sampled in this study, with a total of 5058 individuals recorded from 109 transects on the 13 islands. These were *Batrachylodes elegans*, *Batrachylodes vertebralis*, *Batrachylodes wolfi*, *Ceratobatrachus guentheri*, *Discodeles bufoniformis*, *Discodeles guppyi*, *Discodeles malukuna*, *Litoria lutea*, *Litoria thesaurensis*, *Palmatorappia solomonis*, *Platymantis guppyi*, *Platymantis neckeri*, *Platymantis solomonis*, *Platymantis weberi*, *Rana kreffti* and an undescribed *Platymantis* species. The undescribed species differed from other *Platymantis* species by its call, digital discs, and absence of dorsal stripes and was predominantly found in montane forests (Pikacha, unpubl. data). Density estimates were not generated for two species, *B. wolfi* and *L. lutea*, due to the low number of individuals recorded. In general, the estimated densities of many frog species differed between islands, forest types, and landforms. Several frogs recorded in this study were affected by: forest understorey cover, canopy cover, shrub cover, soil moisture, and leaf litter (Table 2). The model showed higher densities in lowland forests for *B. elegans*, *B. vertebralis*, *C. guentheri*, *P. guppyi*, and *P. weberi*, or a combination of riparian or stream landforms and lowland forests for *D. guppyi*, and freshwater and lowland forests for *P. neckeri*. *Pal. solomonis* was predicted to occur in hill forest. The models are summarised in Table 2.

The factors that most commonly affected frog densities were: island (12 species), landform patterns (11 species), forest types

Table 2. Species recorded in this study, including their distribution, density and abundance

Bo, Bougainville; Ch, Choiseul; Is, Isabel; Ga, Gatokae; Gu, Guadalcanal; Ko, Kolombangara; Ma, Malaita; NG, New Georgia; Ra, Ranongga; Re, Rendova; Te, Tetepare; Va, Vangunu; VL, Vella Lavella. Total transects surveyed = 109

Species	No. of islands present	Islands	No. of transects present in dry season	No. of transects present in wet season	Total no. of transects	Abundance (*n*)	Density (ha^{-1})	
							Range	Mean ± s.e.
Batrachylodes elegans	11	Bo, Ch, Ga, Gu, Is, Ko, Ma, NG, Re, Va, VL	35	56	91	1875	25.1–674.5	232.4 ± 14.8
Batrachylodes vertebralis	6	Bo, Ch, Gu, Is, Ko, NG	15	15	30	184	4.3–200.9	71.0 ± 5.7
Batrachylodes wolfi	1	Ga	1	0	1	2	–	–
Ceratobatrachus guentheri	12	Bo, Ch, Ga, Gu, Is, Ko, Ma, NG, Re, Te, Va, VL	38	53	91	474	5.9–198.8	32.5 ± 3.3
Discodeles bufoniformis	4	Bo, Ch, NG, Ra	9	3	12	21	6.3–12.7	8.7 ± 0.3
Discodeles guppyi	8	Ch, Ga, Gu, Ko, Ma, Re, Va, VL	19	21	40	176	4.3–85.3	19.3 ± 1.9
Discodeles malukuna	9	Bo, Ch, Ga, Gu, Ko, NG, Re, Va, VL	23	27	50	158	4.0–56.0	15.1 ± 1.3
Litoria lutea	1	Ga	0	3	3	4	–	–
Litoria thesaurensis	7	Ch, Ga, Gu, Ko, Re, Va, VL	11	10	21	45	6.3–44.4	13.6 ± 1.2
Palmatorappia solomonis	2	Ch, Is	3	5	8	41	12.7–63.4	34.2 ± 2.2
Platymantis guppyi	12	Bo, Ch, Ga, Gu, Is, Ko, Ma, NG, Re, Te, Va, VL	37	48	85	506	4.4–24.2	28.3 ± 2.3
Platymantis neckeri	8	Ch, Ga, Gu, Ko, NG, Re, Va, VL	14	8	22	65	6.3–63.4	19.0 ± 1.4
Platymantis solomonis	9	Bo, Ch, Ga, Gu, Ko, NG, Re, Va, VL	28	29	57	452	6.2–369.8	54.8 ± 5.9
Platymantis sp.	6	Ga, Gu, Ko, NG, Ra, Va	3	12	15	33	6.3–31.7	13.1 ± 1.0
Platymantis weberi	13	Bo, Ch, Ga, Gu, Is, Ko, Ma, NG, Ra, Re, Te, Va, VL	42	61	103	999	13.3–292.7	74.1 ± 5.1
Rana kreffti	5	Bo, Ch, Is, Gu, Ma	4	5	9	23	6.3–25.4	13.6 ± 0.7
Total						5058		

(10 species), disturbance (4 species), shrub cover (2 species), and understorey cover (2 species). Samples sizes of most (14) of the species were high, providing confidence in the model results: *B. elegans* ($n = 1875$), *B. vertebralis* ($n = 184$), *C. guentheri* ($n = 474$), *D. guppyi* ($n = 164$), *L. thesaurensis* ($n = 43$), *Pal. solomonis* ($n = 41$), *P. guppyi* ($n = 492$), *P. neckeri* ($n = 60$), *P. solomonis* ($n = 430$), *Platymantis* sp. ($n = 33$), and *P. weberi* ($n = 954$). Given the small sample sizes for *B. wolfi* ($n = 2$) and *L. lutea* ($n = 4$), the results for these species are therefore tentative.

The results for each individual species are described as follows:

Batrachylodes elegans. *B. elegans* was most widespread (recorded on 11 of 13 islands) and abundant (1875 individuals counted), recording the highest mean density of 232.4 ± 14.8 (s.e.) ha^{-1} (Table 2). The most parsimonious model consists of four factors: islands, ridge and riparian landforms, and forest types (Table 3, Fig. 3*a*). The model showed mean frog density on Choiseul Island (347.0 ha^{-1}) was higher than on other islands (Bougainville, Gatokae, Guadalcanal, Isabel, Kolombangara, Malaita, New Georgia, Ranongga, Rendova, Tetepare, Vangunu, Vella Lavella, 254.9 ha^{-1}). More frogs occurred on alluvial soils, valleys, and karst landforms (254.9 ha^{-1}), compared with ridge (156.6 ha^{-1}) and riparian (30 ha^{-1}) landforms. Densities were also higher in freshwater, lowland, hill and montane forests (254.9 ha^{-1}), compared with coastal forests (158.5 ha^{-1}) (Fig. 3*a*). In forest understorey, *Cyathea* sp. was noted as a perch plant for *B. elegans*, and it was also found in human-modified habitats such as banana (*Musa* sp.) groves and cassava (*Manihot esculenta*) gardens in lowland forests.

Batrachylodes vertebralis. This species was recorded on six islands. Lowest density per transect (4.3 ha^{-1}) was recorded in lowland forest at Kerugela (225 m above sea level) on Choiseul Island. The highest density (200.9 ha^{-1}) was reported in lowland forest, at the upper Vila River (341 m above sea level), Kolombangara Island (Table 2). The model predicted higher mean densities on Guadalcanal (99.7 ha^{-1}) and Isabel (50.2 ha^{-1}) compared with other islands (Bougainville, Choiseul, Gatokae, Kolombangara, Malaita, New Georgia, Ranongga, Rendova, Tetepare, Vangunu, Vella Lavella) (17.3 ha^{-1}). There were more individuals in sparse shrub cover (17.3 ha^{-1}) compared with dense shrub (4.7 ha^{-1}), in lowland forests (28.1 ha^{-1}) compared with other forest types (coastal, freshwater, hill and montane (17.3 ha^{-1}), and in undisturbed areas (17.3 ha^{-1}), whilst densities were lower in disturbed areas (10.1 ha^{-1}) (Table 3, Fig. 3*b*).

Batrachylodes wolfi. *B. wolfi* was the least common species encountered during the study ($n = 2$) (Table 2). It was recorded at a single site within the Kavolavata River valley, a gorge located on the south-east side of the island of Gatokae. The site was composed of primary forest with low shrubbery and understorey saplings overlapping undisturbed hill/ridge and low montane forests. The data were insufficient (small numbers of individuals observed on transects) for statistical analysis.

Ceratobatrachus guentheri. This species was widespread on all islands except Ranongga (Table 2). Natural coloration in the wild is varied from shades of brown, orange, mottled green, black, and even entire yellow. The statistical model showed higher frog densities on Guadalcanal and Isabel (40.8 ha^{-1}),

Table 3. The most parsimonious model for each species, presented with relevant AIC values

The AIC weights measure the percentage support for each model

Species	Fitted models	R^2 (%)	Adj. R^2 (%)	K	AIC	ΔAIC	W_{AIC}	F	P
Batrachylodes elegans	Density = 254.9 + 87.8 Choiseul I. – 98.4 ridge landform – 227.0 riparian landform – 96.4 coastal forest	32.7	30.1	5	1073.4	1.0	0.5	19.5	<0.0001
Batrachylodes vertebralis	Density = 17.3 + 82.4 Guadalcanal I. + 32.9 Isabel I. – 12.6 dense shrub + 10.8 lowland forest – 7.2 disturbance	35.0	31.8	6	766.8	1.7	0.6	19.6	<0.0001
Ceratobatrachus guentheri	Density = 18.3 + 22.5 Guadalcanal and Isabel Is – thick leaf litter + 46.3 alluvial soil landforms + 27.7 lowland forest	40.9	38.6	5	712.3	2.0	0.5	18.0	<0.0001
Discodeles bufoniformis	Density = 0.01 + 1.96 riparian landform + 6.44 Bougainville and New Georgia Is	48.4	47.4	3	224.4	0.1	0.5	44.8	<0.0001
Discodeles guppyi	Density = 4.6 + 10.3 riparian landform and lowland forest – 3.6 disturbance + 9.7 Choiseul I.	24.6	22.1	4	574.5	1.4	0.5	11.2	<0.0001
Discodeles malukuna	Density = 11.3 + 6.0 lowland forests – 0.2 high understorey canopy – 6.3 Kolombangara I.	9.5	6.0	5	540.9	4.9	0.9	3.6	0.015
Litoria thesaurensis	Density = 1.0 + alluvial soil landform + 2.5 valley landform	15.4	13.8	3	419.6	4.6	0.8	9.6	<0.0001
Palmatorappia solomonis	Density = 0.04 + 9.0 hill forest + 6.8 Bougainville I. – 0.1 dense shrub	15.6	13.2	4	480.2	4.3	0.8	6.5	0.0005
Platymantis guppyi	Density = 18.1 + 9.3 ridge landform + 12.7 high ridge + 30.0 alluvial soil + 7.8 lowland forest – 5.4 disturbance – 11.6 Kolombangara I. + 13.4 Choiseul I.	38.6	34.4	8	644.5	6.3	0.8	9.1	<0.0001
Platymantis neckeri	Density = 1.1 + 4.5 alluvial soil landform + 3.0 freshwater and lowland forest	5.7	3.9	3	493.9	1.3	0.5	3.2	0.04
Platymantis solomonis	Density = 7.0 + 32.0 alluvial soil landform + 52.0 freshwater marshes + 32.4 (Bougainville, Choiseul, Gatokae Is)	27.4	25.3	4	819.0	5.2	0.7	13.2	<0.0001
Platymantis sp.	Density = 1.0 + 9.6 high ridge landform + 1.0 Gatokae I.	21.5	20.0	3	367.3	3.8	0.6	14.5	<0.0001
Platymantis weberi	Density = 54.3 – 18.7 high ridge landform + alluvial soil landform + 27.5 lowland forest – 30.9 Kolombangara I. + 54.9 Choiseul I. + 20.2 Isabel I. – 27.3 Malaita I.	31.3	26.6	8	831.8	3.3	0.7	6.6	<0.0001
Rana kreffti	Density = 10.8 – 0.3 understorey + 2.8 ridge landform and lowland forest + 1.0 disturbance – 3.9 Isabel I. + 4.1 Gatokae I.	31.2	27.8	6	312.7	4.8	0.6	9.3	<0.0001

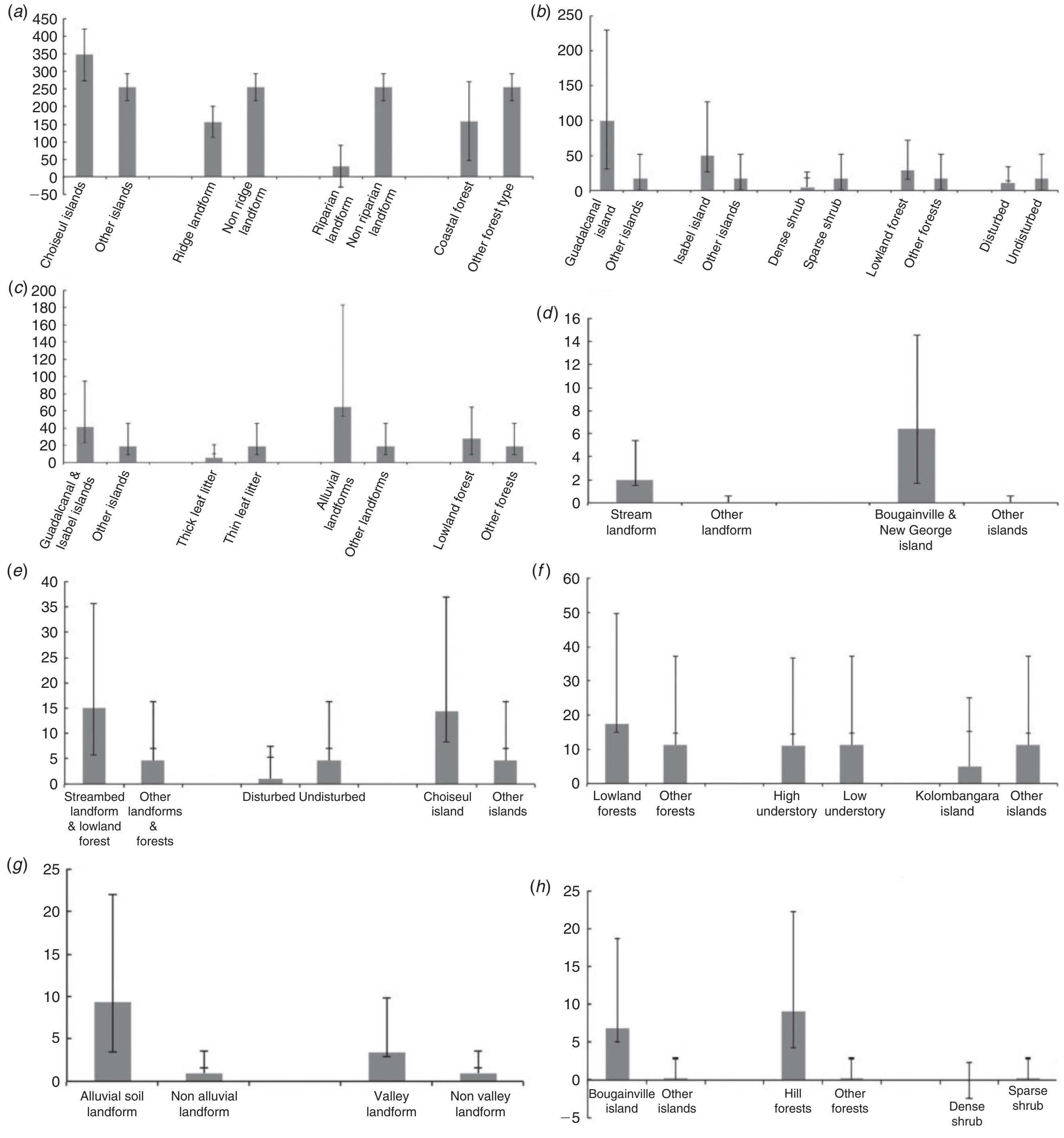

Fig. 3. The effect of various environmental factors (*x* axis) on estimated density (ha^{-1}) (*y* axis) of the following frogs: (*a*) *Batrachylodes elegans*, (*b*) *Batrachylodes vertebralis*, (*c*) *Ceratobatrachus guentheri*, (*d*) *Discodeles bufoniformis*, (*e*) *Discodeles guppyi*, (*f*) *Discodeles malukuna*, (*g*) *Litoria thesaurensis*, (*h*) *Palmatorappia solomonis*, (*i*) *Platymantis guppyi*, (*j*) *Platymantis neckeri*, (*k*) *Platymantis solomonis*, (*l*) *Platymantis* sp., (*m*) *Platymantis weberi*, (*n*) *Rana krefftii*. Other fixed effects are adjusted to zero. The error bar indicates 95% confidence interval.

than other islands (Bougainville, Choiseul, Gatokae, Kolombangara, Malaita, New Georgia, Ranongga, Rendova, Tetepare, Vangunu, Vella Lavella, 18.3 ha^{-1}). Additionally greater density was inferred for areas with thin leaf litter (18.3 ha^{-1}), and lesser in thick litter (5.4 ha^{-1}). Most striking were the high densities indicated for alluvial soil landforms (64.6 ha^{-1}) compared with other landforms (karst, ridge, streambed, valley, 18.3 ha^{-1}). The model presented more frogs in lowland forests (27.7 ha^{-1}) compared with other forest types (coastal, freshwater, hill and montane, 18.3 ha^{-1}) (Table 3, Fig. 3*c*).

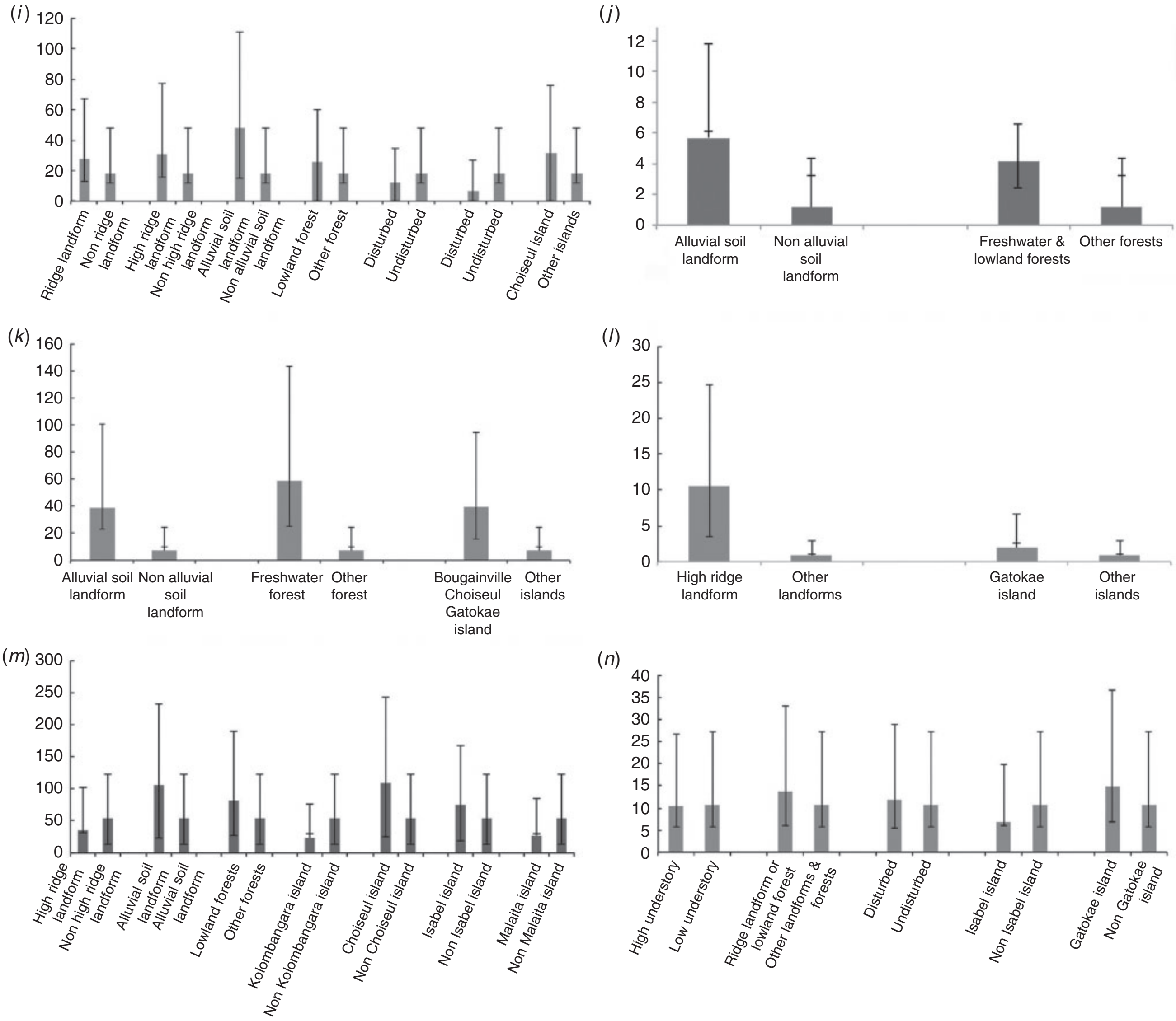

Fig. 3. (Continued).

Discodeles bufoniformis. This species was recorded on transects along the upper Vavudu stream behind Sasamunqa village (Choiseul), Pazuva stream (Ranongga), Sakambare stream (New Georgia), and Parama village (Bougainville) (Table 2). The best-fit model was supported by an AIC weight of 0.49 (Table 3). The model comprised landform and island as factors of density (Fig. 3*d*). The model showed a slight skew towards riparian landforms with a predicted density of 2.0 ha^{-1} and none in other landforms (alluvial soil, karst, ridge, and valley). These frogs were noted to perch on rocks in streams, or hide under them at sections of slow flow. *D. bufoniformis* was also recorded under shrubs or overhanging vegetation growing along stream edges, which was used as retreat sites. Greater densities were predicted on Bougainville or New Georgia (6.4 ha^{-1}), compared with other islands (Choiseul, Gatokae, Guadalcanal, Isabel, Kolombangara, Malaita, Ranongga, Rendova, Tetepare, Vangunu, Vella Lavella) sampled (Table 3, Fig. 3*d*).

Discodeles guppyi. This is a large aquatic frog (110 mm SVL). The best-fit model comprised three factors: a combination of riparian landform and lowland forests, disturbance, and islands. This was supported by an AIC weight of 0.50 (Table 3). The study revealed greater densities in riparian landforms and lowland forests (15.0 ha^{-1}) than other landforms (alluvial soil, karst, ridge, valley) and forest types (coastal, freshwater, hill and montane) (4.6 ha^{-1}). Of the 40 individuals found in the study, 18 were found in rivers and streams in lowland forests, whilst the rest were found close to waterways, and in hill forests. No individuals were recorded in montane forests. This species was also susceptible to disturbance regimes, with the model predicting greater density in undisturbed areas (4.6 ha^{-1}) and lower numbers in disturbed areas (1.1 ha^{-1}). For differences among islands, the model predicted greater densities on Choiseul (14.3 ha^{-1}) compared with other islands (Bougainville, Gatokae, Guadalcanal, Isabel, Kolombangara, Malaita, New Georgia, Ranongga, Rendova, Tetepare, Vangunu, Vella Lavella, 4.6 ha^{-1}) (Table 3, Fig. 3*e*).

Discodeles malukuna. Smallest of the genus, a total of 158 individuals were recorded in 50 transects on nine islands, with mean density of 15.1 ± 1.3 (s.e.) ha^{-1} (Table 2). A strong AIC weight of 0.9 determined the best-fit model, which comprised three factors: forests, understorey, and islands (Table 3, Fig. 3*f*). The model showed greater densities in lowland forests (17.3 ha^{-1}) compared with other forest types (11.3 ha^{-1}) represented by coastal, freshwater, hill and montane forests. Densities are essentially alike in high (11.1 ha^{-1}) and low (11.3 ha^{-1}) understorey cover. On Kolombangara, density is estimated to be lower (5.0 ha^{-1}) than on other islands (Bougainville, Choiseul, Gatokae, Guadalcanal, Isabel, Malaita, New Georgia, Ranongga, Rendova, Tetepare, Vangunu, Vella Lavella, 11.3 ha^{-1}) (Table 3, Fig. 3*f*).

Litoria lutea. This species is listed as vulnerable on the IUCN Red List (Richards and Parker 2004) and was rarely encountered. Even during intensive searches on the large islands it remained elusive. Only four individuals were recorded on Mt Mariu (885 m above sea level), Gatokae Islands, and in understorey (Table 2). Vegetation in the understorey here was dominated by *Freycinetia* sp. (a stifling creeping monocot bush), montane bamboo (*Nastas* sp.), *Alpinia* sp., and *Heliconia* spp. plants. *Heliconia* spp. are commonly used as perch plants by these frogs. The overstorey at this site was dominated by *Cyrtandra laciniata*, *C. filiabracteata*, *C. atherocalyx* and *Syzygium* sp. trees. Given that *L. lutea* was observed at only one site, statistical modelling was not possible.

Litoria thesaurensis. *L. thesaurensis* was found on trees, low shrubs, and on the forest floor. It appears to be a hardy species, commonly encountered in disturbed (logging roads, forest trails, old gardens, forest edges) and undisturbed (swamp areas and temporal forest pools) habitats. A total of 45 individuals were recorded in 21 transects on seven islands, with mean density of 13.6 ± 1.2 (s.e.) (Table 2). A strong AIC weight of 0.8 determined the best-fit model, which comprises two factors: alluvial soil landform and valley landform (Table 3, Fig. 3*g*). The model showed greater densities in alluvial soil (9.3 ha^{-1}) and valley (3.5 ha^{-1}) landforms and lower in other landform types (ridge, valleys, and karst, 1.0 ha^{-1}). Breeding pairs were observed in ponds and ephemeral pools in January 2009 (Choiseul), and January, June, and October 2010 (Kolombangara).

Palmatorrapia solomonis. *P. solomonis* was one of two species listed as vulnerable on the IUCN Red List of threatened species. The best model comprised three factors: forest, island, and shrub cover. The main factor influencing density was hill forest. Densities in hill forest were greater (9.0 ha^{-1}) than in other forest types (coastal, freshwater, lowland and montane, 0.04 ha^{-1}). All 40 individuals recorded in 8 transects in this study were found in hill forest in the understorey trees above shrub cover. Frogs were perched between 1–2 m on low trees. Hill forests (353–413 m above sea level) were composed of trees with closed canopies. Floral diversity in hill forests included *Gymnostoma papuana*, *Xanthostemon melanoxylon*, *Gulubia hombronii*, *Actinorhytis calapparia*, *Gleichenia linearis*, *Racebambos holltumii*, *Gnetum gnemon*, *Lycopodium cernuum*, *Nastus obtusus*, *Dacrydium elatum*, *Fagraea obtusifolia*, *Myrtella beccarii*, *Podocarpus salomoniensis* and several species of *Syzygium* and *Metrosideros* associated with intact primary forests. Sparse and dense shrub cover hardly affected frog densities. Higher densities were predicted on Bougainville (6.8 ha^{-1}) compared with other islands (Choiseul, Gatokae, Guadalcanal, Isabel, Kolombangara, Malaita, New Georgia, Ranongga, Rendova, Tetepare, Vangunu, Vella Lavella, 0.04 ha^{-1}) (Table 3, Fig. 3*h*). The model was supported by a strong AIC weight of 0.81 (Table 3).

Platymantis guppyi. *P. guppyi* is a tree specialist as the 506 records (Table 2) of this frog were made 1–10 m above ground in vegetation. The most parsimonious model comprised four factors: landform (ridge, high ridge, alluvial soil), forest type, disturbance, and islands (Kolombangara and Choiseul) (Table 3, Fig. 3*i*). More frogs were found on ridge (27.4 ha^{-1}), high ridge (30.7 ha^{-1}), and alluvial landforms (48.1 ha^{-1}), than karst, streambeds, and valleys (18.1 ha^{-1}). Lowland forests had greater densities (25.6 ha^{-1}) than other forest types (coastal, freshwater, hill, and montane, 18.1 ha^{-1}). The following plants were noted as perch sites for this species in lowland forests: *Areca macrocalyx*, *Calamus hollrungii*, *Calamus stipitatus*, *Caryota rumphiana*, *Drymophloeus salomonense*, *Gulubia macrospadix*, *Heterospathe minor*, *Heterospathe solomonensis*, *Licuala lauterbachii*, *Ptychosperma salomonense* and *Rhopaloblaste elegans*. The model predicted higher densities in undisturbed (18.1 ha^{-1}) compared with disturbed (12.6 ha^{-1}) sites. Choiseul was estimated to have highest densities (31.4 ha^{-1}), followed by islands (Bougainville, Gatokae, Guadalcanal, Isabel, Malaita, New Georgia, Ranongga, Rendova, Tetepare, Vangunu, Vella Lavella, 18.1 ha^{-1}) other than Kolombangara (6. 4 ha^{-1}) (Table 3, Fig. 3*i*). This model was strongly supported by an AIC weight of 0.95 (Table 3).

Platymantis neckeri. Like *P. guppyi*, this species is a tree specialist. A total of 65 individuals were recorded on eight islands (Table 2). The highest density per transect (63.4 ha^{-1}) was recorded in lowland forests amongst saplings, vines, and understorey trees, which this species used as perch and call sites. In comparison, lowest density was recorded in secondary forest (6.3 ha^{-1}). Mean density over all transects was 19.0 ± 1.4 (s.e.) ha^{-1} (Table 2). The best-fit model predictor accounted for two factors: landform and forest (Table 3). More frogs were found in alluvial soil landform (5.7 ha^{-1}) and a combination of freshwater and lowland forests (4.1 ha^{-1}), than other landforms (karst, ridge, high ridge, streambed, valley, 1.1 ha^{-1}) or forest types (coastal, hill and montane, 1.1 ha^{-1}) (Table 3, Fig. 3*j*). This best-fit model was supported by an AIC weight of 0.48 (Table 3).

Platymantis solomonis. This was one of the most abundant terrestrial species (452 individuals), and occurred in sympatry with *P. weberi*. Lowest recorded density per transect (6.2 ha^{-1}) was in lowland forests and highest density (369.8 ha^{-1}) in freshwater marshes (Table 2). The best-fit model comprised three factors: landform, forests, and islands, and was supported by an AIC weight of 0.70 (Table 3). The model predicted more frogs in the alluvial soil landform (38.95 ha^{-1}) than other landforms (karst, ridge, high ride, streambed, and valley, 6.96 ha^{-1}) (Table 3). Frog densities were estimated higher in freshwater marshes (58.92 ha^{-1}) compared with other forest types (coastal, lowland, hill and montane, 6.96 ha^{-1}). Greater densities were estimated for Bougainville, Choiseul or Gatokae (39.35 ha^{-1}), with much lower densities on other islands (Guadalcanal, Isabel, Kolombangara, Malaita, New Georgia, Ranongga, Rendova, Tetepare, Vangunu, Vella Lavella, 6.7 ha^{-1}) (Table 3, Fig. 3*k*).

Platymantis sp. The undescribed species of *Platymantis* appears to be a scansorial (found on ground but having ability to be arboreal) species found perching on low branches of understorey trees. From 15 transects, 33 individuals were recorded on six islands (Table 2). The most parsimonious model for estimated densities comprised two factors: landform and island. The model revealed greater densities in high ridge landforms (10.6 ha^{-1}) compared with other landforms (alluvial soil, karst, ridge, streambed, valley, 0.9 ha^{-1}). This species was first encountered on high ridges on Gatokae in cloud forest. Indicatively, the model showed slightly higher densities on Gatokae (2.0 ha^{-1}) than other islands (Bougainville, Choiseul, Guadalcanal, Isabel, Kolombangara, Malaita, New Georgia, Ranongga, Rendova, Tetepare, Vangunu, Vella Lavella, 0.9 ha^{-1}) (Table 3, Fig. 3*m*). The predicted model received an AIC weight support of 0.6 (Table 3).

Platymantis weberi. The terrestrial frog *P. weberi* was the most abundant (999 individuals) ground frog, and most widespread species in the study. The lowest density per transect (13.3 ha^{-1}) was recorded in hill forests, and the highest (292.7 ha^{-1}) in freshwater marshes, and the overall mean density was 74.1 ± 5.2 (s.e.) ha^{-1} (Table 2). The most parsimonious model comprised landform factors, forest type and islands, supported by an AIC weight of 0.7 (Table 3). The model predicted highest densities in alluvial soil landforms (105.0 ha^{-1}), followed by landforms (karst, ridge, streambed, valley, 54.3 ha^{-1}) other than high ridge (35.6 ha^{-1}). Higher density was estimated for lowland forests (81.8 ha^{-1}) compared with other forest types (coastal, freshwater, hill and montane, 54.3 ha^{-1}). Highest densities were predicted for two islands – Choiseul (109.3 ha^{-1}) and Isabel (74.5 ha^{-1}) – followed by islands (Bougainville, Gatokae, Guadalcanal, New Georgia, Ranongga, Rendova, Tetepare, Vangunu, Vella Lavella, 54.3 ha^{-1}) other than Malaita (27.1 ha^{-1}) and Kolombangara (23.5 ha^{-1}) (Table 3, Fig. 3*m*).

Rana kreffti. The ground frog *R. kreffti* was recorded at nine transects on five islands. Highest (24.7 ha^{-1}) and lowest density per transect (6.2 ha^{-1}) was recorded in lowland forest. Average density per transect was 13.6 ± 0.7 (s.e.) ha^{-1} (Table 2). The model inferred a very slight difference in densities between areas of high (10.6 ha^{-1}) and low (10.8 ha^{-1}) understorey, or disturbed (11.8 ha^{-1}) and undisturbed (10.8 ha^{-1}) sites (Table 3, Fig. 3*n*). Surveys revealed that alternating wet channels, cyclic wetlands, seeps, streams, and river edges, temporary pools overgrown by *Cynodon dactylon* grass, garden edges, forest edges, and native forest were ideal habitat for *R. kreffti*. A combination of ridge landform and lowland forests was also predicted to have high densities (13.6 ha^{-1}) compared with other landforms and forest types (10.8 ha^{-1}). Population difference among islands revealed highest predicted density (14.9 ha^{-1}) on Gatokae Island, and other islands (Bougainville, Choiseul, Gatokae, Guadalcanal, Kolombangara, Malaita, New Georgia, Ranongga, Rendova, Tetepare, Vangunu, Vella Lavella, 10.8 ha^{-1}), and lowest on Isabel (6.9 ha^{-1}) Island (Table 3, Fig. 3*n*).

Discussion

Our data clearly indicated several trends. The most salient was that island, landform pattern and forest type affected the density of many frog species. For the most part, frog densities were greater on the larger islands (Bougainville, Choiseul, Isabel, Guadalcanal, Kolombangara Malaita, and New Georgia) than on small islands (Tetepare, Gatokae, Ranongga, Rendova, Vangunu, and Vella Lavella). Generally islands can have higher densities of frogs than mainland areas for single species (Rodda and Dean-Bradley 2002). A plausible explanation for such high density of frogs on large islands is the greater diversity of habitats, more large streams, and greater altitude affording greater resources on larger islands (Rodda and Dean-Bradley 2002). Research has already shown that increasing resource availability on islands can lead to higher carrying capacity, and higher densities for other frog species such as the rice frog (*Rana limnocharis*) (Wu and Murray 2006).

A consistent trend was found in how forest type affected all frog guilds. Four tree-dwelling species (*B. elegans*, *B. vertebralis*, *Pal. solomonis*, and *P. guppyi*) and two ground frogs (*D. malukuna* and *P. weberi*) had highest densities and occurred in very different forest types. For example, the highest densities of *Pal. solomonis* almost always occurred in hill forests, while *B. elegans* occurred in all forest types except coastal forest. Lowland forests yielded the highest densities of almost all species sampled. The complexity of such forests provides a variety of habitats suitable for all life cycle stages of different species (Hazell *et al.* 2001). For example, in Australia a variety of understorey plants in the riparian zone and other features such as the presence of palms significantly correlated with the richness and composition of frog assemblages (Parris and McCarthy 1999). The models including the factor ‘forest type’ are consistent with the finding of a previous study of frogs undertaken on Choiseul, where Morrison *et al.* (2008) recorded more frogs in lowland rainforests than hill and montane forests. In the present study most species occurred in lowland forests, although *Pal. solomonis* and *L. lutea* were found only in hill forest and montane forest, respectively. In addition, the attributes of forest area (e.g. areas of large intact forest compared with small forest patches) affected density of frogs; for example, large islands with larger forest areas had greater frog densities. Similarly, other studies in tropical South American forests recorded a higher abundance of frogs in large forest areas than in forest fragments (Marsh and Pearman 1997).

Species such as *Pal. solomonis*, *B. wolfi*, *C. guentheri*, *P. guppyi* and *P. neckeri* were found mainly in primary forest or overgrown secondary forests. In a previous study, Morrison *et al.* (2008) recorded *B. wolfi* in primary ridge forests at 800 m above sea level on the slopes of Mt Maetambe, Choiseul Island, which is consistent with this study, which showed this species to occur in transitional zones between lowland and mid-montane primary forests. Not all frog species occurred in intact forest. Some species like *L. thesaurensis*, *P. solomonis*, *P. weberi* and *R. kreffti* were found in roadside pools, in open garden areas, forest edges, trails and roads, tractor tracks, cassava patches, village edges, and generally in degraded forests. This attests to the generalist nature of these species.

For 11 of the 16 frog species, densities were affected by landform patterns. Frog densities were generally highest in alluvial soil landforms for six species (*C. guentheri*, *L. thesaurensis*, *P. guppyi*, *P. neckeri*, *P. solomonis*, *P. weberi*). Alluvial soil landforms dominate undisturbed lowland and freshwater marshes. Streams generally flowed in alluvial materials, which provided ideal habitats for frogs. In a study of landscape structure on frog occurrences and abundance it was found that local frog population densities were generally lower in agricultural landscapes than in natural forests (Johansson *et al.* 2005), and this is consistent with the results of this study. Additionally, some frogs in Australia are known to use alluvial soils with high organic content as call sites (Wardell-Johnson and Roberts 1993). The frogs *D. guppyi* and *D. bufoniformis* occurred mainly in riparian strips. These large aquatic frogs regularly perched on rocks catching insects. They use streams as retreat sites (Pikacha *et al.* 2008*b*).

Shrub cover, leaf litter, disturbance, and understorey cover were also important factors affecting frog densities. Shrub cover was important for two arboreal species – *B. vertebralis* and *Pal. solomonis* – as shrubs were used for perch sites. Variation between dense and sparse shrub cover reflected different disturbance regimes. Disturbed areas with greater sunlight penetrating to the forest floor allow dense shrub cover, while undisturbed forests with intact canopies and less sunlight reaching the forest floor had relatively sparse shrub growth. Shrub complexes in undisturbed forests are a critical terrestrial habitat necessary for tree frogs (Vos and Stumpel 1996). In Fiji, low-lying herbs and shrubs form perch plants for the Fiji tree frog (Osborne *et al.* 2008). For other species like wood frogs, shrub cover provides retreat and habitat cover (Egan and Paton 2004).

Ceratobatrachus guentheri is a versatile and well adapted species found in disturbed habitat (Menzies 2006; Pikacha *et al.* 2008*b*). Consequently it was not unexpected to find *C. guentheri* densities to be affected by forest floor factors such as leaf litter. Leaf litter and understorey are important features of habitat heterogeneity (Wanger *et al.* 2009), which support dense and diverse frog populations (Fauth *et al.* 1989). This ground frog occurred in higher densities in areas with thin leaf litter. Thick leaf litter occurred in more open secondary forests with large-leafed *Macaranga* sp., and *Campnosperma* sp. trees. Leaf litter is an important microhabitat for many arthropods and invertebrates that form the diet of many ground-dwelling frogs (Heinen 1992; Caldwell and Vitt 1999). This microhabitat is also important to the species' life cycle (Scott 1976). It is likely that leaf litter provides retreat sites for *C. guentheri* (Pikacha 2008).

Palmatorappia solomonis was one of two species listed as vulnerable on the IUCN Red List (Richards and Parker 2004*b*). *Pal. solomonis* is restricted to Isabel (Brown 1952; Pikacha *et al.* 2008*a*), Bougainville (Brown 1952; Pikacha 2008), and Choiseul (Morrison *et al.* 2008), and is typical of many insular species being restricted to a few islands (Paulay 1994). This species was recorded only in hill forest on Isabel. The World Wildlife Fund for Nature (Solomon Islands) also reported this species in primary lowland forests in surveys in the upper Kolombangara River catchment on south-west Choiseul (Pikacha and Sirikolo 2009), where the forest was dominated by hardwoods and a wet and lush understorey cover (McClatchey *et al.* 2005; Pikacha and Sirikolo 2009). These results were also consistent with that of Morrison *et al.* (2008), who recorded populations of *Pal. solomonis* at Sarelata on north Choiseul at 500 m above sea level in primary undisturbed hill forest.

In this study *L. lutea* was recorded only at one site in high ridge forest on the summit of Mt Mariu (885 m above sea level) on Gatokae Island. The site was undisturbed montane and hill forest. Intact forests offer ideal climatic conditions (Pounds *et al.* 1999), breeding habitats (Stewart 1985), and perch sites (Gillespie and Hollis 1996; Osborne *et al.* 2008) for frogs. Pikacha (2008) previously reported this species in lowland forests at a single site in the Mango Bay catchment of south-east Choiseul, although Morrison *et al.* (2008) did not locate this species during extensive surveys around the island. *L. lutea* is reported to be vulnerable to extinction on the IUCN Red List (Richards and Parker 2004*a*), which was consistent with the findings in this study.

The densities of *D. guppyi*, *D. bufoniformis*, and *D. malukuna* were highest within lowland and along streams. Pikacha (2008) also reported densities of these frogs to be highest near aquatic habitats. These three species are widespread in the Solomon Islands (Morrison *et al.* 2008; Pikacha 2008; Pikacha and Sirikolo 2010). *D. guppyi* and *D. bufoniformis* were found within 10 m of waterways, where they perched on rocks. The area was dominated by rotting and waterlogged fallen branches, and logs providing thick cover. Other studies have found *D. guppyi* to be abundant along river gullies, valleys, riverbanks, cave systems, riparian forests and hilly forests (Read and Moseby 2006; Sirikolo and Pikacha 2011). The present study recorded *D. guppyi* at 700 m above sea level on Gatokae but none above this altitude. This is consistent with the result of a previous survey, which noted them absent at altitudes above 1000 m above sea level in areas that lacked extensive surface water on New Britain (Foufopoulos and Richards 2007). In comparison, *D. bufoniformis* was recorded only in lowland forests, while *D. malukuna* was found in lowland to montane forests, which is consistent with the recorded locations of the holotype specimens collected by Preston Webster on 2 July 1968, at 800 m above sea level at Malukuna Village on Guadalcanal (Scoville 2012).

One unknown species was recorded during these surveys. *Platymantis* sp. was first discovered in montane forests on Gatokae Island (Pikacha 2008). Densities for this species were higher on Gatokae Island than other islands (including larger islands). More sampling is needed in montane forests on other islands.

Finally, this present study suggests that population of frogs are higher in undisturbed forests than in disturbed forest. The conservation of frogs of the Solomon Islands should include effectively maintaining natural vegetation characteristics of the representative forest types of the archipelago. Some species, such as the *Discodeles* frogs, were more common in waterways, therefore maintaining clean water catchments is important for some species.

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