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Community ecology

Horizontal and vertical species turnover in tropical birds in habitats with differing land use

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Large tracts of tropical rainforests are being converted into intensive agricultural lands. Such anthropogenic disturbances are known to reduce species turnover across horizontal distances. But it is not known if they can also reduce species turnover across vertical distances (elevation), which have steeper climatic differences. We measured turnover in birds across horizontal and vertical sampling transects in three land-use types of Sri Lanka: protected forest, reserve buffer and intensive-agriculture, from 90 to 2100 m a.s.l. Bird turnover rates across horizontal distances were similar across all habitats, and much less than vertical turnover rates. Vertical turnover rates were not similar across habitats. Forest had higher turnover rates than the other two habitats for all bird species. Buffer and intensive-agriculture had similar turnover rates, even though buffer habitats were situated at the forest edge. Therefore, our results demonstrate the crucial importance of conserving primary forest across the full elevational range available.

1. Background

One of the most documented patterns in ecology is that species richness generally declines with increasing anthropogenic activities. Species composition homogenization is considered to be the underlying mechanism governing such patterns [1–3], with generalist species expanding their ranges, while specialist species ranges contract, leading to specialists being replaced by generalists, and increasing similarities among communities in space and time [4]. Climate change is likely to increase the severity of homogenization, as climate change and land-use change favour the same generalist species, which expand their ranges tracking the climate, while ranges of specialists contract [5]. Studies have repeatedly shown reduced horizontal turnover indicating greater homogenization within human-modified landscapes compared with forests [1–3], but changes in vertical turnover remain unknown. Vertical distances show high variation in temperature (6°C per km), yet all previous studies that measured turnover rates across vertical distances have mainly used natural habitats [6–7]. Human-modified habitats are known to have simplified communities with generalist species that can use multiple habitats [8], leading to the testable hypothesis that vertical turnover in human-modified habitats would be lower compared to less disturbed, proximal habitats.

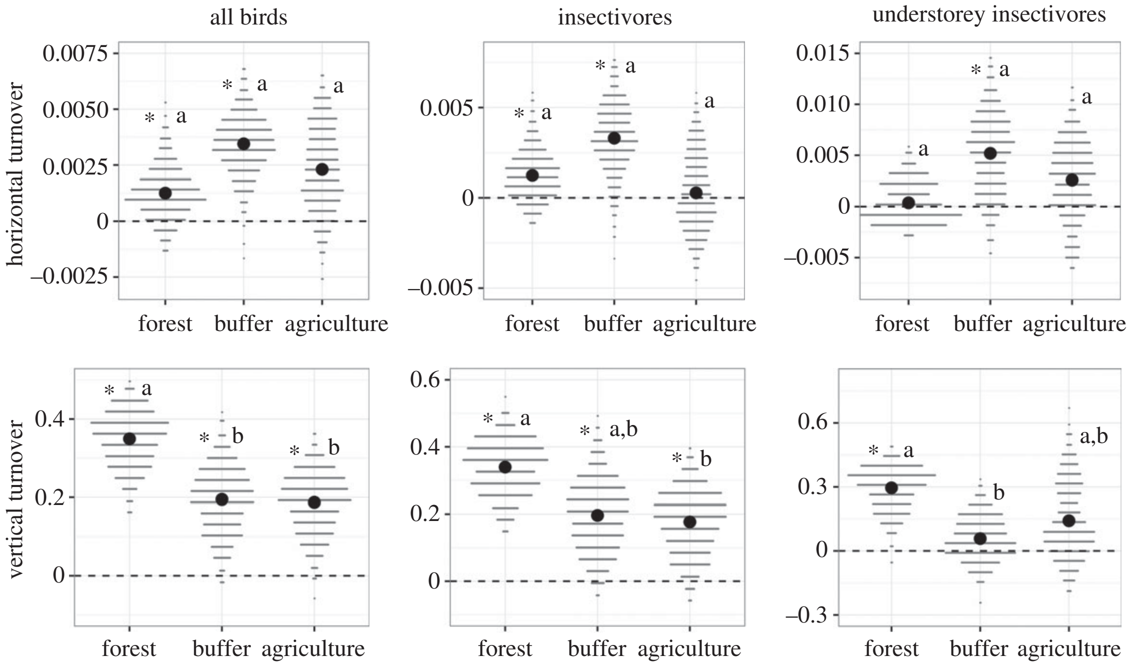

Figure 1. Species turnover per kilometre across horizontal and vertical distances between transects for all birds ($n = 125$ species), insectivores ($n = 70$ species) and understorey insectivores ($n = 23$ species) in forest, buffer and intensive-agriculture habitats. The figure represents mean of 1000 coefficient values (in grey) generated by multiple regression on distance matrices (MRM) after resampling the communities with replacement. The black dashed lines indicate no turnover (table 1), * indicates significant turnover with distance, and habitats with different letters have significantly different turnover rates. Note the *y*-axis of horizontal and vertical turnover are at different scales.

Here we compare species turnover within bird guilds with horizontal and vertical distances across a tropical mountain range in three different land-use types: within relatively undisturbed and protected forest, at the edges of those protected reserves, and in intensive agriculture. We hypothesized that species turnover will be: (i) highest in forest and lowest in intensive-agriculture habitats, because forest species are more specialized, and (ii) higher vertically than horizontally, because the climatic gradient is steeper; and (iii) highest in forest because the vertical gradient in vegetation structure and composition is steeper in natural than anthropogenic habitats. Understanding these patterns is important both for efficient conservation planning and for predicting—and hopefully mitigating—the impacts of on-going climate change.

2. Material and methods

(a) Study site

We conducted this study in wet-evergreen regions of Sri Lanka (electronic supplementary material, figure S1). Forty-one 2 km transects were spaced along an elevational gradient between 90 and 2180 m, in three different land-use types: (i) interior forest transects were inside mature evergreen rainforests within protected areas, (ii) buffer transects were along the boundaries of protected areas, within degraded forests and timber plantations, and (iii) intensive-agriculture transects were in open habitats with intensive agriculture. Mean monthly temperature (range: 14.7–27.1°C) and mean annual precipitation (1972–4273 mm) for each transect were extracted from the WORLDCLIM database (30 arc-seconds resolution; version 1.4 (http://www.worldclim.org/version1); [9]). For every one-kilometre increase in elevation, temperature decreased by c. 5°C and annual precipitation decreased by c. 1000 mm (electronic supplementary material, figure S1). Some amount of caution is required while interpreting the climate data because WORLDCLIM is modelled data and may not exactly represent true climatic parameters. Tree canopy cover for the entire island of Sri Lanka was extracted from the global forest change dataset [10].

(b) Bird data

A team of two walked along the transects at 1 km h^{-1}, identified all the individual birds seen and heard, and recorded their distances from the transect line. Each transect was visited 7.2 ± 4.0 (s.d.) times in 1 year, in both the breeding and non-breeding seasons. The data consist of 27 234 observations of 125 bird species. Transects were horizontal with little variation in elevation and transect coordinates were extracted from the centre of transect. We used DISTANCE software (http://distancesampling.org) to estimate relative densities by accounting for detectability of species (see electronic supplementary material, appendix S1 for details). We recorded all 27 endemic diurnal birds of Sri Lanka, of which 14—all predominantly forest birds—are threatened with extinction (http://www.iucnredlist.org). We divided the birds into three non-exclusive guilds: (i) all birds, (ii) insectivores, with arthropods as their primary diet, and (iii) understorey insectivores, which primarily used the understorey. See previous studies for details [11,12]. All analyses were conducted in the statistical program R (R Core Team, v. 3.3.1). We partitioned Bray–Curtis dissimilarity into nestedness and turnover components, and used the turnover component as a response variable to determine the turnover across horizontal and vertical distances in each habitat and across all three guilds. We used coefficients of each model to estimate the turnover rate (turnover per km) and compared coefficients between habitats and between horizontal and vertical distances. See electronic supplementary material, appendix S1 for details and references.

3. Results

Annual precipitation changed significantly with only vertical (estimate = 1093.35 mm km^{-1}; $p = 0.001$) distance, but not with horizontal distance (estimate = 4.52 mm km^{-1}; $p = 0.087$). Mean monthly temperature changed significantly with both vertical (estimate = 4.73°C km^{-1}, $p = 0.001$) and horizontal distances (estimate = 0.01°C km^{-1}, $p = 0.013$), but much more rapidly vertically than horizontally.

Analysing across increasing horizontal distance, bird turnover in forest habitats increased significantly for all bird and insectivore guilds, though not for the understorey insectivore group (figure 1; asterisk indicates significant turnover). In buffer habitats, bird turnover increased with horizontal distance across all guilds. In contrast, birds in intensive-agriculture habitats remained similar with horizontal distance across all guilds. Analysing across increasing vertical distance, bird turnover increased across all guilds in forest habitats. Bird turnover in buffer and intensive-agriculture habitats increased with vertical distance for all birds and insectivores, though not for the understorey insectivore group (figure 1).

The horizontal turnover rates were similar among habitats for all guilds ($p > 0.05$; figure 1; same letters indicate similar turnover rates). The vertical turnover rates in intensive-agriculture habitats were similar to buffer habitats for all guilds ($p > 0.05$, electronic supplementary material, table S1). However, intensive-agriculture habitats had lower vertical turnover rates than forests for all birds ($p = 0.001$) and insectivore guilds ($p = 0.012$). Similarly, buffer habitats had lower turnover rates than forests for all birds ($p = 0.03$) and understorey insectivore guilds ($p = 0.001$). Vertical turnover of all birds in forest, buffer and intensive agriculture habitats was 287, 60 and 91 times greater than horizontal turnover, respectively (table 1).

Among the 14 threatened endemic forest species, seven preferred low elevations, one preferred middle elevations, five preferred high elevations and one did not show any elevation preference (figure 2; electronic supplementary material, table S2). Both elevation ($p < 0.001$) and land-use ($p < 0.001$) had a significant influence on Sri Lankan bird community composition (electronic supplementary material, figure S2).

4. Discussion

Previous studies on land-use intensification have looked at turnover rates in response to different types of human disturbance across horizontal gradients but not vertical gradients [1–3]. To our knowledge, our results show for the first time that buffer and intensive-agriculture habitats display significant vertical turnover rates, but not as high as forests. Low and high elevation forests harbour markedly different bird communities, but the bird communities in low and high elevation buffer and agriculture are only moderately different. Within forests, although both vertical and horizontal distances influenced forest bird turnover, small vertical distances (c. 2 km; 0.373 per km) had a much bigger effect than large horizontal distances (c. 75 km; 0.0013 per km). Both these results are consistent with a dominant influence of vertical distance on bird turnover in all habitats at regional scales. Recent studies suggest that biotic factors (habitat, diet and interspecific competition) that are indirectly related to temperature may be driving high turnover rates across vertical gradients [13,14].

Table 1. Results of multiple regression of distance matrices with turnover as response variable and horizontal distance and vertical distance as predictor variables.

	estimate	*p*-value
all birds		
forest ($R^2 = 0.86$)		
horizontal	0.0013	0.022
vertical	0.373	0.001
buffer ($R^2 = 0.62$)		
horizontal	0.0034	0.002
vertical	0.203	0.001
agriculture ($R^2 = 0.60$)		
horizontal	0.0022	0.061
vertical	0.200	0.001
insectivores		
forest ($R^2 = 0.85$)		
horizontal	0.0012	0.037
vertical	0.376	0.001
buffer ($R^2 = 0.50$)		
horizontal	0.0032	0.006
vertical	0.215	0.001
agriculture ($R^2 = 0.27$)		
horizontal	−0.0001	0.958
vertical	0.1964	0.005
understorey insectivores		
forest ($R^2 = 0.63$)		
horizontal	−0.0005	0.554
vertical	0.3493	0.001
buffer ($R^2 = 0.30$)		
horizontal	0.0053	0.003
vertical	0.048	0.382
agriculture ($R^2 = 0.27$)		
horizontal	0.0037	0.061
vertical	0.107	0.142

Among forest birds, 14 threatened endemic diurnal forest species showed high turnover with elevation (figure 2). Five preferred high elevation forests (more than 1500 m), increasing their extinction risk due to climate change, especially in islands like Sri Lanka where opportunities for dispersal are limited. Rapid upward shifts in tropical organisms have already been observed with warming of c. 0.5°C in tropical land areas over the past 50 years [15]. A recent study predicted that a 2°C rise in temperature would shift the bird communities upwards by 400 m [15]. For the whole of Sri Lanka, the forested areas (more than 75% tree cover) at elevations higher than 1500 m and 1900 m are 583 km^2 and 152 km^2, respectively. So, a 400 m shift upwards would reduce the potential habitat for high elevation threatened endemic species by 74%. Similar shifts might extirpate entire populations of these species in the isolated Knuckles mountain range where the highest peak is 1863 m (electronic supplementary material, figure S3).

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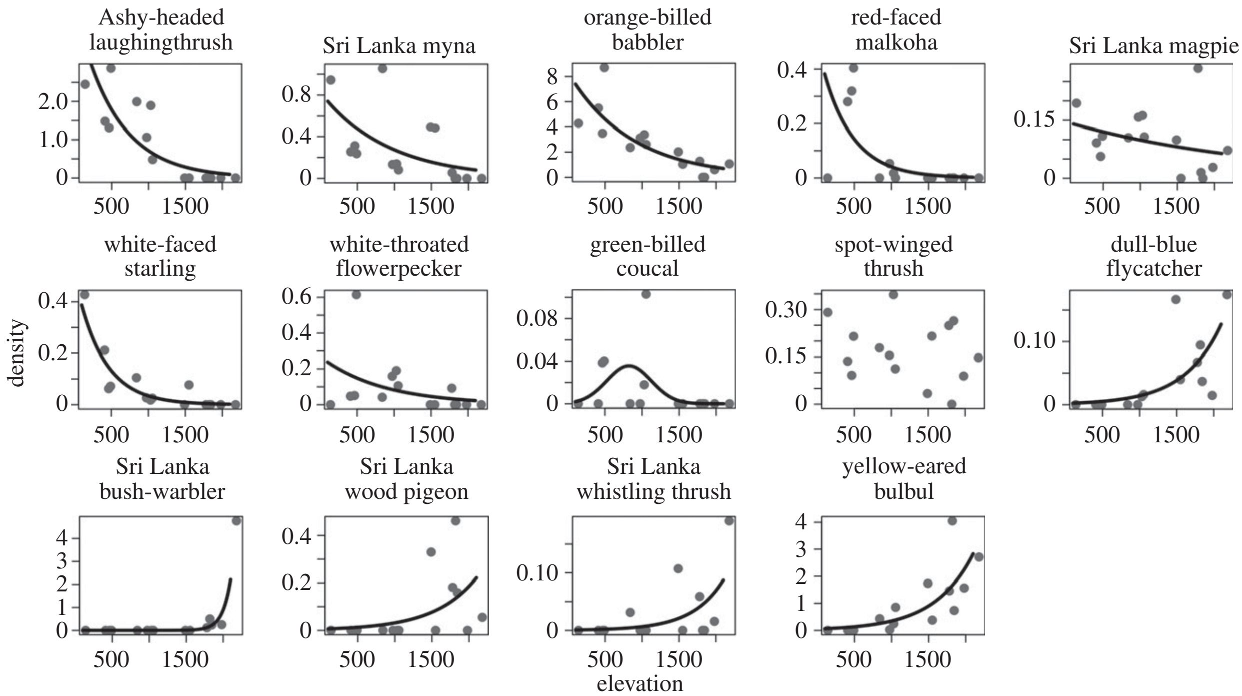

Figure 2. Relative density of threatened Sri Lankan endemic species across an elevation gradient in Sri Lanka showing differences in elevational preferences. See electronic supplementary material, table S2 for details.

In conclusion, our study shows that the turnover rate in tropical birds is very sensitive to vertical distance in all land-use types, and especially high in forests; while turnover with horizontal distance is much smaller. Land-use intensity was also important for turnover in bird communities (electronic supplementary material, figure S2). These results suggest a need to prioritize the protection of sufficient forest area across the full elevational range over protecting additional forest areas at similar elevations, as long as enough habitat is protected at any one elevation to sustain populations. Even though established reserves are relatively well protected in Sri Lanka, the extraordinary level of endemicity, both of fauna and flora [16,17], calls for restoration of degraded areas and expansion of the relatively small size of the existing protected area to cover endemic hotspots. The results also highlight the vulnerability of high-elevation specialists to even moderate global warming and thus emphasize the critical importance of achieving the targets included in the 2015 Paris Agreement.

Ethics. Sri Lanka Forest Department and the Sri Lanka Wildlife Conservation Department approved of this study.

Data accessibility. Data are available from the Dryad Digital Repository [12] http://dx.doi.org/10.5061/dryad.vk070.

Authors' contributions. R.S., R.T.C., S.D., L.P.K. and E.G. designed the study; E.G., U.M.G. and S.W.K. acquired bird data; R.S. and A.K. acquired climate and forest cover data; R.S. analysed the data and drafted the article; all authors revised it critically and approved for publication. All authors agree to be held accountable for the content therein.

Competing interests. The authors have no competing interests.

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