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Foraging niche differentiation among sympatric woodpecker species in forests of north-western India

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Abstract. The sub-Himalayan dipterocarp forests of subtropical region in northwest India support 17 species of woodpecker. From a conservation perspective it is necessary to assess the ecological requirements of woodpeckers in these biologically diverse landscapes, which are experiencing habitat modification and decline in some woodpeckers. We studied the foraging niche differentiation among ten sympatric woodpeckers in the sub-Himalayan forests of northwest India: *Dendrocopos canicapillus*, *D. macei*, *Picus chlorolophus*, *P. xanthopygaeus*, *P. canus*, *Dinopium shorii*, *D. benghalense*, *Chrysophlegma [Picus] flavinucha*, *Chrysocolaptes lucidus*, and *Mulleripicus pulverulentus*. We examined the foraging site preferences of individual woodpecker species and explored the role of inter-specific differences in foraging behaviour as a possible mechanism for their coexistence. Observations on foraging woodpeckers were taken vis-a-vis the following niche dimensions: diameter of the foraging tree, height of the foraging bird, type of substrate on which it was foraging, vertical position with respect to canopy, condition of the forage tree and condition of the substrate. Distinct preferences were evident among species in their foraging tree diameters, foraging heights, vertical positions, and choice of substrate type, while preference for dead substrates was not an important distinguishing factor. Species that overlapped in one dimension generally segregated along other dimensions. Niche segregation in forage tree diameter was associated with body weight. Based on their overall niche overlaps species could broadly be differentiated into groups according to body size viz. small (3 species), medium (3 species), large (3 species), and very large (1 species). Our study demonstrates that differentiation in foraging may be a likely mechanism for coexistence of sympatric woodpeckers in this region. Given that larger species prefer larger substrates, removal of mature trees could affect their abundance, and homogenisation of stand structure could lead to impoverishment of woodpecker diversity.

Key words: foraging behaviour, niche overlap, Picidae, *Shorea robusta*, sub-Himalayan region, substrate selection, sympatric species, woodpecker, flameback, yellownap

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INTRODUCTION

Coexistence of sympatric species can be interpreted on the basis of the ecological niche concept (Chesson 2000, Morin 2011, Mittelbach & McGill 2019). The niche itself is considered as a multi-dimensional hypervolume with each dimension or axis representing a species' requirement for a particular resource (Hutchinson 1957). To understand coexistence among species and to identify traits that determine a species' niche it is necessary to study their resource requirements (Wiens 1992, Chase & Leibold 2003, McGill et al. 2006). Such information is of great consequence in both theoretical and applied ecology.

Studies on birds have found sympatric species to differ in their use of foraging manoeuvres and choice of substrates. Segregation may result from individual species using substrates of different types and dimensions and using disparate vertical or horizontal foraging locations. Such separation has been observed in several bird groups e.g. flycatchers (Qvarnström et al. 2009), tits (Suhonen et al. 1994), kingfishers (Kasahara & Katoh 2008), corvids (Waite 1984) and thrushes (Noon 1981).

Woodpeckers are an avifaunal group of particular interest for assessing differences in foraging behaviour. Since all woodpeckers possess the same general morphological adaptations, they form a distinct functional group with broadly the

same feeding requirements (Short 1978). At the same time, given that many regions have several sympatric species of woodpeckers, it is possible that individual species show finer scale differences in their foraging behaviour, especially among the similar sized species (Short 1978).

Species that have more specific requirements or specialize on particular kinds of foraging resources are likely to be more sensitive to changes in habitat conditions that may be driven by forest management. For example, woodpeckers that require larger trees for feeding are prone to decline when such trees are removed (Roberge et al. 2008). Hence, structural changes due to management operations such as logging can potentially affect the community structure of woodpeckers (Lammertink 2004, Styring & Zakaria 2004a,b).

Foraging niche differentiation among sympatric woodpeckers has been observed in several studies across the world, and has sometimes been linked to variation in morphological characteristics (Schoener 1965, Short 1978, Leonard & Heath 2010). For example, Bull et al. (1986), working on eight woodpecker species in Oregon, USA, found them to differ in foraging location, feeding strategy, substrate type and preference for snags. Askins (1983) investigated foraging niches of woodpeckers in temperate and tropical regions of America. Segregation by occupation of different vertical positions and by choosing substrates of different dimensions among sympatric woodpeckers has been documented in other parts of North America (Williams 1975), and Europe (Török 1990). Such positional and substrate size-related partitioning has been also observed by researchers in tropical regions. For instance, in Southeast Asia, larger woodpecker species were found to prefer larger foraging substrates, and species similar in body size segregated by foraging at different locations in trees (Short 1978, Styring & Zakaria 2004b, Lammertink 2007). Santharam (1995) found evidence of body size-related choice in substrate sizes among eight woodpeckers in Western Ghats in southern India.

Nonetheless, aside from a few exceptions, the foraging ecology of woodpeckers in tropical/sub-tropical regions that harbour a high picid diversity has not been studied in great detail (Mikusiński 2006). Parts of Asia, like north-western India that supports 15 species (of which ca. 12 are sympatric), are well suited to assess foraging niche partitioning among woodpeckers (Styring 2002). Moreover, from a conservation point of view, it is

necessary to assess the ecological requirements of woodpeckers in these biologically diverse regions that are experiencing habitat modification and a resulting decline in some woodpecker species (Lammertink 2004).

We studied the foraging ecology and differentiation among sympatric woodpeckers in the sub-Himalayan region of northwest India. The main research questions of this study were: 1) Do the foraging niches among woodpecker species differ with respect to their choice of substrate characteristics and foraging locations? If so, what are the important dimensions contributing to the segregation?; 2) Are the patterns in niche segregation along different dimensions associated with differences in morphological traits, particularly body weights, of the species?

METHODS

The present study was carried out as part of a larger research project on woodpecker communities in the Ramnagar–Corbett landscape (Fig. 1) in Uttarakhand, northwestern India (Kumar et al. 2011, 2014). The region forms part of the sub-Himalayan foothills in the Himalayan mountain system, lies at 200–900 m elevation, and receives ca. 2000 mm rainfall annually. The vegetation largely comprises tropical moist deciduous forests dominated by dipterocarp *Sal Shorea robusta*. The area is recognized as an important tract for biodiversity conservation, and supports > 500 avian species including 17 woodpeckers (Mohan & Sondhi 2017).

In the area we identified eight study sites representing the structural and compositional diversity of the forests, and established transects of 2.0 km length. At each site we conducted field surveys for woodpeckers by traversing the marked transects on foot at a steady pace of 1–2 km/h, with each site being surveyed 20 times during 2006–2008 (Kumar et al. 2011, 2014).

On these surveys we collected systematic observations on foraging woodpeckers. Upon detecting a woodpecker we identified the species and recorded foraging characteristics at the instant of first sighting. The following foraging niche dimensions were considered: (1) DBH of the foraging tree; (2) height of the foraging bird estimated using a clinometer; (3) substrate type i.e. part of the tree on which it was observed foraging (trunk/ground, primary branch, secondary branch, or terminal branch); (4) vertical position

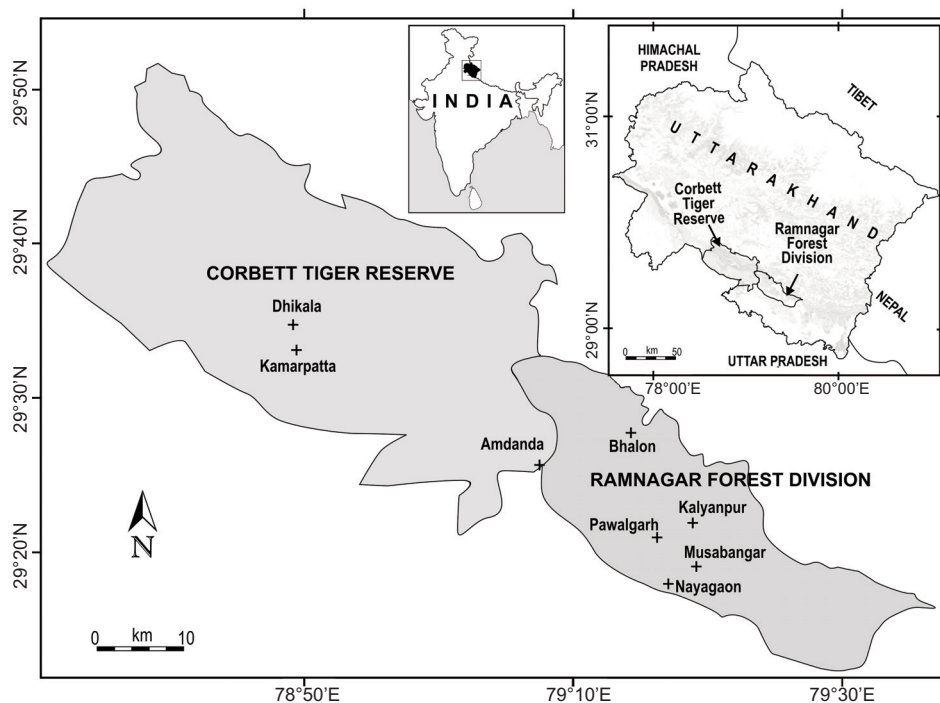


Fig. 1. Map of study area with location of sites.

with respect to canopy (below crown, lower canopy, middle canopy or upper canopy); (5) condition of the forage tree (live or snag); and (6) condition of the substrate (live or dead).

Multiple observations on the same individual were not usually considered. However, in rare cases a second observation was taken after the individual moved to another tree. In addition to systematic observations, ad libitum observations were opportunistically taken whenever a woodpecker was encountered either on the return leg of the survey or while travelling between sites.

We also assessed whether a particular species was selective in its choice of forage tree diameter and tree condition by comparing use (i.e. foraging observations on DBH and tree condition) with availability (i.e. DBH and tree condition of randomly chosen trees in the same stand). The availability data was obtained by measuring DBH of trees in 80 circular plots (10 m radius) in the eight stands (see Kumar et al. 2014 for details).

ANALYSES

Foraging niche segregation along individual dimensions

Those species for which there were at least 10 observations were considered for analysis. For

each species differences in individual niche dimensions between breeding and non-breeding seasons were first investigated using t-tests for continuous variables and chi-square tests (or Fisher's exact tests, depending on sample size) for categorical variables. As differences in foraging variables were on the whole not significantly different between seasons, observations for both seasons were pooled together for further analyses.

Foraging niche segregation along individual dimensions was tested in two stages. First, it was assessed whether there were differences among species in each of the foraging variables. For dimensions that were measured as continuous data (viz. forage tree DBH and foraging height), this was done using ANOVA, while for variables that were categorical (viz. vertical position, substrate type, tree condition and substrate condition) chi-square tests were used. However, when samples were small (< 5), Fisher's exact tests were used in place of chi-square tests. When differences were found to be statistically significant among species, a second level investigation for differences between species was done. This was carried out by means of t-tests for continuous variables and chi-square (or Fisher's exact tests) for categorical dimensions, using Bonferroni adjustments for multiple comparisons.

Selectivity in forage tree diameter for each species was examined by comparing observed DBH values of trees used for foraging with DBH values randomly drawn from among the trees measured during habitat enumeration. Statistical differences between used versus available DBH were examined using resampling methods viz. t-tests bootstrapped over 1000 iterations (Manly 2007). Similarly, a species' preference for snags was assessed by comparing the counts of foraging observations on dead and live trees with counts of dead and live trees obtained from randomly drawn trees with a chi-square test (or Fisher's exact test when samples were less than 5).

Niche overlap

Overlap between species pairs along individual niche dimensions was calculated as follows. For each categorical variable the proportion of observations under each of the component categories was tabulated species-wise. Continuous variables were first converted into frequency distributions and the proportion of observations under each class interval were listed species-wise. Niche overlap between species pairs for each of the six dimensions was calculated using:

$$NO_{ij} = \sum_{k=1}^K \min(p_{ik}, p_{jk})$$

where, NO_{ij} = niche overlap between species i and j for each dimension, and p_{ik} and p_{jk} = proportions of observations in category (or class interval) k for species i and j , respectively (Geange et al. 2011).

Null model permutation tests were used to assess whether the niche overlap between two species was significantly lower than expected by chance (Gotelli & Graves 1996, Geange et al. 2011). Species labels were randomised over 1000 runs to generate a distribution of 'test' niche overlap values. The proportion of iterations returning niche overlap values less than the actual observed niche overlap was taken as 'p-value' to indicate significance of the overlap.

The average niche overlap across all dimensions was computed by

$$NO_{ij} = \frac{1}{T} \sum_{t=1}^T NO_{ijt}$$

where t = number of niche dimensions 1 to T ; NO_{ijt} = niche overlap between species i and j for dimension t (Mouillot et al. 2005).

Niche segregation between species i and j , i.e. the 'distance' in foraging preference between them, d_{ij} , was calculated as the complement of niche overlap [$1 - NO_{ijt}$] (Geange et al. 2011). Distance matrices indicating segregation between

species pairs were constructed for the six niche dimensions as well as for the average foraging niche. On each of these niche segregation matrices we carried out non-metric multidimensional scaling (NMDS; Kruskal 1964) and ordinated the species in niche space. The NMDS plots helped visualise the segregation among species vis-à-vis attributes of foraging behaviour. From NMDS ordination we identified species groups and assessed their distinctiveness using multiple response permutation procedures (MRPP; Mielke & Berry 2001).

Relationship between foraging characteristics and body weight

Correlation between mean forage tree DBH of woodpecker species with their respective median body weights was computed to examine whether woodpeckers had a propensity to forage on tree diameters according to their body weights. Likewise, correlation was also computed between mean foraging height and body weight. Morphometric measurements were obtained from Ali & Ripley (1983) and Winkler et al. (1995). Since bill length was highly correlated with body weight ($r = 0.89$), the relationship between forage tree DBH and body weight applied to bill size also.

The possible relationship between niche segregation and body weight was also explored. Distance matrices representing pairwise differences in body weight were first computed and Mantel's tests of association (Legendre & Legendre 1998) were carried out between the body weight distance matrix and each of the foraging niche segregation matrices (derived previously). The number of iterations in each test was 1000.

All analyses were done using statistical software R version 2.11.1 (R Development Core Team 2010).

RESULTS

Foraging niche segregation along individual dimensions

In total, 1191 foraging observations of ten woodpecker species were obtained (Table 1). Out of these we could successfully determine forage tree DBH for 676 cases, foraging height for 564, vertical position for 1054, tree condition for 1188, and substrate condition for 1190 cases. Although five other species were also observed, these were excluded from analyses owing to insufficient number of observations (< 10).

A broad range of sizes of trees were used for foraging (3 cm to 175 cm DBH). Mean DBH of forage trees for individual species varied from 39.6 cm for Grey-capped Pygmy Woodpecker *Dendrocopos canicapillus* to 64.7 cm for Great Slaty Woodpecker *Mulleripicus pulverulentus* (Fig. 2A).

Forage tree diameters were significantly different among species ($F_{9,666} = 10.57$, $p < 0.001$). Comparing between species pairs (Table 2), the smaller woodpeckers (Grey-capped Pygmy, Fulvous-breasted Woodpecker *Dendrocopos macei* and Lesser Yellownape *Picus chlorolophus*) and one medium-sized species (Streak-throated Woodpecker *Picus xanthopygaeus*) chose distinctly smaller tree sizes for foraging than did large bodied species (Grey-headed Woodpecker *Picus canus*, Greater Flameback *Chrysocolaptes lucidus* and Great Slaty Woodpecker). One medium-sized woodpecker (Himalayan Flameback *Dinopium shorii*) chose intermediate diameter trees for foraging. Black-rumped Flameback *Dinopium benghalense*, also medium-sized, had a DBH preference similar to the smaller woodpeckers. Greater Yellownape *Chrysophlegma [Picus] flavinucha*, although a large woodpecker, did not show significant differences in choice of forage tree DBH with any other woodpecker.

All woodpecker species, except Streak-throated, were found to select significantly larger trees than those sampled at random (Table 3), with the

difference between mean forage tree DBH and average available DBH generally increasing with body size. However, the Black-rumped Flameback was an exception: although being medium-sized it appeared to be less selective than even the smallest species (Grey-capped Pygmy and Fulvous-breasted).

The heights at which woodpeckers foraged ranged from the ground level to more than 30 m. Foraging height was significantly different among species ($F_{9,554} = 11.7$, $p < 0.001$). Grey-headed Woodpecker tended to forage much lower (< 10 m) than other species, and was often observed on the ground (Fig. 2B). Similarly, Black-rumped Flameback also occupied a lower height profile. On the other hand, Lesser Yellownape and Great Slaty foraged at the greatest heights (> 20 m). Greater Yellownape, Grey-capped Pygmy and Fulvous-breasted mostly foraged at 16–19 m from the ground. Three species — Streak-throated, Himalayan Flameback and Greater Flameback — occupied intermediate heights (13–15 m). Between-species comparisons (Table 2) showed that Grey-headed Woodpecker and Lesser Yellownape had significantly different choice of foraging heights from other species.

There were significant differences among species in their vertical positions used for foraging ($\chi^2_{27} = 325$; Fisher's exact test $p < 0.001$). Six species tended to forage mostly below the tree

Table 1. The size of ten woodpecker species with sample size for foraging analyses considered in the present study. Species arranged from smallest to largest. ^a — median body weight as given by Winkler et al. (1995), ^b — median bill length as given by Ali & Ripley (1983).

Species	Code	Size category	Number of foraging observations	Body weight ^a (g)	Bill length ^b (mm)
Grey-capped Pygmy Woodpecker <i>Dendrocopos canicapillus</i>	DECA	Small	296	22.0	17.0
Fulvous-breasted Woodpecker <i>Dendrocopos macei</i>	DEMA	Small	137	43.0	22.5
Lesser Yellownape <i>Picus chlorolophus</i>	PICH	Small	97	79.0	30.5
Streak-throated Woodpecker <i>Picus xanthopygaeus</i>	PIXA	Medium	66	104.5	31.5
Himalayan Flameback <i>Dinopium shorii</i>	DISH	Medium	184	101.0	40.3
Black-rumped Flameback <i>Dinopium benghalense</i>	DIBE	Medium	132	105.0	37.0
Grey-headed Woodpecker <i>Picus canus</i>	PICA	Large	122	152.5	44.3
Greater Yellownape <i>Chrysophlegma [Picus] flavinucha</i>	PIFL	Large	36	181.5	41.0
Greater Flameback <i>Chrysocolaptes lucidus</i>	CHLU	Large	91	207.5	57.3
Great Slaty Woodpecker <i>Mulleripicus pulverulentus</i>	MUPU	Very Large	34	430.0	64.5

Table 2. Inter-specific differences between species pairs for forage tree diameter (below diagonal) and foraging height (above diagonal). Figures indicate t-test statistics with p-values in parentheses; differences significant at $\alpha = 0.05$ are shown in bold. Superscript letters S, M, L and V denote small-, medium-, large- and very large-sized species, respectively. See Table 1 for key to species code names.

	DECA ^S	DEMA ^S	PICH ^S	PIXA ^M	DISH ^M	DIBE ^M	PICA ^L	PIFL ^L	CHLU ^L	MUPU ^V
DECA ^S		0.87 (1.000)	2.15 (0.001)	0.57 (1.000)	2.09 (1.000)	0.98 (< 0.001)	0.05 (< 0.001)	1.04 (1.000)	0.94 (1.000)	1.33 (0.327)
DEMA ^S	1.44 (1.000)		1.68 (0.015)	0.26 (1.000)	1.40 (1.000)	0.55 (< 0.001)	0.18 (< 0.001)	1.18 (1.000)	0.58 (1.000)	1.16 (1.000)
PICH ^S	0.14 (1.000)	0.45 (1.000)		1.20 (< 0.001)	0.63 (< 0.001)	1.14 (< 0.001)	1.43 (< 0.001)	2.19 (1.000)	0.98 (0.001)	0.29 (1.000)
PIXA ^M	4.47 (0.001)	0.57 (1.000)	0.99 (1.000)		0.82 (1.000)	0.21 (1.000)	0.36 (1.000)	1.26 (1.000)	0.26 (1.000)	0.98 (0.008)
DISH ^M	0.30 (1.000)	2.97 (0.195)	2.6 (1.000)	3.31 (0.179)		0.71 (0.290)	1.12 (0.080)	1.98 (1.000)	0.55 (1.000)	0.62 (0.008)
DIBE ^M	2.98 (0.001)	0.41 (1.000)	0.83 (1.000)	0.14 (1.000)	3.1 (0.045)		0.57 (1.000)	1.49 (0.071)	0.08 (0.099)	0.90 (< 0.001)
PICA ^L	3.47 (0.089)	2.49 (0.026)	2.29 (0.131)	2.75 (0.021)	1.09 (1.000)	2.65 (0.008)		0.89 (0.025)	0.60 (0.028)	1.16 (< 0.001)
PIFL ^L	5.63 (< 0.001)	2.83 (0.499)	2.59 (1.000)	3.11 (0.310)	1.12 (1.000)	2.99 (0.240)	0.14 (1.000)		1.48 (1.000)	1.74 (1.000)
CHLU ^L	6.67 (< 0.001)	4.54 (< 0.001)	4.29 (0.002)	4.78 (< 0.001)	2.39 (0.471)	4.6 (< 0.001)	0.37 (1.000)	0.63 (1.000)		0.84 (0.172)
MUPU ^V		5.73 (< 0.001)	5.52 (< 0.001)	5.91 (< 0.001)	3.91 (0.016)	5.76 (< 0.001)	1.54 (1.000)	1.95 (1.000)	1.62 (1.000)	

crowns (Grey-headed, Black-rumped Flameback, Greater Yellownap, Streak-throated, Himalayan Flameback and Greater Flameback; Fig. 3A). Great Slaty Woodpecker was observed to forage most of the time in the upper or middle canopy, as were two of the smaller species — Grey-capped Pygmy and Lesser Yellownap. Fulvous-breasted Woodpecker foraged mostly in the lower or middle canopy.

Four species (Grey-capped pygmy, Fulvous-breasted, Lesser Yellownap and Great Slaty) used vertical positions that were significantly distinct patterns from almost all other species (Table 4). The remaining six species occupied vertical positions significantly different from smaller species and the Great Slaty.

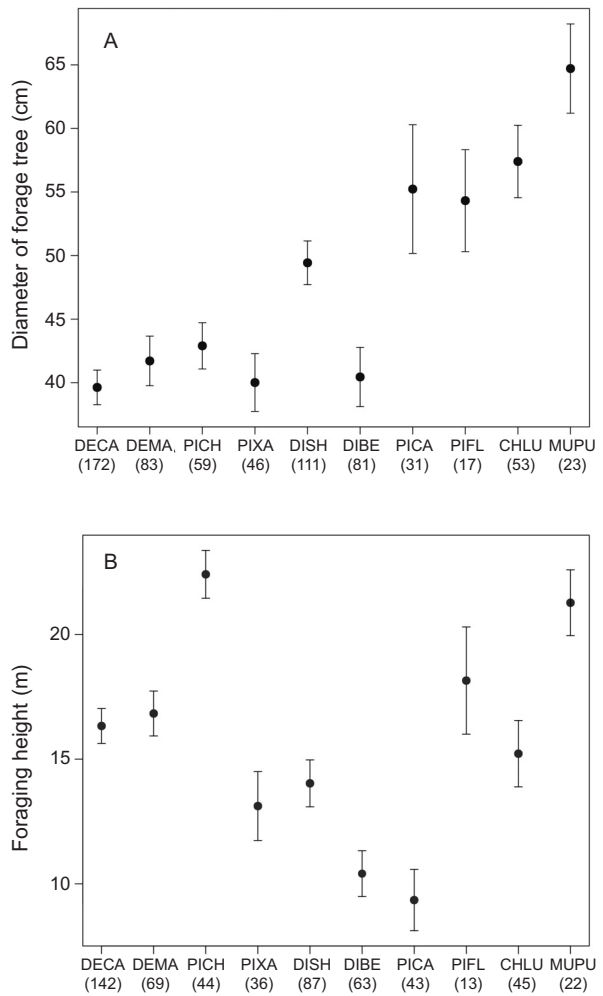


Fig. 2. Foraging of ten woodpecker species in NW India. A — mean forage tree DBH (\pm SE); B — mean foraging height above ground (\pm SE). Sample sizes indicated in parentheses. See Table 1 for key to species codes.

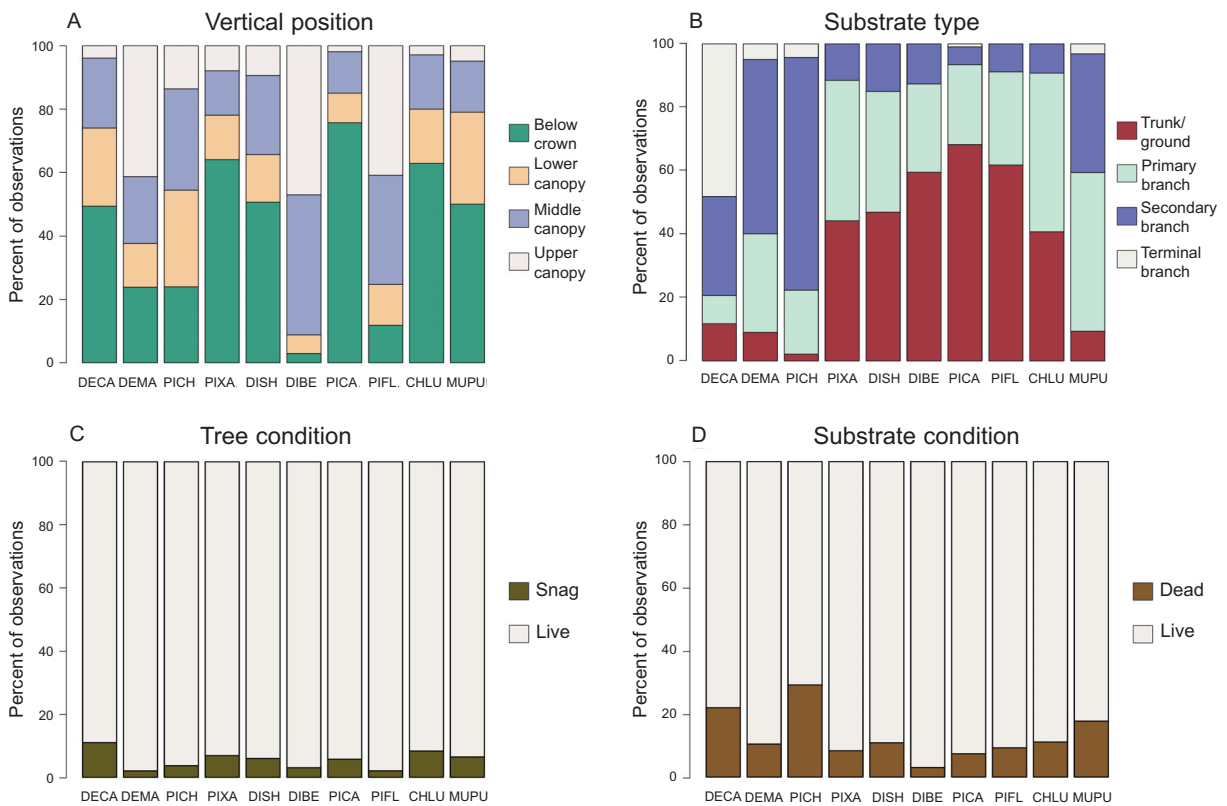


Fig. 3. Frequency of ten woodpecker species foraging in relation to vertical position (A), substrate type (B), tree condition (C) and substrate condition (D). Species arranged in ascending order of body weight. See Table 1 for key to species codes.

The proportional use of substrate types i.e. parts of a tree for foraging differed significantly among species (Fisher's exact test $p < 0.001$). The Grey-capped Pygmy, was conspicuous in its preferential use of terminal branches (Fig. 3B). Secondary branches were very strongly preferred by Lesser Yellownappe (73%) and Fulvous-breasted (55%), while Greater Flameback and Great Slaty mostly used primary branches (50%). Three species — Grey-headed, Greater Yellownappe and

Black-rumped Flameback — selectively chose tree trunks and occasionally foraged on the ground. Streak-throated and Himalayan Flameback foraged on trunk/ground and primary branches in nearly equal proportions. On the whole, four species had the most distinctive patterns in use of different substrate types (Table 4). These included three of the smaller species (Grey-capped Pygmy, Fulvous-breasted, and Lesser Yellownappe) and the Great Slaty. The medium-bodied species

Table 3. Mean diameters of trees used for foraging by individual species versus those available, compared using bootstrap t-tests. Species showing significant differences between used and available DBH are indicated in bold. See Table 1 for key to species code names.

Species	Size	Estimated mean DBH of trees (in cm)		Critical values (95%) of t	
		Used	Available	Lower	Upper
DECA	Small	39.5	28.8	3.87	7.91
DEMA	Small	41.5	30.1	2.18	6.17
PICH	Small	42.3	30.5	1.94	6.26
PIXA	Medium	39.0	35.3	-0.92	3.02
DISH	Medium	49.6	31.5	5.67	10.10
DIBE	Medium	38.6	30.0	1.72	5.54
PICA	Large	51.0	29.9	2.11	6.81
PIFL	Large	54.9	31.4	1.68	6.14
CHLU	Large	57.7	32.2	4.31	8.98
MUPU	Very Large	66.8	31.4	2.21	7.97

Table 4. Inter-specific differences between species pairs for vertical position (below diagonal) and substrate type (above diagonal). Figures indicate p-values from Fisher's exact tests; differences significant at $\alpha = 0.05$ are shown in bold. Superscript letters S, M, L and V denote small-, medium-, large- and very large-sized species, respectively. See Table 1 for key to species code names.

	DECA ^S	DEMA ^S	PICH ^S	PIXA ^M	DISH ^M	DIBE ^M	PICA ^L	PIFL ^L	CHLU ^L	MUPU ^V
DECA ^S		< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
DEMA ^S	< 0.001		0.990	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	1.000
PICH ^S	0.945	< 0.001		< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.045
PIXA ^M	< 0.001	0.090	< 0.001		1.000	1.000	0.450	1.000	1.000	< 0.001
DISH ^M	< 0.001	< 0.001	< 0.001	1.000		1.000	0.045	1.000	1.000	< 0.001
DIBE ^M	< 0.001	< 0.001	< 0.001	1.000	1.000		1.000	1.000	0.450	< 0.001
PICA ^L	< 0.001	< 0.001	< 0.001	0.090	< 0.001	1.000		1.000	0.045	< 0.001
PIFL ^L	< 0.001	< 0.001	< 0.001	1.000	1.000	1.000	1.000		1.000	< 0.001
CHLU ^L	< 0.001	0.045	< 0.001	1.000	1.000	1.000	0.090	1.000		< 0.001
MUPU ^V	0.045	< 0.001	1.000	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	

were largely similar vis-à-vis type of substrate used.

Proportional use of snags and live trees appeared to differ significantly among species (Fisher's exact test $p = 0.025$; Fig. 3C). Only one species pair (Greater Flameback vs. Grey-capped Pygmy Woodpecker) showed statistically significant differences in the use of snags (Table 5). Greater Flameback was found to use snags in greater proportion than were randomly available.

Significant differences were found among species in their use of dead versus live branches for foraging (Fisher's exact test $p < 0.001$). Notable use of dead substrates was observed in Fulvous-breasted Woodpecker and the Greater Flameback (respectively, 30% and 22%), which was higher than for other species that used dead branches infrequently (20% or less; Fig. 3D). The Fulvous-breasted Woodpecker differed from all other woodpeckers except Streak-throated, Greater Yellownape and Greater Flameback in its preference for dead substrates (Table 5).

Niche overlap

Of the ten species analysed, the Great Slaty had the most distinct overall foraging niche that did not overlap much with other species (Fig. 4). Larger woodpeckers, particularly Great Slaty and Greater Flameback, had relatively lower overlaps in their choice of forage tree DBH than did smaller species (Figs. 4, 5). In terms of their foraging heights, Greater Flameback, Himalayan Flameback, Great Slaty, Greater Yellownape and Streak-throated showed a high degree of overlap with most other species. With regards to vertical position, low overlap were observed for Great Slaty, Grey-capped Pygmy, Fulvous-breasted, Grey-headed and Lesser Yellownape. Choice of substrate type appeared to be a distinguishing factor between species, as overlap value for this dimension were generally low. As far as the condition of trees used for foraging was concerned, the high values of overlap suggested that there was little segregation between species along this dimension. Similarly, overlaps were high among species vis-à-vis their proportionate choice of

Table 5. Inter-specific differences between species pairs for tree condition (below diagonal) and substrate condition (above diagonal). Figures indicate p-values from Fisher's exact tests; differences significant at $\alpha = 0.05$ are shown in bold. Superscript letters S, M, L and V denote small-, medium-, large- and very large-sized species, respectively. See Table 1 for key to species code names.

	DECA ^S	DEMA ^S	PICH ^S	PIXA ^M	DISH ^M	DIBE ^M	PICA ^L	PIFL ^L	CHLU ^L	MUPU ^V
DECA ^S		< 0.001	1.000	1.000	1.000	1.000	1.000	1.000	0.315	1.000
DEMA ^S	1.000		< 0.001	1.000	< 0.001	< 0.001	< 0.001	1.000	1.000	0.045
PICH ^S	1.000	1.000		1.000	1.000	1.000	1.000	1.000	1.000	1.000
PIXA ^M	1.000	1.000	1.000		1.000	1.000	1.000	1.000	1.000	1.000
DISH ^M	1.000	1.000	1.000	1.000		1.000	1.000	1.000	0.810	1.000
DIBE ^M	0.900	1.000	1.000	1.000	1.000		1.000	1.000	0.225	1.000
PICA ^L	1.000	1.000	1.000	1.000	1.000	1.000		1.000	0.180	1.000
PIFL ^L	1.000	1.000	1.000	1.000	1.000	1.000	1.000		1.000	1.000
CHLU ^L	0.045	1.000	0.720	1.000	1.000	1.000	1.000	1.000		0.585
MUPU ^V	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	

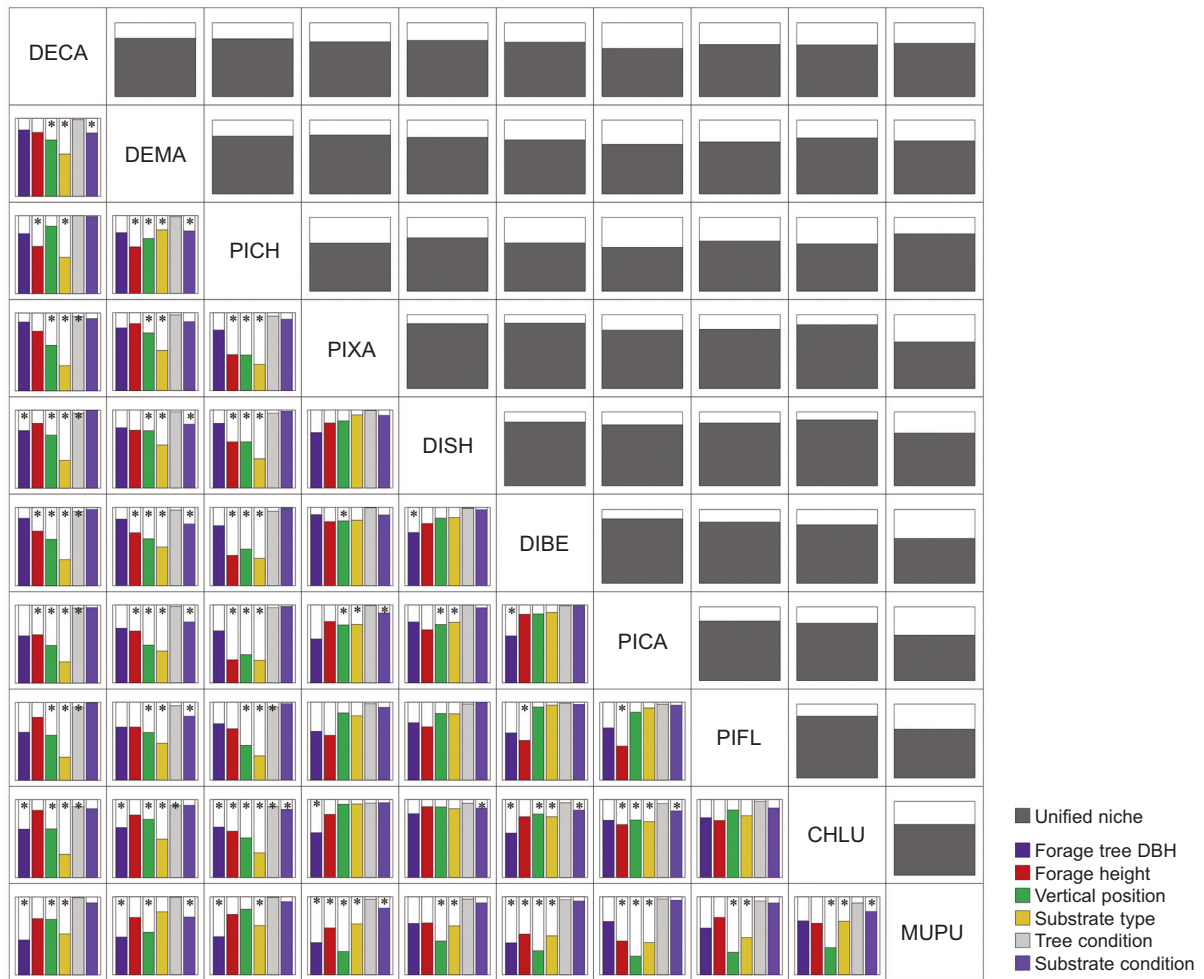


Fig. 4. Foraging niche overlaps between species pairs for individual dimensions (below diagonal) and overall niche overlap (above diagonal). The y-axis scale indicates overlap values, ranging from 0 (empty) to 1 (completely filled). Overlaps significantly lower than expected are indicated by asterisks. Species arranged in ascending order of body weight. See Table 1 for key to species codes.

dead/live branches for foraging except for Fulvous-breasted and Greater Flameback that showed some degree of segregation from other picids.

The Great Slaty Woodpecker had the most distinct overall foraging niche that had much lower overlap with other species when compared with the overall mean of 0.75 for the entire community (Fig. 4). Grey-capped Pygmy, Fulvous-breasted, Lesser Yellownappe and Grey-headed Woodpeckers also showed comparatively lower overlaps. Medium-sized species and the larger-bodied Greater Yellownappe all had overlaps that were moderately large. Greater Flameback and Himalayan Flameback had the most similar foraging niches (overlap of 0.89), while Lesser Yellownappe and Grey-headed had the most distinct foraging niches (overlap 0.59).

NMDS indicated that the species fell into four distinct groups (Fig. 5) — small (Grey-capped Pygmy, Fulvous-breasted and Lesser Yellownappe), medium (Streak-throated, Himalayan Flameback and Black-rumped Flameback), large (Grey-headed, Greater Yellownappe and Greater Flameback) and very large (Great Slaty). Results from MRPP showed that differences between these groups were significant ($A = 0.56$; $d_{\text{observed}} = 0.09$, $d_{\text{expected}} = 0.2046$; $p < 0.001$).

Relationship between foraging characteristics and body weight

A strong relationship was observed between mean diameter of trees used by woodpecker species and their body weights. There was a significant correlation between mean forage tree DBH of woodpecker species with their respective

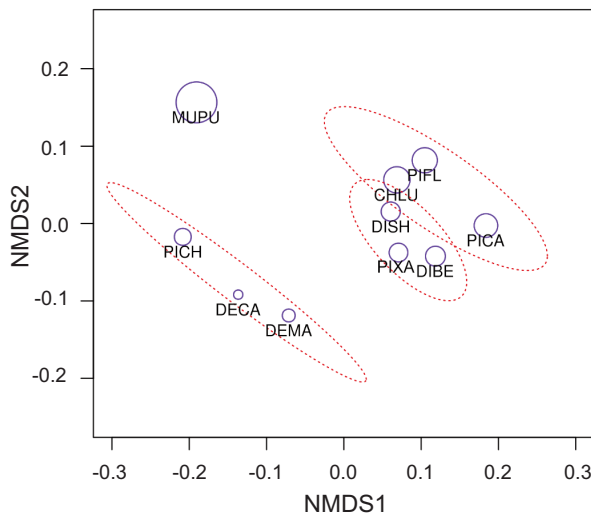


Fig. 5. NMDS ordination plot of average foraging niches of the ten woodpecker species. Area of circle is proportional to body weight of each species. Dotted ellipses indicate 0.95 confidence limits of the ordinated groups. See Table 1 for key to species codes.

body weights ($r = 0.86$, $p = 0.001$). However, no significant relationship was observed between mean foraging height and body weight.

Overall foraging niche segregation between species was highly associated with their respective differences in body weight (Mantel's $r = 0.48$, $p = 0.011$). Regarding individual niche dimensions, forage tree DBH had very high associations with body weight (Mantel's $r = 0.70$, $p = 0.002$), while body weight also had a moderately high association with vertical position (Mantel's $r = 0.50$, $p = 0.037$). None of the other dimensions were found to be related to morphometrics (Table 6).

DISCUSSION

The present study shows that woodpeckers differentiate their foraging niches by having different preferences for substrates as well as choosing distinct vertical positions. Forage tree diameter emerged as an important factor of niche segregation. Research done in the Western Ghats, southern India, also reported segregation among woodpeckers by substrate size (Santharam 1995). Selectivity in forage tree diameter by picids has been documented in several other studies: Diameter of trees selected by Lesser Spotted Woodpecker *Dendrocopos minor* was lower than those for Great Spotted Woodpecker *D. major* in Italy (Laiolo et al. 2003). Large trees were

Table 6. Relationship between body weight and foraging niche (overall and individual dimensions) analysed using Mantel's tests of association. Relationships significant at $p < 0.05$ are indicated in bold.

Distance matrix 1	Distance matrix 2	Mantel's r	p-value
Body weight	Overall niche segregation	0.48	0.011
Body weight	Foraging tree DBH	0.70	0.002
Body weight	Foraging height	0.05	0.430
Body weight	Vertical position	0.50	0.037
Body weight	Substrate type	0.13	0.223
Body weight	Tree condition	0.07	0.285
Body weight	Substrate condition	0.17	0.158

preferred by Middle Spotted Woodpecker *D. medius* (Pasinelli & Hegelbach 1997, Robles et al. 2007), Pileated Woodpecker *Dryocopus pileatus* (Newell et al. 2009), and White-backed Woodpecker *D. leucotos* (Melletti & Penteriani 2003), while Downy Woodpeckers *Dryobates pubescens* foraged on smaller diameter substrates (Conner et al. 1994).

The present study also shows that large trees are important not only for larger species but generally for all woodpeckers. Larger woodpeckers showed a greater segregation in their choice of forage tree diameter than did smaller species, possibly because substrates smaller than a threshold size (which depends on body size) are not conducive for obtaining forage. Support comes from our concurrent study, which found that the abundance of large trees was an important determinant of woodpecker diversity (Kumar et al. 2014). Preference for large-diameter trees has also been observed in the picid community in Western Ghats, India (Santharam 1995). Styring (2002) also found that substrate use among woodpeckers in Malaysia was associated with body size and other morphological characteristics. Similarly, studies in the Americas also found that larger trees were used in greater proportion to availability by Red-cockaded Woodpecker *Leuconotopicus borealis* (Engstrom & Sanders 1997), American Three-toed Woodpecker *Picoides dorsalis* (Gagne et al. 2007) and the Magellanic Woodpecker *Campephilus magellanicus* (Vergara & Schlatter 2004).

Foraging height and vertical position were vital distinguishing elements among sub-Himalayan woodpeckers. Spatial partitioning has also been noted in previous studies. For example, foraging height was an important factor segregating foraging among woodpecker species in the Southeast Asia (Short 1978, Styring & Zakaria 2004a, Lamertink 2007) as well as in Europe (Török 1990, Böhm & Kalko 2009) and North America (Williams

1975, Conner et al. 1994). It was also found that individual species largely followed segregation patterns like the ones observed in other parts of the subcontinent e.g. Brown-capped Pygmy Woodpecker *Dendrocopos nanus*, which is equivalent in body size to Grey-capped Pygmy Woodpecker in this study, was found to occupy the highest stratum for foraging (Santharam 1995).

The study species, especially the smaller ones, differed appreciably in their choice of substrate type (i.e. tree parts). This result is consistent with previous research in south India (Santharam 1995), USA (Kisiel 1972, Reller 1972, Williams 1975) and Britain (Smith 2007). Notably, Santharam (1995) had also reported the smaller species (Brown-capped Pygmy, Yellow-crowned *D. mahratensis* and Lesser Yellownappe) to prefer higher order substrates, a trend that was also apparent in the present study.

Regarding preferences for substrate condition, results of this study conform with Santharam (1995) who, too, found no interspecific differences in the use of foraging substrate condition in the woodpecker community of Western Ghats. Deadwood has been considered an important resource for many woodpecker species (Winkler et al. 1995), and research from our region suggests that snag density is an important determinant of woodpecker abundance and species richness (Kumar et al. 2014). However, as no clear differentiation vis-à-vis substrate condition was observed across species in this study, it may be that dead substrates are uniformly important for all species.

Body size influenced selection in tree size used for foraging. Selection of substrate sizes for foraging may be due to 'optimal trunk diameter' to balance vigilance and foraging, as in case of the Downy Woodpecker (Lima 1992). Another possible reason for body-size related patterns in foraging could be biomechanical capabilities and limitations that are a function of body mass (Lammertink 2007). As body weight is highly correlated with bill length, the morphological basis for the relationship between body weight and tree DBH is likely due to skull morphology, which has been linked with foraging behaviour (Short 1978, Leonard & Heath 2010). Size-related patterns were not apparent in foraging height. Great Slaty Woodpecker, although the largest species, foraged much higher than most other species, resembling Lesser Yellownappe, which is only one-fifth as heavy. The species has been observed to occupy a similar vertical stratum in Borneo (Lammertink 2007).

Certain niche dimensions appeared to be concurrent. Niche separation along vertical position was connected to segregation by the part of the tree used. This is an expected relationship, since substrates like tree trunks are naturally present at lower heights than for example terminal branches which occur higher up in the vertical profile. Segregation along foraging height was, to some extent, related to vertical position.

The present study shows that woodpecker species that overlap along one dimension of the foraging niche usually segregate in other dimensions. It also demonstrates that differentiation in foraging ecology may be a potential mechanism of coexistence in the woodpecker community of the sub-Himalayan region. Moreover, segregation along certain dimensions is linked to morphological traits of the species. Further research to explore the relation between foraging behaviour and phylogeny will shed light on the evolution of this divergence. Moreover, further investigation of resource availability (e.g. insect prey abundance, nesting and roosting sites) is required for a more complete understanding of the possible mechanisms of coexistence among the woodpecker community of the region.

Certain aspects of foraging behaviour underscored in this study are valuable from the point of view of conservation: The distinct size of trees chosen by different woodpecker species is likely to have an implication on their abundance if the preferred diameter classes of trees are removed. Also, considering the distinctive preferences among species in other aspects, e.g. foraging height and substrate type, modification of stand structure in other ways (for example, by cutting limbs and branches) could alter the availability of preferred foraging resources. Such changes in habitat structure could, in turn, lead to an impoverishment of woodpecker diversity.

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STRESZCZENIE

[Zróżnicowanie nisz żerowiskowych u sympatrycznie występujących dzięciołów w lasach północno-zachodnich Indii]

W pracy analizowano zróżnicowanie nisz żerowiskowych gatunków dzięciołów występujących sympatrycznie w wilgotnych lasach liściastych w północno-zachodnich Indiach. Badania prowadzono na ośmiu powierzchniach różniących się strukturą i składem drzewostanu (Fig. 1). Na każdej powierzchni w latach 2006–2008 20-krotnie prowadzono obserwacje żerujących dzięciołów na transektach o długości 2,0 km każdy. Badano preferencje poszczególnych gatunków względem miejsc żerowania oraz rolę międzygatunkowych różnic w ekologii żerowania jako potencjalnego mechanizmu leżącego u podstaw ich współwystępowania. W przypadku obserwacji żerującego ptaka zapisywano następujące parametry: 1) pierśnicę drzewa, na którym żerował, 2) wysokość żerowania, 3) miejsce żerowania, 4) wysokość żerowania względem korony drzewa, 5) kondycję drzewa (żywe lub martwe) oraz 6) kondycję miejsca żerowania (żywe lub martwe).

W analizach uwzględniono gatunki dzięciołów, dla których zebrano co najmniej 10 obserwacji żerowania, czyli w sumie 10 gatunków. Ze względu na wielkość ciała dzięcioły przyporządkowano do jednej z czterech kategorii: 1) gatunki małe — dzięcioły: drobny, płowy i żółtoczuby; 2) gatunki średniej wielkości — dzięcioł białobrewy oraz sułtany: himalajski i żółto-grzbiety, 3) gatunki duże — dzięcioły: zielonosiwy i żółtoczuby, sułtan złotogrzbiety, 4) gatunki bardzo duże — mohun wielki (Tab. 1).

Stwierdzono wyraźne różnice w pierśnicy drzew, na których żerowały poszczególne gatunki dzięciołów. Ogólnie, gatunki mniejsze żerowały na wyraźnie cieńszych drzewach niż gatunki większe (Tab. 2, Fig. 2A). Ponadto, wszystkie gatunki poza jednym wybierały spośród dostępnych drzew te o większej pierśnicy (Tab. 3). Wysokość żerowania także różniła się pomiędzy gatunkami (Tab. 2), dzięcioł zielonosiwy był obserwowany niżej niż pozostałe gatunki, często na ziemi (Fig. 2B). Istniały wyraźne różnice między gatunkami w wysokości żerowania względem korony drzewa, z sześcioma gatunkami żerującymi głównie poniżej korony (Tab. 4, Fig. 3A). Także częstość żerowania w poszczególnych miejscach (pień, konary i gałęzie) różniła się pomiędzy gatunkami dzięciołów, dzięcioł drobny preferował najdrobniejsze gałęzie (Fig. 3B). Mimo, że kondycja samego drzewa oraz miejsca żerowania różniła się pomiędzy gatunkami dzięciołów, gdy analizowano cały badany zespół (Fig. 3C,D), to analizując pary gatunków najczęściej nie stwierdzano istotnych różnic w odniesieniu do tych dwóch parametrów (Tab. 5). Analizując nisze żerowiskowe stwierdzono, że gatunki, które silnie pokrywały się w jednej z charakterystyk żerowania, na ogół różniły się w innych. Gatunkiem, którego nisza w najmniejszym stopniu pokrywała się z niszami innych gatunków był mohun wielki (Fig. 4). Analiza segregacji nisz wyróżniła cztery grupy dzięciołów, co miało związek z wielkością ich ciała (Fig. 5, Tab. 6). W przypadku poszczególnych parametrów niszy tylko pierśnica oraz wysokość względem korony drzewa wykazywały związek z wielkością ciała (Tab. 6).

Badania wykazały, że zróżnicowanie nisz żerowiskowych może tłumaczyć współwystępowanie tak dużej liczby gatunków dzięciołów w wilgotnych lasach liściastych północno-wschodnich Indii. Biorąc pod uwagę, że większe gatunki preferują większe drzewa, to szczególnie usunięcie dojrzałych drzewostanów może wpłynąć negatywnie na ich liczebność.