

Impact of the invasive plant, *Lantana camara*, on bird assemblages at Malé Mahadeshwara Reserve Forest, South India

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Abstract: *Lantana camara* is an invasive species that is widespread in India. Using birds as an indicator taxon, we investigated whether *Lantana* invasion was correlated with changes in ecosystem health of the moist and dry deciduous forests at the Malé Madeshwara Hills, Karnataka. We studied *Lantana* at four densities, low, medium, and high, and a no-*Lantana* control. Bird species diversity, species richness, and abundance were lower at high densities of *Lantana* in both forest types. Evenness increased with increase in *Lantana* density. To better understand the observed changes in bird community composition, we segregated birds into 2 guild types: microhabitat guilds and foraging guilds. An increase in *Lantana* density was correlated with a decline in canopy birds (of the canopy microhabitat guilds) and insectivores (of the insectivore foraging guilds). Our results suggest that *Lantana* affects the structure of the bird community by decreasing diversity, and that *Lantana* affects certain guilds more than others.

Resumen: *Lantana camara* es una especie invasora ampliamente distribuida en la India. Usando a las aves como un taxón indicador, investigamos si la invasión de *Lantana* estaba correlacionada con cambios en la salud ecosistémica de los bosques húmedos y secos caducifolios en las Colinas Male Madeshwara, Karnataka. Estudiamos *Lantana* a cuatro densidades, baja, media y alta y un testigo sin *Lantana*. La diversidad, la riqueza y la abundancia de especies de aves fueron menores cuando la densidad de *Lantana* era alta en ambos tipos de bosque. La equitatividad se incrementó conforme aumentó la densidad de *Lantana*. Para comprender mejor los cambios observados en la composición de la comunidad de aves, segregamos a las aves en dos tipos de gremios: gremios de microhábitat y gremios de forrajeo. El incremento en la densidad de *Lantana* se correlacionó con un decremento en las aves del dosel (de los gremios de microhábitat de dosel) e insectívoros (de los gremios de forrajeo insectívoros). Los resultados sugieren que *Lantana* afecta a la estructura de la comunidad de aves reduciendo su diversidad, y que afecta más a ciertos gremios que a otros.

Resumo: A *Lantana camara* é uma espécie invasiva muito espalhada na Índia. Utilizando as aves como um Taxa indicador, investigou-se se a invasão da *Lantana* estava correlacionada com as mudanças na saúde do ecossistema da floresta húmida e seca decídua nas colinas de Malé Madeshwara, Karnataka. Estudou-se a *Lantana* em quatro densidades, baixa, média e alta e sem lantana como controlo. A diversidade específica em aves, a riqueza específica, e a

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abundância eram baixas nas altas densidades de *Lantana* em ambos os tipos florestais. A semelhança aumentou com o acréscimo na densidade de *Lantana*. Para melhor compreender as alterações observadas na composição da comunidade de aves, separámos as aves em dois tipos de estratos: o do grupo do microhabitat e o das forrageadoras. Um aumento na densidade da *Lantana* apresentava-se correlacionado com o declínio nas aves da copa (da copa no estrato do microhabitat) e insectívoras (no estrato das forrageadoras insectívoras). Os nossos resultados sugerem que a *Lantana* afecta a estrutura da comunidade de aves pelo decréscimo da diversidade, e que os efeitos da *Lantana* afectam mais certos estratos do que outros.

Key words: Bird diversity, guilds, indicator taxa, invasion, *Lantana camara*.

Introduction

Declining biodiversity is one of the most dramatic and irreversible aspects of anthropogenic global change, and biological invasions are believed to be the second largest cause of current biodiversity loss after habitat destruction (Cronk & Fuller 1995; Usher 1991; Vitousek *et al.* 1996). Most studies have looked at the impact of invasion in general on vegetation structure, and have attempted to test the diversity-stability hypothesis (Elton 1958), and the diversity-invasibility hypothesis (Case 1990; Law & Morton 1996; Rejmanek 1989, 1996; Tilman 1997). It is also shown that exotic species invasions influence distribution and abundance of native species (D'Antonio & Vitousek 1992; Vitousek *et al.* 1987), and affect regeneration of native flora (Tireman 1916). Exotic plant species can also divert pollinators and dispersers of native species towards themselves, thus hindering the reproductive success of native species (Brown *et al.* 2002; Feinsinger 1987; Schurkens & Chittka 2001)

Lantana camara L. (Verbenaceae; hereafter, *Lantana*), a native of tropical America (Holm *et al.* 1977), is found in 47 countries and has been described as one of the world's ten worst weeds (Cronk & Fuller 1995). It has invaded millions of hectares of grazing land globally and is of serious concern for the production of 14 major crops including coffee, tea, rice, cotton and sugarcane (Day *et al.* 2003). *Lantana* berries attract frugivorous birds and mammals that help to disperse its seeds widely. *Lantana* forms dense, impenetrable thickets that smother native vegetation and pasture (Day *et al.* 2003).

Lantana was introduced to India in 1807 as an ornamental plant at the National Botanical Garden of Calcutta (Thakur *et al.* 1992). It soon escaped into the wild and has established itself all over

the Indian subcontinent, stretching from the submontane regions of the outer Himalayas to the southernmost part of India. Previous studies on *Lantana* in India have mainly focused on its physiology and its impact on pollination (Mathur & Mohan Ram 1986), but there have been very few studies done with respect to the ecological impact of *Lantana* at larger scales (Hegde *et al.* 1996; Murali & Setty 2001; Raizada *et al.* 2008).

The spread of *Lantana* in forests is a special cause for concern as it may change forest structure and composition, affecting native species assemblages (Aravind *et al.* 2006). *Lantana* can outcompete native plants because it can grow on nutritionally poor soils (Bhatt *et al.* 1994). *Lantana* flowers year-round and the large amounts of nectar it produces could draw away potential pollinators (Brown *et al.* 2002; Schurkens & Chittka 2001). *Lantana* alters forest structure by replacing the native understorey species, and this, in turn, can affect the distribution and behaviour patterns of animal populations.

There are very few studies that have looked at the impact of invasive plants on fauna (Knops *et al.* 1999). In this study, we assess the impact of *Lantana camara* on birds. Birds are considered to be good indicators of ecosystem health because they are easily identified and are known to be sensitive to changes in the ecosystem (Blair 1996). Our main objective was to assess the impact of *Lantana* on bird species richness and diversity, and to assess changes in bird guild composition under different levels of *Lantana* invasion.

We expected birds to respond to change in forest structure due to the presence of *Lantana* in different ways based on their individual preferences. Since *Lantana* changes the structure of the forest within a relatively short time, we expected that highly mobile animals such as birds would

respond by moving to more preferred habitats within the same forest type. Hence, we expected changes in species diversity, species richness, evenness, and abundance with an increase in *Lantana* density. Furthermore, following the established trends of changes in diversity with respect to disturbance, we expected highest diversity values in areas of intermediate *Lantana* density. Here we consider *Lantana* not only as an agent of niche change but also as a source of disturbance.

We also expected different guilds of birds to respond differently to *Lantana* presence. Birds can be categorized based on two types of guild schemes: (1) foraging guilds composed of insectivores, nectarivores, frugivores, omnivores, carnivores and granivores; and (2) microhabitat guilds composed of open-area birds, canopy birds, ground birds and undergrowth birds. With respect to foraging guilds, we expected an increase in the number of insectivores, nectarivores and frugivores with an increase in *Lantana* density, since *Lantana* is known to produce high nectar-content flowers as well as berries all year round, thereby attracting more insect and nectar-feeding birds as well as frugivores. We expected little or no change in the other categories of foraging guilds. With respect to microhabitat guilds, we expected a decrease in open-area birds and undergrowth birds since an increase in *Lantana* density implies that the structure of the forest is more closed and this makes it difficult for these birds to move around freely. We expected little or no change in canopy birds with change in the density of *Lantana* since *Lantana* rarely reaches the canopy of the forest.

Materials and methods

Study site

We conducted this study in the Malé Mahadeshwara Hills (MM Hills) range, which is located in Chamara Nagar District, Karnataka, India, along the junction of the Eastern and Western Ghats, the two most biologically diverse ranges of South India (Fig. 1). The MM Hills range lies between 11° 55' and 12° 13' N and between longitudes 77° 30' to 77° 47' E. The area under the MM Hills Reserve Forest is around 291 km², with highly undulating terrain.

The area has a mild climate throughout the year. The months of April and May are the hottest, with temperatures reaching 40 °C, while the months of December and January are the coldest with minimum temperatures as low as 13 °C. The

MM Hills receive rainfall from the northeast as well as the southwest monsoon. However, most of the rain is derived from the northeast monsoon during September and October. The different types of vegetation found in the MM Hills reserve forest are dry deciduous forest (64.34 %), scrub woodland (20.50 %), and moist deciduous and riparian forest (2.47 %) (Uma Shaanker *et al.* 2005). These forests harbour about 25 species of mammals, 150 species of birds, 80 species of butterflies, and 700 species of angiosperms (Aravind *et al.* unpublished.).

There are about 12 human settlements scattered within the reserve forest limits. The communities depend on non-timber forest product (NTFP) harvesting, quarrying, and daily wage labour for basic livelihood. The MM Hills forest is highly disturbed due to a variety of human activities such as agriculture, quarrying, NTFP harvesting, fuelwood collection, road construction, etc. (Uma Shaanker *et al.* 2005).

For the present study we selected two vegetation types in MM Hills, the dry deciduous forest and the moist deciduous forest. In both these forest types *Lantana* invasion is very high compared to in the scrub woodland. *Lantana* presence was classified into three categories (low, medium and high) based on total cover by visual estimation. *Lantana* cover of 10-30 % was categorised as low, 30-60 % as medium, and > 60 % as high. Plots were laid at random in areas that had been visually identified as having varying *Lantana* density, and in areas without *Lantana*. A total of twelve, 50 x 50 m plots, i.e., three plots for each category of *Lantana* density were laid. Plots were separated by a minimum distance of 300 m. We counted the number of stems of *Lantana* per plot and used a Chi-square test of goodness-of-fit to compare the visual estimation of *Lantana* cover to actual stem counts.

Bird sampling

Birds were observed using the point count method. All birds seen and heard within a 50 m radius were recorded. Each observation lasted for 5 minutes with 10-minute intervals between observations (Krebs 1989) for a total of four observations per hour. Sampling was carried out 3 times per plot per season. The seasons in which bird observations were conducted were summer (March-April), early monsoon (September-October) and winter (December-January). All birds were identified based on Ali & Ripley (1983). All sampling was carried out during 2000 and 2001, and a single observer was in charge of all data

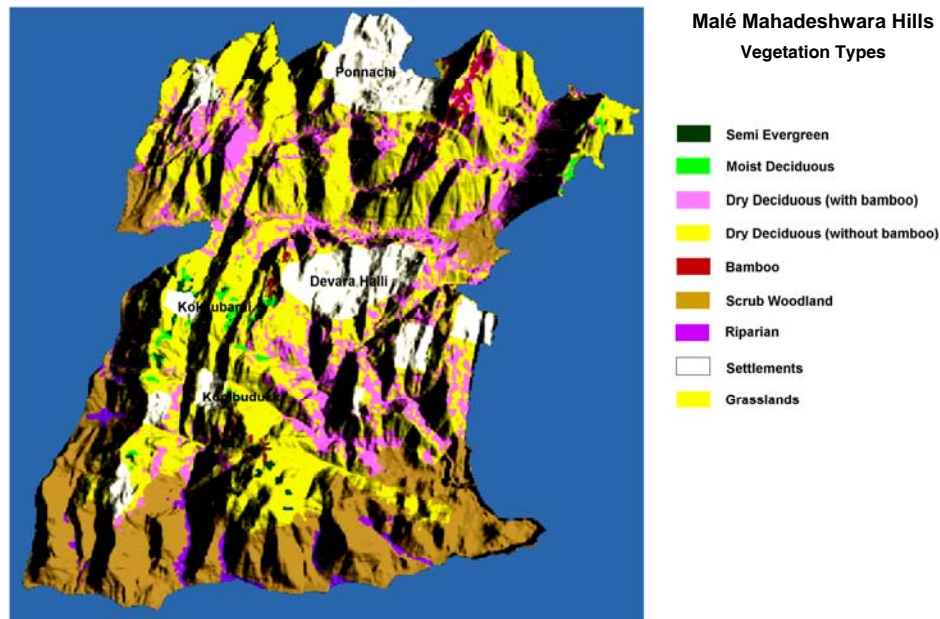


Fig. 1. Digital Elevation Map of the MM Hills Reserve Forest (Inset: location of MM Hills in south India). The map is derived from IRS 1D LISS III imagery acquired on April 15th 1999 and digital elevation model is derived from the contour lines of 1:25,000 Survey of India toposheets.

collection. Subsequently, data from the 3 seasons were pooled for further analysis.

Several diversity measures have been calculated for the data collected (see Statistical analysis) and these measures provide basic information about bird community structure associated with different levels of *Lantana* invasion. However, these diversity measures provide only partial information about the structure of the community. Therefore, birds were also classified into two guild schemes related to feeding habits and to microhabitat preference based on our observations and on the available literature. The feeding guilds include insectivores, frugivores, nectarivores, granivores, omnivores and carnivores (Ali & Ripley 1983) and the microhabitat preference guilds are based on habitats occupied by the birds, i.e., whether canopy, open area, ground or understorey. This separation into guilds along different axes provides further insight into how bird communities change in association with varying *Lantana* density.

Statistical analysis

We pooled all the data from each plot according to forest type (i.e., dry deciduous and moist deciduous) and *Lantana* category (i.e. control, low,

medium, high) in order to compute diversity measures of community structure. Diversity was computed using the Shannon-Weiner index (Magurran 1988):

$H' = - \sum p_i * \log(p_i)$; where, p_i is the proportion of the i^{th} species

Since all the plots were of the same dimension, we calculated species richness as the total number of species present per plot (Ludwig & Reynolds 1988), and abundance as the total number of individuals per plot. Evenness was calculated according to the following equation:

$Evenness = H'/H'_{max}$; where, H' is the Shannon Diversity and H'_{max} is the total number of species recorded.

To determine the impact of *Lantana* on bird diversity measures, we analysed bird diversity using an ANCOVA, with forest type as covariate. The dependent variables were species richness, species abundance, Shannon diversity index and evenness, and the independent variable was the density of *Lantana* stems in the plots.

For the guild analysis, we segregated all the recorded species based on guilds. Subsequently we analysed the number of individuals of each guild recorded in all the plots. We conducted an ANCOVA with the number of individuals as the dependent

variable, *Lantana* density as the independent variable, and forest type as the covariate. In case of significant results, subsequent post-hoc analyses were conducted using the Tukey HSD method.

Regression analysis was performed to assess the response of the ten most abundant species of birds with increase in *Lantana* density. This analysis was done for both moist deciduous and dry deciduous forests.

Species abundance curves were computed for birds in different densities of *Lantana* in both the vegetation types using BioDiversity Pro Software for Windows (<http://the-natural-history-museum-the-scottish.software.informer.com/>). The input variables were abundance of species at each density of *Lantana*.

Results

Lantana cover and density

There was a significant correspondence between visual estimation of *Lantana* cover and the total number of stems of *Lantana* in the plots ($\chi^2 = 21.56$, $p < 0.0001$, $df = 3$; Fig. 2). Therefore, we used *Lantana* stem density rather than visually estimated *Lantana* cover in subsequent analyses.

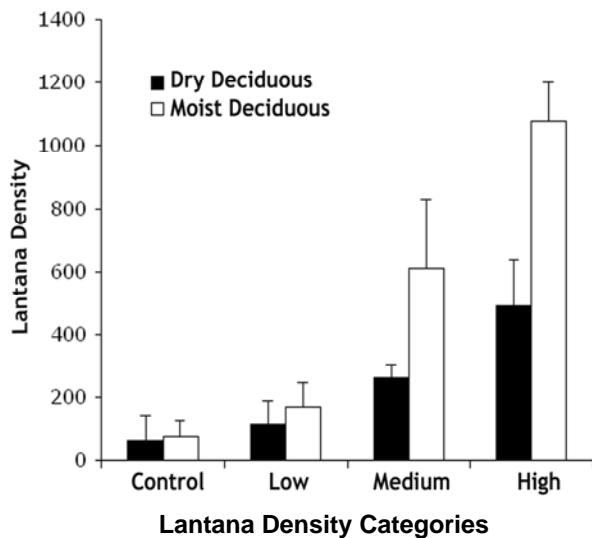


Fig. 2. Correspondence between the categorisation of *Lantana* density based on visual estimation of *Lantana* cover and the number of *Lantana* stems recorded in plots laid in each of the visually estimated *Lantana* categories. *Lantana* density denotes average number of stems per 2500 m² plot (n=3 plots per category).

There was a significant decrease in the density of *Lantana* stems as tree cover increased. This was observed both in the dry-deciduous ($R^2 = 0.69$, $p < 0.001$, $n = 12$), as well as the moist-deciduous ($R^2 = 0.71$, $p < 0.001$, $n = 12$) forest types.

Lantana density and bird community structure

A total of 5706 individuals belonging to 102 bird species were recorded during the study period. Of these, 2524 individuals of birds belonging to 65 species were recorded in the moist deciduous forest and 3184 individuals of birds belonging to 85 species were recorded in dry deciduous forest across all *Lantana* densities. *Lantana* density was significantly related to the diversity parameters for birds in both dry deciduous (Fig. 3) and moist deciduous (Fig. 4) forest. Irrespective of the forest type, as the *Lantana* density increased, there was a significant decline in species richness, abundance, and species diversity (Shannon-Wiener index; Table 1). However, there was a significant increase in the evenness of the species recorded (Table 1).

Computed species-abundance curves for birds in dry deciduous forest showed that the community is almost saturated. In moist-deciduous forest, on the other hand, the community is yet to saturate, and this was the case at all densities of *Lantana* (Fig. 5).

Among the microhabitat guilds, only the canopy birds responded significantly to an increase in *Lantana* density (Table 2). Among the foraging guilds, there was a significant decline in the number of insectivores with an increase in *Lantana* density (Table 2). The other guilds did not show a significant response to the presence of *Lantana*.

Relation between dominant bird species and *Lantana* density

Of the 95 species of birds recorded, 88 species have been identified to species level (see Appendix Table 1) and the remainder up to the genus or group. Of these, 48 species were common to both vegetation types, 30 species were unique to dry deciduous forest and 13 species were unique to moist deciduous forest. Among dominant species, five species of frugivores, namely, the red-whiskered bulbul, common iora, Tickell's flower-pecker, whitebrowed bulbul, and red-vented bulbul were common to both vegetation types.

Among frugivorous birds, the densities of white-browed bulbuls and red-vented bulbuls increased

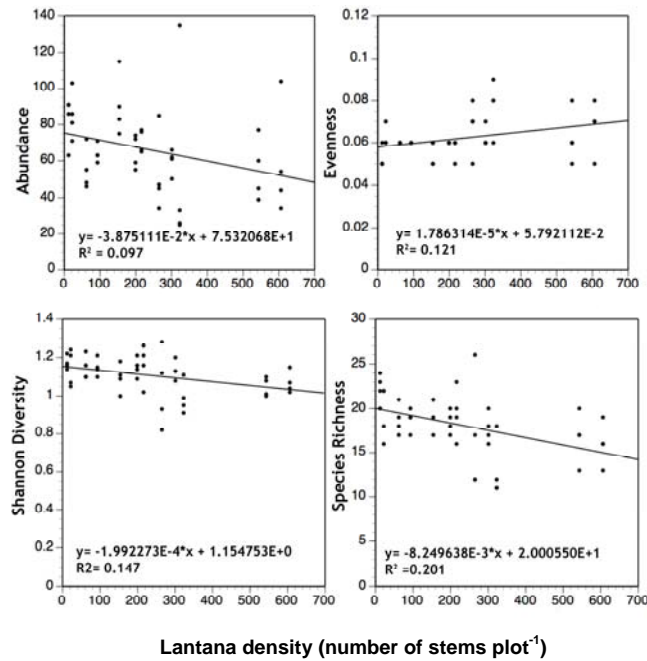


Fig. 3. Relationship between diversity parameters of birds as a function of *Lantana* density (number of stems per 2500 m² plot) in dry deciduous forest (n=3 replicate plots per *Lantana* density category).

significantly with an increase in *Lantana* density in moist deciduous forest (Table 3), whereas in dry deciduous forest the density of red-whiskered bulbuls increased significantly with an increase in *Lantana* density (Table 3). The density of the Malabar shama, common iora, and small green barbet decreased significantly in moist deciduous forest (Table 3) as *Lantana* density increased. In dry deciduous forest, on the other hand, densities of the Indian robin, purple sunbird, tailorbird, and purple-rumped sunbird decreased significantly as *Lantana* density increased (Table 3).

Discussion

Birds are good bio-indicators of ecosystem health (Blair 1996) and are also most likely to be affected by the increase in *Lantana* density. For example, *Lantana*'s fruits are fleshy and available year-round, making them an ideal food source for frugivores such as bulbuls, who are one of the main dispersers of *Lantana* seeds. Furthermore, *Lantana* forms dense thickets in the understorey (Holm *et al.* 1977), thereby altering the structure of the forest. Thus it is expected that birds would be one of the taxa most affected by presence of *Lantana*.

We had expected that at low levels of *Lantana* invasion there would be little or no impact on the bird species diversity, i.e., the diversity of birds would more or less reflect the 'background' diversity seen in these patches. At increasing levels of *Lantana* density, the system seems to be affected as is seen by the decrease in diversity. At the highest density of *Lantana*, there is a drop in the diversity values, implying that there is a definite impact of *Lantana* density. An important indicator of change in diversity parameters between the levels of *Lantana* density is seen with respect to evenness (Table 1). In both forest types, evenness of species increased. This, combined with the general decline in diversity, suggests that increase in *Lantana* density benefits a few species, thus leading to greater homogeneity. Such biotic homogenization in relation to invasion by alien species has also been shown to occur in several other taxa such as plants (Hejda *et al.* 2009), ants (Holway & Suarez 2006), and fish (Olden *et al.* 2004).

While patterns of diversity do tell us something about the changes in the structure of the community, it is difficult to know what mechanisms underlie these changes. Hence an analysis of feeding and microhabitat guilds could be more useful in determining the nature of *Lantana*'s impact on the

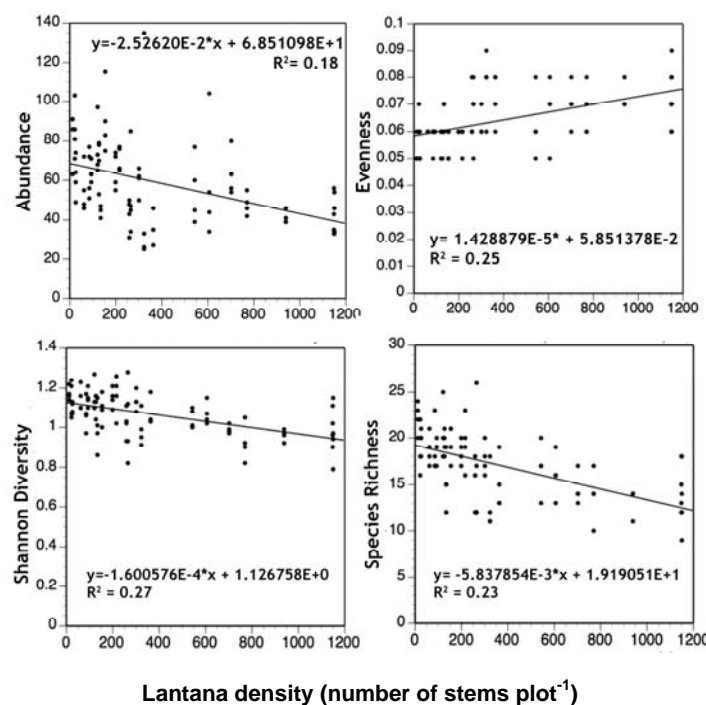


Fig. 4. Relationship between diversity parameters of birds as a function of *Lantana* density (number of stems per 2500 m² plot) in moist deciduous forest (n=3 replicate plots per *Lantana* density category).

ecosystem. We expected the omnivore and the frugivore guilds to increase in response to increased *Lantana* density, as *Lantana* provides a new food source, and we expected the insectivorous birds to decrease because dense *Lantana* thickets act as barriers to fast flight associated with these insectivorous birds that feed in mid-air (e.g., drongos and flycatchers). However, only the insectivores showed a marked response to the presence of *Lantana*, with a significant decline in areas of high *Lantana* density.

Table 1. Results of ANCOVA for different diversity parameters for birds in relation to *Lantana* density in moist and dry deciduous forests. The dependent variables were species richness, abundance, Shannon diversity index and evenness, and the independent variable was the density of *Lantana* stems in the plots; forest type was treated as a covariate.

| Parameters | df | Sum of Squares | F ratio | p |
|-------------------|------|----------------|---------|----------|
| Species Richness | 2,95 | 297.25 | 34.77 | < 0.0001 |
| Abundance | 2,95 | 4176.05 | 12.24 | < 0.001 |
| Evenness | 2,95 | 0.002 | 32.76 | < 0.0001 |
| Shannon Diversity | 2,95 | 0.186 | 23.98 | < 0.0001 |

Microhabitat guilds also proved to be useful in revealing a response to *Lantana* invasion. Ground, understory and open-area birds, which are expected to be the most affected by the increase in *Lantana* density, did not show any changes. However, canopy specialists decreased in both forest types. This is a counterintuitive, since *Lantana* is an understory species and, in principle, should have had little or no impact on canopy species. The reason for the decrease in canopy birds may be attributed to the overlap between canopy birds and insectivorous birds. Furthermore, the decrease in canopy specialists could also be related to disturbance that presumably preceded invasion by *Lantana*. We observed a negative correlation between *Lantana* density and tree cover in both vegetation types, which would further support this explanation. Thus, a decline in canopy birds could be related to a decline in tree cover rather than to presence of *Lantana* and is in accordance with studies from northern India (Raizada *et al.* 2008).

To our surprise, densities of the two frugivorous birds of open habitats, white-browed bulbul and red-vented bulbul, significantly increased with increase in *Lantana* in moist deciduous forest (Table 3). On the other hand, in dry deciduous for-

est, it was the density of the red-whiskered bulbul - a frugivore that prefers dense forest - that increased significantly (Table 3). These species could be used as indicators of habitat change due to invasion of *Lantana*.

There are indications that *Lantana* invasion is significantly correlated with changes in bird assemblages - both diversity and community structure in the Malé Mahadeshwara Reserve Forest. Decrease in diversity estimates was a consistent pattern in both the vegetation types that we studied.

Repeated sampling over a longer period of time could be crucial in determining patterns at a larger scale. Birds respond in different ways to the presence of *Lantana*, and it may be more relevant to choose a particular species or guild as a bio-indicator rather than the entire community, based on the questions addressed. We suggest that future studies should focus on either insectivores or canopy birds in determining the exact nature of *Lantana*'s impact.

Table 2. Results of ANCOVA for different guilds of birds in relation to *Lantana* density. The numbers of individuals in each microhabitat and feeding guild were used as the dependent variables and *Lantana* density was the independent variable, with forest type as the covariate. In case of significant results, subsequent post-hoc analyses were conducted using the Tukey HSD method.

| | Guild | Nparm | df | Sum of Squares | F Ratio | p |
|--------------|-------------|-------|----|----------------|---------|----------|
| Microhabitat | | | | | | |
| | Open | 3 | 3 | 13.36 | 3.52 | 0.02 |
| | Ground | 3 | 3 | 0.33 | 0.23 | 0.87 |
| | Canopy | 3 | 3 | 156.25 | 13.96 | < 0.01* |
| | Understorey | 3 | 3 | 14.78 | 1.98 | 0.12 |
| Feeding | | | | | | |
| | Carnivore | 3 | 3 | 0.11 | 0.03 | 0.99 |
| | Frugivore | 3 | 3 | 12.11 | 2.15 | 0.09 |
| | Granivore | 3 | 3 | 1.71 | 1.75 | 0.16 |
| | Insectivore | 3 | 3 | 224.54 | 15.99 | < 0.01** |
| | Nectarivore | 3 | 3 | 1.50 | 1.83 | 0.14 |
| | Omnivore | 3 | 3 | 0.03 | 0.03 | 0.99 |

* Tukey HSD, $Q = 2.6$, $\alpha = 0.05$; ** Tukey HSD, $Q = 2.8$, $\alpha = 0.05$

Table 3. Relationship (Pearson's correlation) between *Lantana* density and abundance of the ten most abundant species of birds in dry deciduous and moist deciduous forests (df = 10).

| Dry Deciduous Forest | | | Moist Deciduous Forest | | |
|------------------------|--------|------------|------------------------|--------|------------|
| Species | r | p | Species | r | p |
| red-whiskered bulbul | 0.769 | $p < 0.01$ | red-whiskered bulbul | -0.569 | NS |
| common iora | -0.041 | NS | common iora | -0.615 | $p < 0.05$ |
| Tickell's flowerpecker | -0.375 | NS | Tickell's flowerpecker | 0.204 | NS |
| white-browed bulbul | 0.417 | NS | white-browed bulbul | 0.618 | $p < 0.05$ |
| red-vented bulbul | -0.426 | NS | red-vented bulbul | 0.802 | $p < 0.01$ |
| whiteheaded babbler | -0.282 | NS | leaf warbler | -0.482 | NS |
| purple sunbird | -0.727 | $p < 0.01$ | small green barbet | -0.661 | $p < 0.02$ |
| tailorbird | -0.603 | $p < 0.05$ | magpie robin | -0.299 | NS |
| Indian robin | -0.695 | $p < 0.02$ | Blyth's reed warbler | -0.069 | NS |
| purple-rumped sunbird | -0.669 | $p < 0.02$ | Malabar shama | -0.75 | $p < 0.01$ |

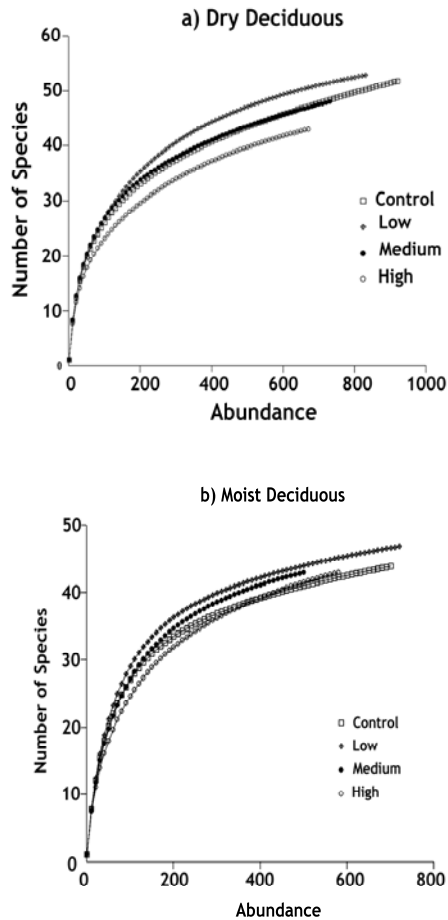


Fig. 5. Computed species-abundance curves for birds associated with different densities of *Lantana* in (a) dry deciduous and (b) moist deciduous forest.

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References

Ali, S. & S.D. Ripley. 1983. *Handbook to the Birds of India and Pakistan* (Compact edn.). Oxford University Press and BNHS, New Delhi.

Aravind, N.A., Dinesh Rao, G. Vanaraj, K.N. Ganeshaiyah, R. Uma Shaanker & J.G. Poulsen. 2006. Impact of *Lantana camara* on plant communities at

Malé Mahadeshwara reserve forest, South India. pp. 1-12. In: L.C. Rai & J.P. Gaur (eds.) *Invasive Alien Species and Biodiversity in India*. Banaras Hindu University, Varanasi.

Bhatt, Y.D., Y.S. Rawat & S.P. Singh. 1994. Changes in ecosystem functioning after replacement of forest by *Lantana* shrubland in Kumaun Himalaya. *Journal of Vegetation Science* **5**: 67-70.

Blair, R.B. 1996. Land use and avian species diversity along an urban gradient. *Ecological Applications* **6**: 506-519.

Brown, B.J., R.J. Mitchell & S.A. Graham. 2002. Competition for pollination between an invasive species (purple loosestrife) and a native congener. *Ecology* **83**: 2328-2336.

Case, T.K. 1990. Invasion resistance arises in strongly interacting species-rich model competition communities. *Proceedings of National Academy of Sciences* **87**: 9610-9614.

Cronk, Q.C.B. & J.L. Fuller. 1995. *Plant Invaders*. Chapman and Hall, London.

D'Antonio, C.M. & P.M. Vitousek. 1992. Biological invasion by exotic grasses, the grass/fire cycle and global climate change. *Annual Review of Ecology and Systematics* **23**: 63-87.

Day, M.D., C.J. Wiley, J. Playford & M.P. Zalucki. 2003. *Lantana: Current Management Status and Future Prospects*. Australian Centre for International Agricultural Research: Canberra.

Elton, C.S. 1958. *The Ecology of Invasions by Animals and Plants*. Methuen and Co. London.

Feingsinger, P. 1987. Effects of plant species on each other's pollination: Is the community structure influenced? *Trends in Ecology and Evolution* **2**: 123-126.

Hegde, R., S. Suryaprakashi, L. Achoth & K.S. Bawa. 1996. Extraction of forest products in the forests of Biligirirangan Hills, India. 1: Contribution to rural income. *Economic Botany* **50**: 243-251.

Hejda, M., P. Pyšek & V. Jarošík. 2009. Impact of invasive plants on the species richness, diversity and composition of invaded communities. *Journal of Ecology* **97**: 393-403.

Holm, L.G., D.L. Plucknett, J.V. Pancho & J.P. Herberger. 1977. *The World's Worst Weeds*. University Press of Hawaii, Honolulu.

Holway, D.A. & A.V. Suarez. 2006. Homogenization of ant communities in mediterranean California: The effects of urbanization and invasion. *Biological Conservation* **127**: 319-326.

Knops, J.M.H., N.M. Haddad, S. Naeem, C.E. Mitchell, J. Haarstad, M.E. Ritchie, K.M. Howe, P.B. Reich, E. Siemann & J. Groth. 1999. Effects of plant rich-

- ness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecology Letters* **2**: 286-293.
- Krebs, C.J. 1989. *Ecological Methodology*. Harper and Row, New York.
- Law, R. & R. D. Morton. 1996. Permanence and the assembly of ecological communities. *Ecology* **77**:762-775.
- Ludwig, J.A. & J.F. Reynolds. 1988. *Statistical Ecology. A Primer on Methods and Computing*. John Wiley & Sons, New York.
- Magurran, A. 1988. *Ecological Diversity and its Measurement*. Croom Helm, London.
- Mathur, G. & H.Y. Mohan Ram. 1986. Floral biology and pollination of *Lantana camara*. *Phytomorphology* **36**: 79-100.
- Murali, K.S. & R. Siddappa Setty. 2001. Effect of weeds *Lantana camara* and *Chromelina odorata* growth on the species diversity, regeneration and stem density of tree and shrub layer in BRT sanctuary. *Current Science* **80**: 675-678.
- Olden, J.O., N. L. Poff, M. R. Douglas, M.E.E. Douglas & K.D. Fausch. 2004. Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology and Evolution* **19**: 18-24.
- Raizada, P., G.P. Sharma & A.S. Raghubanshi. 2008. Ingress of *Lantana* in dry tropical forest fragments: Edge and shade effects. *Current Science* **94**: 180-182.
- Rejmanek, M. 1989. Invasibility of plant communities. pp. 369-388. In: J.A. Drake, H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmanek & M. Williamson (eds.) *Biological Invasions*. John Wiley and Sons, New York.
- Rejmanek, M. 1996. Species richness and resistance to invasion. pp. 153-172. In: G.G. Orians, R. Dirzo & J.H. Cushman (eds.) *Biodiversity and Ecosystem Processes in Tropical Forests*. Springer, Berlin.
- Schurkens, S. & L. Chittka. 2001. The significance of the invasive crucifer species *Bunias orientalis* (Brassicaceae) as a nectar source for central European insects. *Entomologia Generalis* **25**: 115-120.
- Thakur, M.L., M. Ahmad & R.K. Thakur. 1992. *Lantana* weed (*Lantana camara* var. *aculeata* Linn.) and its possible management through natural insect pests in India. *Indian Forester* **118**: 466-488.
- Tilman, D. 1997. Community invisibility, recruitment limitation and grassland biodiversity. *Ecology* **78**: 81-92.
- Tireman, H. 1916. *Lantana* in the forests of Coorg. *Indian Forester* **42**: 385-392.
- Uma Shaanker, R., K.N. Ganeshaiah, Smitha Krishnan, R. Ramya, C. Meera, N.A. Aravind, Aravind Kumar, Dinesh Rao, G. Vanaraj, J. Ramachandra, R. Gathier, J. Ghazoul, N. Poole & B.V. Chinnapa Reddy. 2004. Livelihood gains and ecological costs of NTFP dependence: assessing the roles of dependence, ecological knowledge and market structure in three contrasting human and ecological setting in south India. *Environmental Conservation* **31**: 242-253.
- Usher, M.B. 1991. Biological invasions into tropical nature reserves. pp. 21-34. In: P.S. Ramakrishnan (ed.) *Ecology of Biological Invasions in the Tropics*. International Scientific Publications, New Delhi.
- Vitousek, P.M., C.M. D'Antonio, L.L. Loope & R. Westbrooks. 1996. Biological invasions as global environmental change. *American Scientist* **84**: 468-478.
- Vitousek, P.M., L.L. Loope & C.P. Stone. 1987. Introduced species in Hawaii: Biological effects and opportunities for ecological research. *Trends in Ecology and Evolution* **2**: 224-227.

Appendix Table 1. List of bird species along with their abundances recorded in the two vegetation types across all *lantana* densities. Also shown is the classification of each species by feeding (G= granivore, F= frugivore, I= insectivore, N= nectarivore, C= carnivore, O= omnivore) and microhabitat (O= open, C=canopy, U=understorey, G= ground) guild.

| Family | Common Name | Scientific Name | Guilds | | Vegetation | |
|--------------|-----------------|-----------------------------|---------|---------------|---------------|-----------------|
| | | | Feeding | Micro habitat | Dry deciduous | Moist deciduous |
| Accipitridae | Shikra | <i>Accipiter badius</i> | C | O | 3 | 1 |
| Phasianidae | Red Spurfowl | <i>Galloperdix spadicea</i> | O | G | 4 | 1 |
| | Grey Junglefowl | <i>Gallus sonneratii</i> | O | G | 20 | 27 |

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Appendix Table 1. Continued.

| Family | Common Name | Scientific Name | Guilds | | Vegetation | |
|--------------|---|-------------------------------------|---------|---------------|---------------|-----------------|
| | | | Feeding | Micro habitat | Dry deciduous | Moist deciduous |
| Columbidae | Green Imperial Pigeon | <i>Ducula aenea</i> | F | C | 4 | |
| | Little Brown Dove | <i>Streptopelia senegalensis</i> | G | O | 4 | |
| | Eurasian Collared-Dove (Collared Turtle or Indian Ring Dove) | <i>Streptopelia decaocto</i> | G | O | 4 | |
| | Spotted Dove | <i>Streptopelia chinensis</i> | G | O | 37 | |
| Psittacidae | Roseringed Parakeet | <i>Psittacula krameri</i> | F | C | 20 | 11 |
| | Plum-headed Parakeet (Blossom Headed Parakeet) | <i>Psittacula cyanocephala</i> | F | C | 45 | 13 |
| | Malabar Parakeet (Bluewinged Parakeet) | <i>Psittacula columboides</i> | F | C | 18 | 13 |
| Cuculidae | Coucal | <i>Centropus sinensis</i> | C | U | 1 | |
| | Koel | <i>Eudynamys scolopacea</i> | F | C | | 1 |
| | Small Greenbilled Malkoha | <i>Phaenicophaeus viridirostris</i> | C | U | 5 | |
| | Common Hawk Cuckoo (Brainfever Bird) | <i>Cuculus varius</i> | I | C | 8 | |
| | Sirkeer Cuckoo | <i>Phaenicophaeus leschenaultii</i> | I | U | 1 | |
| Apodidae | Creasted Tree Swift | <i>Hemiprocne coronata</i> | I | C | 2 | |
| Alcedinidae | White-throated Kingfisher | <i>Halcyon smyrnensis</i> | C | O | 2 | |
| Meropidae | Small Green Bee-eater | <i>Merops orientalis</i> | I | O | 23 | |
| Upupidae | Hoopoe | <i>Eurasian Hoopoe</i> | I | G | 4 | |
| Bucerotidae | Indian Grey-Hornbill (Common Grey-Hornbill) | <i>Ocyeros birostris</i> | F | C | 3 | |
| Megalaimidae | White-cheeked Barbet (Small Green Barbet) | <i>Megalaima viridis</i> | F | C | 3 | 195 |
| | Brown-headed Barbet (Large Green Barbet) | <i>Megalaima zeylanica</i> | F | C | 9 | 54 |
| | Coppersmith Barbet (Crimson Breasted Barbet) | <i>Megalaima haemacephala</i> | F | C | 3 | 14 |
| Picidae | Black-rumped Flameback (Lesser Goldenbacked Woodpecker) | <i>Dinopium benghalense</i> | I | C | 5 | 16 |

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Appendix Table 1. Continued.

| Family | Common Name | Scientific Name | Guilds | | Vegetation | |
|---------------|--|---------------------------------------|---------|---------------|---------------|-----------------|
| | | | Feeding | Micro habitat | Dry deciduous | Moist deciduous |
| | Common Flameback (Indian Goldenbacked Three Toed Woodpecker) | <i>Dinopium javanense</i> | I | C | 2 | |
| | Yellow-crowned Woodpecker (Yellow Fronted Pied Woodpecker) | <i>Dendrocopos mahrattensis</i> | I | C | 3 | |
| | Brown-capped Woodpecker (Pigmy Woodpecker) | <i>Dendrocopos nanus</i> | I | C | | 1 |
| | Woodpecker sp. | ? | I | C | 2 | 4 |
| Hirundinidae | Swallow | <i>Hirundo rustica</i> | I | O | 7 | |
| Laniidae | Brown Shrike | <i>Lanius cristatus</i> | I | U | 3 | |
| | Baybacked Shrike | <i>Lanius vittatus</i> | I | O | 1 | |
| | Long-tailed Shrike (Rufousbacked Shrike) | <i>Lanius schach</i> | I | O | | 4 |
| Oriolidae | Golden Oriole | <i>Oriolus oriolus</i> | F | C | 10 | 3 |
| | Black-hooded Oriole (Black-headed Oriole) | <i>Oriolus xanthornus</i> | F | C | 12 | 3 |
| Dicruridae | Whitebellied Drongo | <i>Dicrurus caerulescens</i> | I | U | 31 | 7 |
| | Black Drongo | <i>Dicrurus macrocercus</i> | I | O | 16 | 19 |
| | Bronzed Drongo | <i>Dicrurus aeneus</i> | I | C | | 9 |
| Sturnidae | Common Myna | <i>Acridotheres tristis</i> | O | O | 4 | |
| | Jungle Myna | <i>Acridotheres fuscus</i> | O | O | 1 | 2 |
| Corvidae | Jungle Crow | <i>Corvus macrorhynchos</i> | O | G | | 8 |
| | Treepie | <i>Dendrocitta vagabunda</i> | C | C | 24 | 4 |
| Campephagidae | Large Cuckoo-Shrike | <i>Coracina macei</i> | I | C | | 2 |
| | Common Wood-Shrike | <i>Tephrodornis pondicerianus</i> | I | C | 12 | |
| | Blackheaded Cuckoo- Shrike | <i>Coracina melanoptera</i> | I | C | 8 | |
| | Bar-winged Flycatcher- shrike (Pied Flycatcher Shrike) | <i>Hemipus picatus</i> | I | C | 1 | |
| | Scarlet Minivet | <i>Pericrocotus flammeus</i> | I | C | 10 | 56 |
| | Small Minivet | <i>Pericrocotus cinnamomeus</i> | I | C | 37 | 1 |

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Appendix Table 1. Continued.

| Family | Common Name | Scientific Name | Guilds | | Vegetation | |
|--------------------------|---|--------------------------------------|-----------------------|---------------|---------------|-----------------|
| | | | Feeding | Micro habitat | Dry deciduous | Moist deciduous |
| Irenidae | Goldfronted Chloropsis | <i>Chloropsis aurifrons</i> | F | C | 30 | 15 |
| | Common Iora | <i>Aegithina tiphia</i> | I | C | 145 | 81 |
| | Fairy Bluebird | <i>Irena puella</i> | F | C | | 31 |
| Pycnonotidae | Redvented Bulbul | <i>Pycnonotus cafer</i> | F | U | 461 | 108 |
| | Redwhiskered Bulbul | <i>Pycnonotus jocosus</i> | F | U | 106 | 670 |
| | Whitebrowed Bulbul | <i>Pycnonotus luteolus</i> | F | U | 403 | 160 |
| Muscicapidae | Puff-throated Babbler (Spotted Babbler) | <i>Pellorneum ruficeps</i> | I | U | | 2 |
| Subfamily: Timaliinae | Jungle Babbler | <i>Turdoides striatus</i> | I | U | 45 | 26 |
| | Common Babbler | <i>Turdoides caudatus</i> | I | U | 5 | 5 |
| | Indian Scimitar-Babbler (Slatyheaded Scimitar- Babbler) | <i>Pomatorhinus horsfieldii</i> | I | U | 5 | 22 |
| | Quaker Babbler | <i>Alcippe poiocephala</i> | I | U | | 53 |
| | Rufous Babbler | <i>Turdoides subrufus</i> | I | U | 1 | |
| | Rufousbellied Babbler | <i>Dumetia hyperythra</i> | I | U | 2 | |
| | Yellow-billed Babbler (Whiteheaded Babbler) | <i>Turdoides affinis</i> | I | O | 161 | 6 |
| Muscicapinae | Tickell's Blue Flycatcher | <i>Cyornis tickelliae</i> | I | U | 3 | 42 |
| | Paradise Flycatcher | <i>Terpsiphone paradisi</i> | I | C | 1 | 17 |
| | Whitebrowed Fantail Flycatcher | <i>Rhipidura aureola</i> | I | U | 3 | |
| | Flycatcher sp. | | I | U | | 1 |
| | Black-naped Monarch Flycatcher | <i>Hypothymis azurea</i> | I | C | 2 | 28 |
| | Greyheaded Canary Flycatcher | <i>Culicicapa ceylonensis</i> | I | C | 1 | 38 |
| | Subfamily: Sylviinae | Lesser Whitethroat | <i>Sylvia curruca</i> | I | G | 1 |
| | Greenish Warbler | <i>Phylloscopus trochiloides</i> | I | C | 30 | 4 |
| | Grey-Breassted Warbler (Franklin's Wren Warbler) | <i>Prinia hodgsonii</i> | I | U | 95 | 2 |
| | Blyth's Reed Warbler | <i>Acrocephalus dumetorum</i> | I | U | 74 | 58 |
| | Ashywren Warbler | <i>Prinia socialis</i> | I | U | 1 | |
| | Booted Warbler | <i>Hippolais caligata</i> | I | U | 68 | 52 |
| | Tailorbird | <i>Orthotomus sutorius</i> | I | U | 185 | 18 |
| Subfamily: Turdinae | Magpie Robin | <i>Copsychus saularis</i> | I | U | 77 | 63 |
| | Indian Robin | <i>Saxicoloides fulicata</i> | I | O | 155 | 11 |

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Appendix Table 1. Continued.

| Family | Common Name | Scientific Name | Guilds | | Vegetation | |
|---------------|--|--------------------------------|---------|---------------|---------------|-----------------|
| | | | Feeding | Micro habitat | Dry deciduous | Moist deciduous |
| | White-rumped Shama (Malabar Shama) | <i>Copsychus malabaricus</i> | I | U | 4 | 68 |
| | Orangeheaded Ground Thrush | <i>Zoothera citrina</i> | I | G | | 15 |
| Paridae | Great Tit (Grey Tit) | <i>Parus major</i> | I | C | | 5 |
| Sittidae | Velvetfronted Nuthatch | <i>Sitta frontalis</i> | I | C | 2 | 37 |
| Motacillidae | Yellow Wagtail | <i>Motacilla flava</i> | I | O | 1 | |
| Dicaeidae | Pale-billed Flycatcher (Tickell's Flowerpecker) | <i>Dicaeum erythrorhynchos</i> | F | C | 209 | 145 |
| Nectariniidae | Purple Sunbird | <i>Nectarinia asiatica</i> | N | U | 166 | 15 |
| | Purplerumped Sunbird | <i>Nectarinia zeylonica</i> | N | U | 215 | 30 |
| Zosteropidae | Oriental White Eye | <i>Zosterops palpebrosus</i> | F | C | | 36 |
| Ploceidae | Chestnut-shouldered Petronia (Yellow throated Sparrow) | <i>Petronia xanthocollis</i> | G | O | | 3 |
| | White-rumped Munia (Whitebacked Munia) | <i>Lonchura striata</i> | G | O | 1 | |
| | Scaly-breasted Munia (Spotted Munia) | <i>Lonchura punctulata</i> | G | O | 1 | |
| Fringillidae | Rose Finch | <i>Carpodacus erythrinus</i> | G | O | 3 | |