Species-specific bird functions in a forest-canopy food web

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Bird functions in a forest-canopy food web were evaluated by a large-scale field experiment using 'canopy' enclosures. By controlling the presence of two bird species, great tits (*Parus major*; foliage gleaner) and nuthatches (*Sitta europaea*; trunk gleaner), in the enclosures, their effect on predatory insects (ants), herbivorous insects (Lepidoptera larvae) and producers (oak trees) was quantified. Great tits reduced the density of Lepidoptera larvae and, indirectly, leaf damage, but had no impact on ants. Nuthatches decreased the density of ants but did not influence either Lepidoptera larvae or leaf damage. These results highlight species-specific functions of birds in the maintenance of forest ecosystems.

Keywords: cascading effects; canopy enclosure; avian predation; ants; Lepidoptera larvae; oak

1. INTRODUCTION

The linkage between biodiversity and maintenance of an ecosystem is a prime directive in ecological research (Naeem *et al.* 1994; Lawton 1994; Tilman & Downing 1994; Tilman *et al.* 1996). Previous studies have emphasized the general concept that all species are not equal in regard to their ecological functions (Tilman & Downing 1994), providing evidence that species richness can strongly affect ecosystem properties (Bengtsson *et al.* 1997). Although the fact that an increasing number of species enhances the productivity or stability of an ecosystem has been well established (Tilman *et al.* 1996), our understanding of the variations in functions between species is still insufficient to understand fully the mechanisms behind this phenomenon. For instance, ecologists have long attempted to answer the question 'Why is the world green?' (Hairston *et al.* 1960) by examining predator-induced top-down control over interactions between lower trophic levels, this being considered as one of the most important mechanisms balancing natural ecosystems. Species-specific features of such predator functions, however, have received little attention to date, although the maintenance of the system, in reality, may be achieved by the net effect of multiple predatory species.

In forest ecosystems, trophic cascading effects of birds remain controversial (Holmes *et al.* 1979; Marquis 1996). Predation by birds has been shown reduce the population sizes of herbivorous insects, which, in turn, decrease herbivory, at least on juvenile trees (Marquis & Whelan 1994). However, the role of the birds' predation has never been assessed in forest canopies, probably because of logistical difficulties associated with structural complexity and scale (Lawton 1995). In forest canopies, in which a great proportion of primary production occurs and diverse organisms coexist to form complex food webs, do insectivorous birds produce apparent cascading effects on lower trophic levels? If so, the functions can be expected

to vary among bird species with a variety of foraging habits (Norberg 1977; Wiens 1989). A typical food web for forest ecosystems has often been represented as having four trophic levels: carnivorous vertebrates as top predators, invertebrates as intermediate predators, herbivorous invertebrates, and trees as primary producers (Holmes *et al.* 1979; Spiller & Schoener 1990; Gunnarsson 1996). However, careful consideration of the function of each species in the web shows the trophic structure of such communities to be much more complex.

Foraging habits differ clearly between tits (*Parus* spp.) and nuthatches (*Sitta* spp.), which are often major components of the insectivorous bird assemblage in the cool-temperate deciduous forests of the Northern Hemisphere. In Japan, for instance, great tits (*Parus major*) primarily capture Lepidoptera larvae (herbivores) on canopy foliage (i.e. foliage gleaners), whereas nuthatches (*Sitta europaea*), except parents feeding fledglings, generally forage for ant species (intermediate predators) on tree trunks (trunk gleaners) (Royama 1969; Yamashina 1980). The food web can therefore be regarded as having three trophic levels when focusing on the role of tits, but four levels when considering that of nuthatches. Foliage-gleaning birds are predicted to decrease the number of herbivores, in this case Lepidoptera larvae, and, in turn, reduce herbivory on trees (figure 1, model A). In contrast, trunk-gleaning birds are expected to decrease the number of intermediate predators (i.e. carnivorous ants), thereby having a negative effect on trees by indirectly increasing the number of herbivorous insects via a cascading effect (figure 1, model B). Here we present experimental evidence that insectivorous birds have prominent effects on canopy food-web structures by controlling insects at multiple trophic levels in a species-specific manner.

2. MATERIAL AND METHODS

A field experiment was conducted in the Tomakomai experimental forest (TOEF; 42°43'N, 141°36'E) in Hokkaido, the northernmost island of the Japanese archipelago. This cool-temperate (5.6 °C mean annual temperature; 1161 mm mean annual precipitation) secondary-growth deciduous forest is dominated by oak (*Quercus crispula*), together with a mixture of

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Figure 1. Models of a food web in forest canopies. Model A illustrates how the predation of birds affects lower trophic levels in a three-level scheme of the HSS hypothesis (Hairston *et al.* 1960). Model B illustrates effects of bird predation in a four-level scheme. Arrows indicate the effect of consumers on their prey in the presence of all effects among each component in the web. Arrow thickness indicates per-capita effect.

15 other canopy tree species. Most of the trees break bud in mid-May and shed their leaves in mid-October. Three common bird species in the forest are the great tit (*P. major*), marsh tit (*Parus palustris*) and nuthatch (*S. europaea*) (Ishigaki & Matsuoka 1972). The herbivorous-insect assemblage on oak is dominated by Lepidoptera larvae (*ca.* 80% by number), while the remaining taxa account for only small proportions (*ca.* 8% Homoptera, *ca.* 6% Hymenoptera larvae and *ca.* 6% others). The carnivorous-invertebrate assemblage is dominated by ants (*ca.* 75%), with other taxa being of lesser importance (*ca.* 20% spiders and *ca.* 5% others) (Murakami 1998).

The experiment was carried out during June and July of 1997. The four treatments (natural condition as control; great tit only present; nuthatch only present; and birds absent) with three replicates each were randomly assigned to 12 sites (15 m × 15 m) distributed over a 12 ha area of the forest. Each experimental site, which contained 16–19 canopy oaks (10–20 cm diameter at breast height (DBH), 6–9 m height) plus 21–32 individuals of other canopy species, was separated from adjacent sites by at least 50 m. Nine ‘canopy’ enclosures (15 m × 15 m area, 10 m height) were constructed so as to control the presence of birds within the experimental sites (figure 2). An entire forest canopy was covered with 17 mm nylon mesh supported by four iron posts. The mesh allowed the passage of all invertebrates except large moths and stag beetles but completely excluded birds. On 1 June, three non-breeding males of both great tit and nuthatch were captured by mist-nets at locations over 1 km distant from the nearest enclosure. Six enclosures were then stocked with one bird each, the remaining three were left as ‘no bird’ treatments. This density (equivalent to *ca.* 40 individuals per hectare) was *ca.* 1.5 times greater than the overall natural density of insectivorous birds in this forest (Ishigaki & Matsuoka 1972). Experimental birds were released from the enclosures immediately after completion of the experiment. The masses of individual

Figure 2. Canopy enclosure in early June, 1997.

birds did not change significantly during the experiment (great tit, $t = -1.3$, $p = 0.321$; nuthatch, $t = 0.20$, $p = 0.863$, by paired t -test). In addition to controlling bird presence, ant density on the oak trees was also manipulated. Since ant manipulations potentially affect bird foraging behaviour (Haemig 1992), the former were carried out in the three ‘no bird’ enclosures. The ants were experimentally excluded from eight oak trees (reduced ant treatment) by placing a tanglefoot (Fuji Co. Ltd., Tokyo, Japan) ring around the lower trunks (at < 0.5 m height). Within the enclosures three ant species, *Myrmica ruginodis*, *Lasius hayashi* and *Formica japonica*, were dominant on the oak trees.

During the two-month experimental period, we observed bird foraging behaviour both inside and outside (control sites) the enclosures and we recorded the foraging sites (foliage, twigs or trunks, or ground) and prey types (Lepidoptera or Hymenoptera larvae, ants, or other invertebrates). All bird-enclosure sites were visited during the experiment in a random order once every six days (ten visits for each site) and the control sites once every three days (20 visits for each). During each visit, bird-foraging behaviour was observed for 1 h at various times during daylight hours (05.00–16.00). Within the enclosures, great tits primarily captured caterpillars (72% of the total foraging attacks) with most of them expected to be Lepidoptera larvae and other invertebrates (18%) on foliage, with only occasional attacks on the ground and twigs or trunks (10% total). In contrast, nuthatches frequently fed on ants (63%) and other invertebrates (18%) on twigs or trunks, with foliage gleaning (mainly preying on caterpillars) making up only 19% of the total attacks. The proportions for foraging sites and prey types did not differ significantly inside and outside the

enclosures for either the great tit (χ^2 -test, foraging site, d.f. = 2, $\chi^2 = 1.57$, $p = 0.456$; prey type, d.f. = 2, $\chi^2 = 1.60$, $p = 0.449$; total number of foraging attacks observed inside the enclosures, $n = 284$, and in natural conditions, $n = 299$) or nuthatch (foraging site, d.f. = 2, $\chi^2 = 3.68$, $p = 0.16$; prey type, d.f. = 2, $\chi^2 = 3.18$, $p = 0.204$; inside, $n = 201$, natural, $n = 134$). Each of the three control sites was visited by both great tits (2.17 ± 1.54 individuals h^{-1}) and nuthatches (1.08 ± 0.42 individuals h^{-1}).

We measured three key parameters of the canopy food web: the abundance of ants (intermediate predators) on tree trunks, Lepidoptera larvae (herbivores) on foliage and the degree of oak leaf (producers) damage. This was done immediately after oak budbreak but before the experimental manipulation (27–31 May) to assess the initial condition, and on two occasions thereafter, in the middle (18–21 June; first sampling) and at the end (20–24 July; second sampling) of the experiment. For each sampling, all invertebrates on a 1 m^2 trunk surface at $> 5\text{ m}$ height were collected by a vacuuming technique (Elton 1972) on eight randomly chosen oak trees (DBH $> 10\text{ cm}$) in each of the 12 study sites. Invertebrates on foliage ($> 8\text{ m}$ height) were also collected quantitatively from 40 shoots of the year on each of the eight oak trees in each study site. Each shoot was cut and immediately put into a plastic sack before transfer to the laboratory. In the ‘no bird’ treatment sites, eight additional oak trees with the ‘reduced ant’ treatment (i.e. ‘no bird plus reduced ant’) were sampled. Samples were preserved in 70% ethanol, sorted and classified as either Lepidoptera or Hymenoptera larvae, ants and others. In the present study, because the density of Hymenoptera larvae was quite low on the oaks, only Lepidoptera larvae and ants were examined from the foliage and trunk samples, respectively. The degree of leaf damage was calculated as the mean percentage area missing from the restored leaf area, measured to the nearest 0.1% by National Institutes of Health Image software for 50 leaves randomly collected from the canopies ($> 8\text{ m}$ height) of eight oaks. The values for the initial conditions and those during the experiment were separately analysed. Mean values ($n = 3$) for the numbers of ants and Lepidoptera larvae and percentage leaf damage in each site under initial conditions were analysed with one-way ANOVA (main factor = treatment). Those during the experiment were analysed with repeated-measures ANOVA (main factor = treatment, repeated factor = sampling period). All exact values were $\log_{10}$ transformed and percentage values were arcsine transformed.

3. RESULTS

As a consequence of the experimental manipulation, we found a striking difference in the cascading effects between the bird species in the canopy food web (figure 3). Before the manipulation, none of the three parameters differed between the sites for the five treatments (ant, d.f. = 4,10, $F = 0.92$, $p = 0.490$; Lepidoptera larvae, d.f. = 4,10, $F = 2.62$, $p = 0.099$; oak, d.f. = 4,10, $F = 0.11$, $p = 0.978$; by one-way ANOVA). During the experiment, the density of ants, however, came to differ significantly between the treatments but was not affected by either repeated factors or interaction effects (figure 3a and table 1). The increasing values from the initial to the experimental periods in all but the nuthatch treatments may have resulted from growth of the ant colonies. The density of Lepidoptera larvae also differed significantly between

Figure 3. Mean values (± 1 s.e.m., $n = 3$) of (a) the density of ants, (b) the density of Lepidoptera larvae and (c) the degree of leaf damage on oak canopies, before (initial condition) and on two occasions during the experiment. Data are shown for natural conditions, great tit presence, nuthatch presence, ‘no bird plus natural ant’ and ‘no bird plus reduced ant’ treatments. Different letters indicate significant differences between treatments during the experimental period with $p < 0.05$ (post-ANOVA by Fisher’s LSD).

treatments and was affected by repeated factors but not by interaction effects (figure 3b and table 1). The increase from the first to the second sampling was due to the emergence of newly hatched larvae. The densities of ants in the control, great tits and ‘no bird plus natural ant’ treatments were greater than that in the nuthatch treatment (figure 3a). In the ‘no bird plus reduced ant’ treatment, the ants were completely removed from the oak canopies. The density of Lepidoptera larvae in the ‘no bird plus reduced ant’ treatment was greater than those in both the

Table 1. *Results of repeated-measures ANOVAs on the effect of experimental manipulations on the density of ants, density of Lepidoptera larvae and degree of leaf damage on oak trees*

(MS, mean squares.)

source of variation	d.f.	MS	F	p
density of ants				
treatment	4	0.976	46.65	< 0.001
sampling period	1	0.003	0.43	0.529
sampling period	4	0.005	0.68	0.624
× treatment				
error	10	0.007		
density of Lepidoptera larvae				
treatment	4	0.221	11.65	< 0.001
sampling period	1	0.300	19.04	0.001
sampling period	4	0.006	0.41	0.800
× treatment				
error	10	0.021		
degree of leaf damage on oak				
treatment	4	0.014	6.21	0.009
sampling period	1	0.008	61.58	< 0.001
sampling period	4	< 0.001	0.05	0.995
× treatment				
error	10	< 0.001		

nuthatch and ‘no bird plus natural ant’ treatments, and was lowest in the control and great tit treatments (figure 3*b*). Moreover, differences in the degree of leaf damage between the treatments perfectly mirrored the trends observed for the Lepidoptera larvae (figure 3*c*). The degree of leaf damage differed significantly between treatments and was affected by repeated factors but not by interaction effects (figure 3*c* and table 1). The leaf damage in the ‘no bird plus reduced ant’ treatment was greater than those in the nuthatch and ‘no bird plus natural ant’ treatments, and lowest in the control and great tit treatments.

4. DISCUSSION

This large-scale manipulative experiment revealed that the natural bird assemblage dramatically reduces the density of Lepidoptera larvae and, in turn, leaf damage on oaks in the canopy of cool-temperate deciduous forest. In such a habitat of great structural complexity, the predators could have trophic-cascading effects on the producers. The previous studies that found top-down control of food-web structure in a wide array of natural systems, e.g. the tundra (Oksanen *et al.* 1981), intertidal zones (Menge 1991), lakes (Carpenter *et al.* 1987), streams (Power 1990; Nakano *et al.* 1999), mangroves (Spiller & Schoener 1990) and tree saplings (Marquis & Whelan 1994), have pointed at various factors that alter the outcome of cascading interactions. The present results, however, argue that species-specific features of predators are an important element explaining variation in the outcome.

The two bird species fulfilled species-specific functions in the canopy food web. Great tits, which are typical foliage gleaners, had a direct negative effect on the density of Lepidoptera larvae and an indirect positive effect on oak trees but had no impact on ants. This finding was in line with our specific prediction based on the three-level scheme of the HSS hypothesis (figure 1,

model A). Contrary to our prediction, the trunk-gleaning nuthatches reduced ants by *ca.* 60% but had an overall neutral effect on Lepidoptera larvae and oaks. Ants reduced the density of Lepidoptera larvae and, subsequently, leaf damage on oaks. However, behavioural observations of nuthatches showed that these birds occasionally captured Lepidoptera larvae in the canopy. The neutral effect of nuthatches on Lepidoptera density could therefore have resulted from the confounding effect of such direct predation and the decreased ant density that enhanced Lepidoptera larval survival. In terrestrial food webs including both top and intermediate predators, the former often feed on the latter as well as on herbivores (i.e. omnivory) and so their overall effect on primary producers could be weakened (Schoener 1989; Spiller & Schoener 1990). It was concluded that the ecological functions of the two bird species in the canopy food web differed considerably.

The responses of Lepidoptera larvae and oak foliage to great tit predation were similar to those observed at sites with natural bird-predation pressure. This can be explained by the fact that foliage-gleaning birds accounted for *ca.* 60% by mass of the total insectivorous bird assemblage in the forest; the other groups were trunk gleaners (15%) and ground gleaners or trunk peckers (together 25%). The relatively low abundance of trunk-gleaning birds in the assemblage may explain the weak impact of birds on ants under natural conditions. Nevertheless, omnivorous nuthatches may play a considerable role in stabilizing food-web dynamics, as pointed out by a recent model (McCann *et al.* 1998) that predicted that the weak links provided by omnivory dampen oscillations between trophic levels.

Our results provide a basic understanding of the importance of bird-species diversity in the maintenance of forest ecosystems. Recently, concern has grown that rapid loss of biodiversity will lead to degradation of ecosystem functions (Naeem *et al.* 1994; Lawton 1994; Bengtsson *et al.* 1997). Worldwide loss and degradation of forests certainly will impact on bird-species diversity (Holmes *et al.* 1986; Askins *et al.* 1990), which has often been shown to be delimited by the structural (spatial and species) complexity of vegetation (MacArthur & MacArthur 1961). Therefore, we can expect accelerated destruction of forest ecosystems as a whole due to a negative feedback between decreasing balancing forces of the system associated with bird diversity loss and human-induced direct degradation of forest environments.

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