

FOREST PRODUCTIVITY PREDICTS INVERTEBRATE BIOMASS AND OVENBIRD (*SEIURUS AUROCAPILLUS*) REPRODUCTION IN APPALACHIAN LANDSCAPES

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Abstract. Forest-floor detrital food webs are sustained by annual inputs of leaf fall. However, it is unknown whether this bottom-up effect extends to vertebrates feeding on the detrital food web. We hypothesized that reproductive success of Ovenbirds (*Seiurus aurocapillus* L.) is a function of macroinvertebrate biomass within the detrital food web, and that both macroinvertebrate biomass and Ovenbird reproduction can be predicted from forest productivity (measured by site index). We found that across diverse topography within two physiographic provinces of the central Appalachian Mountains macroinvertebrate biomass is correlated with forest site index. Furthermore, Ovenbird reproduction is a significant, positive function of both site index and macroinvertebrate biomass. We conclude that bottom-up effects of forest productivity propagate through the detrital food web to secondary/tertiary vertebrate predators. Thus site productivity is an effective tool for predicting landscape-scale variation in avian productivity and the strength of bottom-up effects within the forest food web.

Key words: Appalachian Plateau; bottom-up control; deciduous forest; food web structure; invertebrate biomass; Ovenbird reproduction; Ridge-and-Valley province; site index; topography.

INTRODUCTION

The debate over factors that control food web structure is classically polarized between bottom-up (resource availability) and top-down (predation) factors. While there is strong logical and empirical evidence that bottom-up forces are important within food webs (Hunter and Price 1992, Polis 1994), the argument for top-down trophic effects (Carpenter et al. 1985) within food webs is both strong and persistent (Hairston et al. 1960, Fretwell 1977, 1978, Oksanen 1991, Hairston and Hairston 1993). Both older theory (Oksanen et al. 1981) and recent empiricism (Meserve et al. 2003) indicate that it is too simplistic to assume that either bottom-up or top-down processes alone control most food webs, but there are compelling analyses suggesting the primacy (sensu Power 1992) of bottom-up effects. For example, McNaughton et al. (1989) found that herbivore productivity was correlated with primary productivity across a variety of ecosystems and herbivore taxa. Although extension of this correlation to higher trophic levels is less common, one compelling and practical aspect of such correlations is the blossoming potential for predicting spatial variation in food web properties by remote sensing of primary production or through correlation of primary production with

mapped physical conditions (e.g., topography). Such predictions open new frontiers for studying landscape-scale variation in food web structure, but are predicated on defining strong statistical relationships across trophic levels under differing levels of primary production.

In eastern U.S. deciduous forests, most annual primary production enters the detrital food web of the forest floor (Edwards et al. 1970, Bormann and Likens 1981, Coleman et al. 1983, Reiners 1988, Hairston and Hairston 1993). In examining the deciduous forest detrital (leaf litter) food web, Wise and Chen (1999) found that top vertebrate predators do not limit population density of at least one major group of invertebrate predators (wolf spiders, Family Lycosidae), suggesting that top-down control in this system is weak. Chen and Wise (1997, 1999) demonstrated that addition of detritus to forest-floor food webs increased population sizes of both fungivores and their invertebrate predators. In addition, Scheu and Schaefer (1998) experimentally manipulated carbon, nitrogen and phosphorus in decomposing leaf litter and found a doubling of predaceous centipede numbers in response to higher nutrient availability. Collectively these studies strongly suggest that forest-floor detrital food webs are under bottom-up control, but extension of bottom-up effects to the productivity of vertebrates feeding on the forest-floor detrital food web has not been demonstrated.

Spatial variation is seldom addressed in the discussion of control over forest-floor food web structure and

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productivity. As demonstrated by Scheu and Schaefer (1998) nutrient additions to the forest-floor can stimulate productivity of the detrital food web. But within forest ecosystems there is natural spatial variation in detritus quality that accrues from multiple factors, including composition of the tree community (Pastor and Post 1986) and microenvironmental influences on the growth and activity of fungal and bacterial decomposers (Coleman and Crossley 1996). Thus, although bottom-up control of forest-floor food webs is important, considerable variation in the magnitude of this effect may occur across the forest-floor within single forest stands. Likewise, landscape topography induces predictable spatial variation in forest tree species composition, forest microenvironment (e.g., soil moisture; Iverson et al. 1997), and forest-floor nutrient concentrations (Garten et al. 1994).

The effects of spatial variation in site primary productivity on vertebrate predators at the top of the forest-floor detrital food web should be most clearly apparent for vertebrate species that (1) are highly mobile and thus can select among sites of varying productivity, and (2) depend solely on forest-floor habitats for energy and nutrients. Neotropical songbirds annually migrate between southern/tropical wintering grounds and their breeding areas within the eastern deciduous forest and other habitats of North America. Of these migratory species, the forest-interior specialists breed within contiguous forests or large forest fragments (Whitcomb et al. 1981), feeding largely on invertebrates occupying a variety of structural niches within the forest. The Ovenbird (*Seiurus aurocapillus* L.) is one very common forest-interior species that feeds on invertebrates of the forest-floor detrital food web (Stenger 1958). Ovenbirds select territories based on habitat structural cues and food abundance (Smith and Shugart 1987, Burke and Nol 1998). Nonetheless, territoriality and an abundance of individuals force Ovenbirds to occupy a range of site "quality" within forest habitat (Smith and Shugart 1987). Thus spatial variation in forest-interior habitat productivity and food availability should elicit corresponding variation in Ovenbird productivity.

Within the central Appalachian Mountains, topography creates spatial variation in forest productivity across the landscape (Trimble 1964). We hypothesize that this variation in productivity creates spatial variation in bottom-up effects within forest-floor foodwebs. Thus we predict that spatial variation in forest productivity caused by topography will be positively correlated with invertebrate detrital food web productivity, and subsequently with vertebrate predator productivity. If these predictions hold true, then landscape-scale spatial variation in forest-floor food web productivity is ultimately controlled by the distribution of forests relative to topography.

METHODS

Study sites

Eight 10-ha (250 × 400 m) study sites were selected in western Maryland; four in Savage River State Forest (SRSF) within the Appalachian Plateau physiographic province, and four in Green Ridge State Forest (GRSF) which is within the Ridge-and-Valley province (Fig. 1). The Appalachian Plateau receives the highest mean annual precipitation within the state of Maryland (114–140 cm/yr; Brown and Brown 1992), and creates a rain shadow that results in the Ridge-and-Valley province to its east having the lowest mean rainfall (76–88 cm/yr; Brown and Brown 1992). In SRSF, northern red oak (*Quercus rubra*), white oak (*Q. alba*), and sugar maple (*Acer saccharum*) dominate the overstory, with chestnut oaks (*Q. prinus*) common on drier slope positions (Brown and Brown 1992, Brush et al. 1980). Red maple (*A. rubrum*) is common in the subcanopy. Forests at GRSF are dominated by oak and hickory species (red oak, white oak, chestnut oak, scarlet oak [*Q. coccinea*], pignut hickory [*Carya glabra*], mockernut hickory [*C. tomentosa*]), interspersed with pine (*Pinus* spp.) on the driest slopes (Brown and Brown 1992, Brush et al. 1980). In the early 1990s, an outbreak of gypsy moth (*Lymantria dispar*) defoliated large areas of GRSF and also affected dry ridge tops in SRSF. Stands heavily damaged by gypsy moth were avoided for this study.

Within each province, potential study sites were identified along topographic gradients defined by (1) convergent topographic positions where downslope drainage patterns would cause water to accumulate (i.e., topographic convergence index; Beven and Kirkby 1979), (2) relative slope position (Wilds 1996) to indicate lower sheltered slope positions (lower quartile of a slope) and higher elevation exposed slope positions (upper quartile of a slope), and (3) slope aspect to indicate exposure to prevailing westerly winds and heat loading from solar radiation. By overlaying these indicators of "wetness" with forest cover distributions (Anderson Level II USGS classification from the Maryland Office of State Planning) and using 100 m of forest cover as a buffer from other land uses, all potential forest-interior study sites within SRSF and GRSF were delineated. To standardize forest composition, potential sites with large amounts of coniferous (*Tsuga canadensis* or *Pinus* spp.) basal area were eliminated; all potential study sites eventually included in this study had less than 15% coniferous basal area and all but three had less than 10%. Potential study sites were also eliminated if field examination revealed unmapped disturbance or fragmentation (e.g., recent logging roads or forest harvesting). Twenty-two study sites representing a range of wet to dry topographic conditions were chosen to study avian reproduction in 1999 and 2000. In 2000, eight of these study sites were selected to represent the range of variation in forest-interior growing conditions (two wet and two dry within each

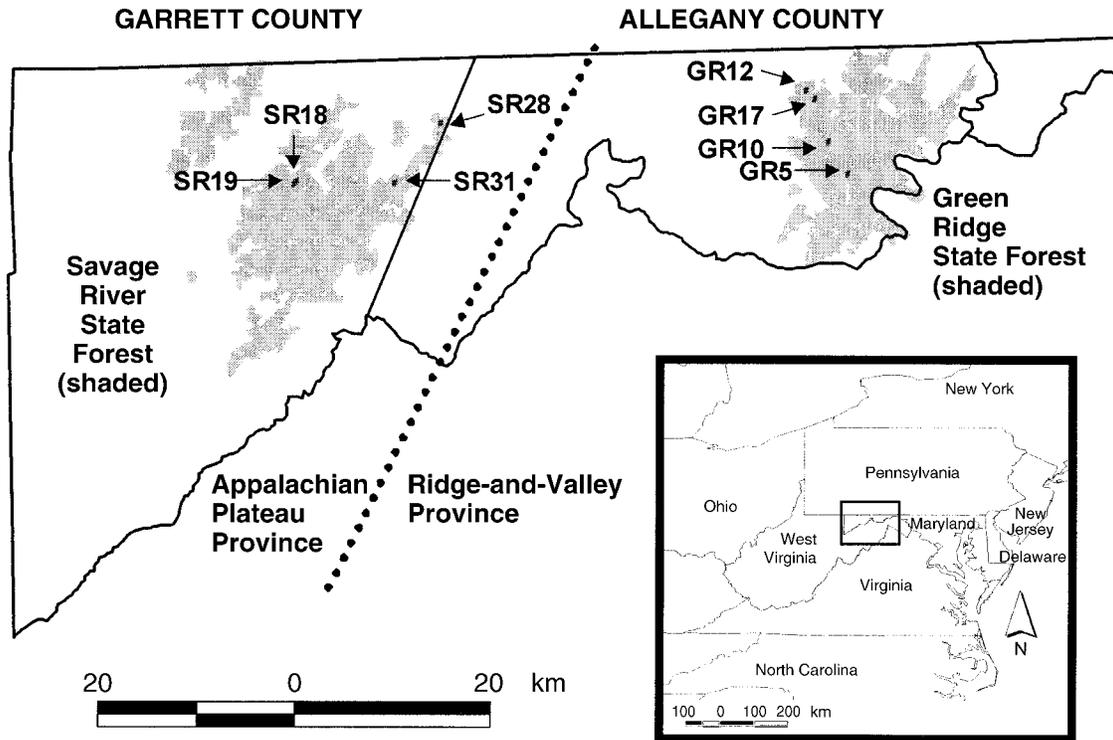


FIG. 1. Location of field sites within the Savage River State Forest (SRSF) and Green Ridge State Forest (GRSF), Maryland, USA. SRSF is located on the Appalachian Plateau physiographic province in Garrett County, and GRSF is in the Ridge-and-Valley province in Allegany County. Each field site is 10-ha of forest interior habitat, and is denoted by the state forest initials and a unique numeric code to identify it within a wider range of potential study sites. Within each province, sites are arrayed across aspect and slope position gradients to capture a wide range of topographic exposures. SR19, SR31, GR5, and GR17 are low slope position, relatively mesic sites. SR18, SR28, GR10, and GR12 are located at higher slope positions and are relatively xeric.

province) that are common across the landscape and studies for these sites were expanded to include forest litter invertebrates. Results from these eight sites are presented here.

Forest productivity

Site index (Carmean 1975) is a metric commonly used to describe forest productivity. Site index integrates forest growth temporally by empirically characterizing the relationship between tree height and tree age to predict the height of a tree at a reference age (usually 50 yr). Although originally applied to even-aged, single-species stands, site index has proven applicable in defining relative site productivity for the mixed oak forests of western Maryland (Sturtevant and Seagle 2004).

To measure site index, trees were sampled in five circular (30 m radius) plots within each 10-ha study site between October 1999 and March 2001. Plots were stratified across each rectangular study area by placing one at its geometric center and the remaining four equidistant between the center and a corner of the study area. Within each plot, five healthy canopy dominant or codominant trees ($N = 25$ per site) were selected and cored using a 40.6-cm Suunto increment borer

(Suunto Corporation, Vantaa, Finland). Diameter at breast height (dbh, at 1.37 m) was recorded to the nearest 0.5 mm for each tree and height was measured to the nearest 0.5 m using an impulse laser rangefinder (Laser Technology, Inc., Centennial Colorado, USA). Height–age relationships vary among tree species. Thus, to standardize site index measures across study sites, sampling focused on northern red oak (Trimble and Weitzman 1956, Stout and Shumway 1982) which was widely distributed across study sites. If red oak was not present at a plot, either white oak or chestnut oak was sampled. All extracted tree cores were placed in plastic straws, returned to the lab, mounted on grooved strips of plywood, sanded, and aged using an Olympus SZ60 microscope (Olympus America, Melville, New York, USA).

Site index was calculated from the equation for upland oaks formulated by Carmean et al. (1989) who used height–age curves by Olson (1959):

$$SI = BH + 0.7709H^{1.0063}(1 - e^{-0.0356A})^{-1.5038H^{-0.0419}} \quad (1)$$

where SI is site index (height in feet with base age of 50 yr), BH is a constant to correct for measuring tree age at a height of 1.37 m, H is average height (in feet) of dominant and codominant oaks (by species), and A

is the average age of the same dominant and codominant trees (by species) that were cored. English units of measure were used for consistency with the voluminous literature on site index. The resulting SI values indicated that Eq. 1 underestimated white oak and chestnut oak growth (Sturtevant and Seagle 2004). These two species responded very similarly to a wide range of site quality and thus a single regression equation was derived ($R^2 = 0.73$, regression MSE = 1.81 m, $P < 0.0001$; Sturtevant and Seagle 2004) to adjust white oak and chestnut oak SI values and make them comparable to red oak:

$$SI_{\text{adj}} = 3.87 + 0.84 SI_{\text{orig}} \quad (2)$$

SI_{adj} represents the adjusted SI for either white oak or red oak, while SI_{orig} is the original SI calculated for each species.

Litter invertebrates

While having some species in common, the forest-floor invertebrate community has relatively little interaction with the underlying soil community (Heal and Dighton 1986). Most common among the fungivores of the forest floor are the springtails (Collembola), mites (Acari), and millipedes (Class Diplopoda) (Chen et al. 1996, Chen and Wise 1997). Fungivores are prey for a variety of other arthropods (Swift et al. 1979, Coleman and Crossley 1996), including predaceous mites, spiders (Order Arachnida), beetles (Coleoptera), pseudoscorpions (Pseudoscorpionida), and centipedes (Class Chilopoda). Ants (Formicidae) are also common. Vertebrates that feed on the invertebrates groups include shrews, mice (e.g., *Peromyscus* spp.), ground foraging birds (e.g., the Ovenbird), and amphibians.

The abundance of litter invertebrates on the eight study sites was determined during spring and summer of 2000 using five 0.5×0.5 m samples of the forest-floor litter (collected down to the mineral soil) taken from each plot that was used to sample forest trees for site index calculations. Each of these five samples was taken at random distances along one of five 5-m transects radiating outward in equal 72° increments from the center of each plot. Sampling was replicated temporally during the avian breeding season by collecting samples in May, June, and July. Thus each site was represented by 75 litter samples. All litter samples were placed in plastic bags, returned to the laboratory, and placed in modified Tulgren funnels with a 100-W light bulb as the heat source to extract invertebrates into a 70:30 ethanol:water solution. After extraction, dry litter samples were examined by hand to insure that all macroinvertebrates were being removed. Other studies (e.g., Mazerolle and Hobson 2003) have assumed that invertebrates larger than 3.0 mm could be located and consumed by foraging birds. To avoid omitting any potential food items we extended the lower size limit to 2.0 mm, although these individuals added very little to total macroinvertebrate biomass. These macroinver-

tebrates were removed from solution, rinsed with ethanol, and identified to class or genus. After identification, macroinvertebrates were dried at 105°C for 48 h and total dry mass measured. Litter samples from which invertebrates were extracted were also dried (70°C for 48 h in a forced-air oven) and weighed. Thus, the macroinvertebrates could be expressed as densities (numbers/m² or g dry mass/m²) or as g dry mass invertebrates/g dry mass litter. Smaller invertebrates, numerically dominated by Collembola and mites, were counted in the ethanol solution in a gridded pan using an Olympus SZ60 microscope.

Ovenbird reproductive success

Based on Vickery et al. (1992), an elaboration of the spot-mapping technique (Kendeigh 1944) was used to assess the diversity, density, and relative fledging success of forest songbirds on each study site during the 2000 breeding season. An observer experienced in forest songbird identification by sight and sound visited each study site twice per week beginning in mid-May and ending in mid-August. Five observers were rotated among sites to avoid observer bias. Sampling for each site was alternated between early (sunrise to 08:30) and late morning (09:00 to 12:00). Avian observations were mapped to 50 m outside the study site boundaries to account for edge territories. All songbirds, excluding the woodpeckers (Family Picidae), were recorded, although only Ovenbirds are reported on here. Observers recorded all sight and sound occurrences of individual birds and their observed behavior. Observations also included long-distance movements (>50 m) and counter-singing between males on adjacent territories. Aural and visual detections of fledglings were investigated to count the number of fledglings, estimate their age class based on plumage and agility (Appendix), and determine sex and number of attending parents. Territories were delineated by the minimum convex polygon method; territory density was calculated as the number of territories per 10-ha study area (Appendix). Successful fledging for a territory was determined by observation of fledglings. Ovenbird relative reproductive success was calculated as the density of successful territories divided by the density of all territories. Edge territories with $<25\%$ of the territory inside the site boundary were excluded in this calculation.

Statistical analyses

Three successively finer scales of analysis were used: sites ($N = 8$), plots from the four study sites within each physiographic province ($N = 20$), and total plots from all eight sites (total $N = 40$). No temporal trends in population densities were apparent for invertebrate groups, thus all densities and biomasses represent means of data aggregated across the three invertebrate samplings. Macroinvertebrate biomass was described as a function of site index at both the plot and site scale using simple linear regression (SAS Institute Inc.

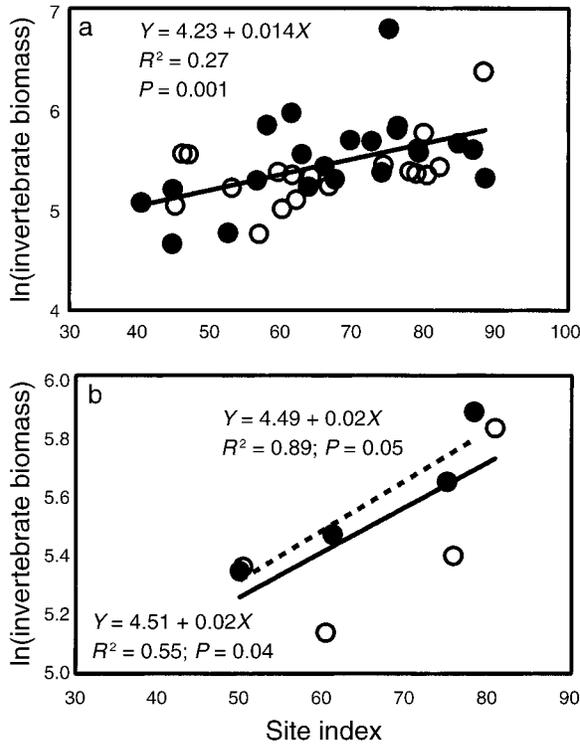


FIG. 2. Forest-floor litter macroinvertebrate biomass (log-transformed; originally measured as $\text{g/m}^2 \times 10^3$) as a function of forest site index. Site index is a temporally integrative measure of forest productivity interpreted as expected height (in feet) at a base age of 50 yr. Analyses related invertebrate biomass to site index for (a) multiple plots located within eight 10-ha study sites, and (b) plot means for each of the study sites. Open circles are plots from the Appalachian Plateau, filled circles are data from the Ridge-and-Valley. Solid regression lines are analyses lumped across provinces. The dashed line in (b) is a regression for the Ridge-and-Valley only.

1990). Ovenbird reproductive success was also analyzed by regression at the site scale as a function of both macroinvertebrate biomass and site index.

RESULTS

Litter macroinvertebrate biomass was positively correlated with site index at both the plot and study site scales (Fig. 2). Thus the large variation in site index evident for both the Appalachian Plateau and Ridge-and-Valley study sites (Fig. 2) capture a wide range of environmental conditions that influence invertebrate populations. At the plot scale of analysis (Fig. 2a), the ranges of invertebrate biomass for the two provinces were very similar, indicating that province effects are minimal. Nonetheless, separate regressions (not shown) at the plot level for the Ridge-and-Valley ($R^2 = 0.33, P = 0.008$) and Appalachian Plateau ($R^2 = 0.16, P = 0.09$) indicate a stronger relationship between site index and invertebrate biomass for the Ridge-and-Valley. Macroinvertebrate biomass is more strongly re-

lated to forest site index when these variables are averaged to the site level (Fig. 2b; results for both provinces combined, $R^2 = 0.55, P = 0.04$). Like the plot-level analysis, invertebrate biomass is not as closely correlated with site index for the Appalachian Plateau (not shown in Fig. 2b; $R^2 = 0.57, P = 0.25$) as for the Ridge-and-Valley ($R^2 = 0.89, P = 0.05$).

The proportion of Ovenbird territories fledging young was strongly and positively correlated with both invertebrate biomass (Fig. 3a) and with site index (Fig. 3b). Thus study sites that have higher forest productivity and higher mean litter invertebrate biomass also are more productive of this forest-interior bird species. Except for one outlier from the Appalachian Plateau data, no distinctions in fledging data distributions were found between Ridge-and-Valley and Appalachian Plateau study sites (Fig. 3). That outlier was a study site on the Appalachian Plateau with only one Ovenbird territory in 2000. Based on its invertebrate biomass ($5.15 \times 10^3 \text{ g/m}^2$) and site index (59) relative to other

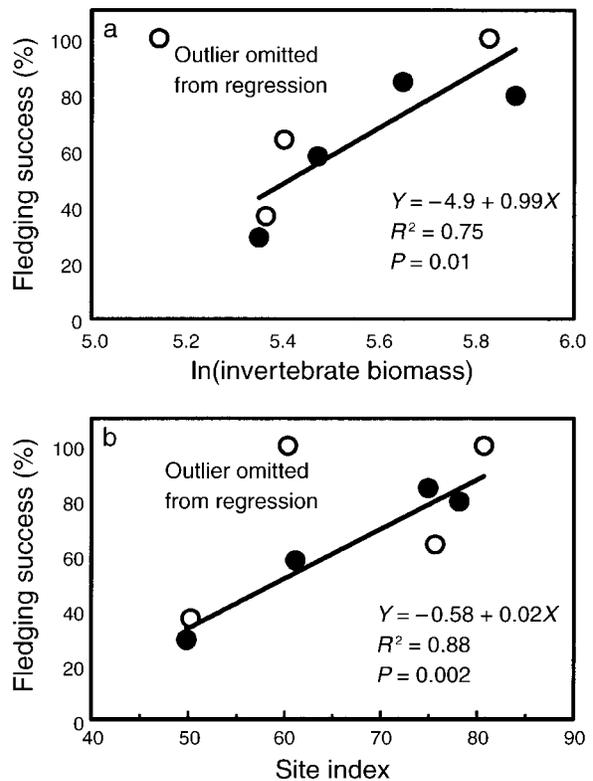


FIG. 3. Relationship of Ovenbird territory fledging success (%) to (a) macroinvertebrate biomass (log-transformed; originally measured as $\text{g/m}^2 \times 10^3$), and (b) site index. Fledging success was measured on each 10-ha study site via behavior mapping. Invertebrate biomass is the mean for 75 samples per site. Site index is a measure of forest productivity and measures expected tree height (in feet) at a base age of 50 yr. Open circles are plots from the Appalachian Plateau; closed circles are data from the Ridge-and-Valley study sites. Note that the regression results presented omit one outlying data point.

study sites (Fig. 2b), this outlier had a relatively low macroinvertebrate biomass for its site index. Thus the fledging success of this site is attributed to high within-territory invertebrate biomass and perceptible habitat/microhabitat selection by the nesting pair within a study site that is on average low in invertebrate biomass. With this outlier in the regression, Ovenbird nesting success was still significantly related with site index ($R^2 = 0.56$, $P = 0.03$); outlier inclusion in the regression of nesting success on macroinvertebrate biomass resulted in nonsignificant results ($P = 0.15$).

DISCUSSION

Within the deciduous forest-floor invertebrate food web, population sizes of fungivore and predator species are under bottom-up control by resources (Chen and Wise 1999). Other studies (Smith and Shugart 1987, Burk and Nol 1998) have demonstrated that Ovenbird territories have greater invertebrate food resources than surrounding forest-floor habitat, and Wise and Chen (1999) presented evidence that vertebrate predators do not limit litter invertebrate populations. Collectively, these studies suggest that bottom-up effects could extend to vertebrate predators of the litter invertebrate community. Our results support this hypothesis by demonstrating that Ovenbird fledging success is positively correlated with forest site index and forest litter macroinvertebrate biomass. The overall strength of these relationships suggests a strong bottom-up linkage across trophic levels, propagating from primary producers to a vertebrate species that is a secondary, and often tertiary, predator.

We have also found that hillslope topography creates spatial variation in forest productivity in central Appalachian landscapes, resulting in predictable effects on invertebrate detrital food web productivity and, consequently, productivity of vertebrates feeding on the detrital food web. Beyond the landscape scale, these predictable relationships may shift at physiographic province or ecoregion (e.g., Bailey 1995) boundaries where large changes in climate can ameliorate the effects of hillslope topography. This shift is evident in comparing our results from the wetter Appalachian Plateau and the drier Ridge-and-Valley. Although separate analyses demonstrated that prediction of invertebrate biomass and Ovenbird reproductive success from site index is viable for each physiographic province, these relationships were always stronger for the Ridge-and-Valley. Because the topographic positions (i.e., elevation, slope, and aspect) analyzed for the two provinces were similar, it is likely that the greater annual precipitation and lower potential evapotranspiration of the Appalachian Plateau partially ameliorate the effects of hillslope topography.

Physical landscape characteristics as key drivers of trophic interactions, particularly bottom-up effects, are found across diverse ecosystems. For example, Garrott et al. (2002) found that spatial variation in geothermal

activity and geochemistry influences quality of ungulate forage, subsequently altering adult ungulate senescence and susceptibility to predation. Although ecologists have long focused on the response of herbivores to food quantity and quality (e.g., Mattson 1980, Seagle and McNaughton 1992), our work suggests that greater focus on relating spatially variable drivers of primary production to multiple trophic levels will further define the extent and spatial predictability of bottom-up effects in food webs.

From a temporal perspective, we also suggest that annual variation in precipitation can intensify or ameliorate hillslope topography effects and, perhaps, provincial effects. This impact obviously is not apparent in the single season results presented here, but significant differences in bird reproduction do occur between drought and normal rainfall years in the central Appalachians (Sturtevant 2001). This situation is analogous to studies in other ecosystems. For example, Meserve et al. (2001) suggested that the small mammal community in semiarid thorn scrub habitat is heavily influenced by the bottom-up effect of plant productivity which is, in turn, a function of oscillations in precipitation. For Appalachian landscapes topography apparently serves as a long-term integrator of environmental conditions and thus a spatial predictor of the range in magnitude of bottom-up effects, while annual precipitation may determine short-term variation within that range.

The existence of high- and low-quality habitat/territories for breeding songbirds is not a new concept (Krebs 1970) but it has been most often examined in terms of density-dependent vs. density-independent control over population size and more recently as site-dependent control over population size (Rodenhouse et al. 1997). Site-dependent regulation suggests that avian populations are controlled by the distribution of breeding individuals or pairs among territories with differing abilities to support successful reproduction. We have not attempted to account for all impacts on Ovenbird reproduction and population size, although nest parasitism was minimized by working only in forest-interior habitat (Sturtevant 2001). Nonetheless, our results strongly suggest that the food component of habitat/territory quality for forest-interior songbirds is under bottom-up control and can be predicted from forest growth data. This result provides a potential means for assessing habitat quality, independent of actual avian breeding success, that can serve as (1) a null hypothesis for field studies of the site-dependence hypothesis, (2) a prediction of the overall breeding quality for a landscape, or (3) a template for simulation studies of avian population dynamics in spatially heterogeneous landscapes or landscapes subject to human alteration.

Although bottom-up effects imposed by topography are apparent in our study, variation in detrital food web structure with spatial scale must be considered in future studies. For example, we found that site index is a

stronger predictor of invertebrate biomass at the 10-ha site level than at the plot (approximately 0.1-ha) level, suggesting microtopographic variation is important for local invertebrate productivity. In general, neotropical migratory birds establish summer breeding territories that integrate food resources over areas small enough to be influenced by microtopographic features. Because producing and rearing offspring are energetically expensive, food resource levels within these territories are crucial to reproductive success. Unfortunately, experimental studies of terrestrial detrital food webs at or larger than the spatial scale of bird territories are nonexistent. While experimental manipulations of finer scale systems are elegant and insightful in terms of mechanisms, they can be difficult to relate to spatial resource effects at the scale of vertebrate habitat use. For example, Chen and Wise (1999) supplemented detritus for a forest litter invertebrate community and convincingly demonstrated the importance of detritus quantity for productivity of both detritivores and their invertebrate predators. Nonetheless, this demonstration of bottom-up control over system productivity is problematic for explaining spatial variation in the forest ecosystem or landscape in which the experiments were embedded because (1) the amount of leaf detritus input to forest-floor food webs is naturally rather consistent from year to year and thus does not resemble experimental supplementation; (2) barring significant disturbances, detrital inputs to the forest-floor have low temporal, but potentially high spatial, variation in quality because of the longevity and spatial distribution of tree species; and (3) factors such as microtopography are not considered. Thus, understanding forest food web interactions for species that integrate resources over heterogeneous areas larger than typical experimental manipulations, such as Ovenbird territories, requires the mechanistic understanding produced by fine scale experiments in conjunction with broader scale correlations such as those presented here.

It is important to consider the mechanism by which forest site index influences litter invertebrate biomass. Forest site index is a long-term integrative measure of forest productivity that, in the central Appalachians, is highly correlated with site wetness, which is in turn controlled by topography (Iverson et al. 1997). Mesic conditions apparently provide more suitable habitat and environmental conditions for invertebrate populations to carry out their life cycles, for those plant species that provide higher quality detritus for invertebrate detritivores, and/or for growth of decomposing fungal populations on which the invertebrates feed. By any or all of these means, mesic conditions facilitate the bottom-up dynamics of the leaf litter invertebrate food web, resulting in greater food availability and greater fledging success for Ovenbirds.

Factors that drive spatial and temporal variation in food webs have historically been difficult to define, and results presented here leave open a variety of questions

about the hierarchical effects of abiotic and biotic factors on food web structure, as well as the effect of scales of observation/experimentation on perceived food web structure. Yet generalizations about food web structure are crucial for management of harvested food webs and central to conservation of others. Our results lend evidence to the primacy and trophic extent of bottom-up effects for structuring the forest-floor detrital food web across diverse landscapes. Although spatial and temporal variation in the strength of bottom-up effects may be introduced by forest tree succession, topographic distributions of tree species, and forest disturbances, our results suggest that a large portion of this variation is predictable from site productivity. In application, measurement and predictive spatial modeling of site index (Trimble 1964) or other measures of forest productivity should provide one means of ranking forest stands for detrital food web productivity and thus for conservation value to neotropical migratory birds such as the Ovenbird.

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APPENDIX

Definitions of bird age classes, and a discussion of territory definition and the calculation of fledgling success is available in ESA's Electronic Data Archive: *Ecological Archives* E086-083-A1.