

## THE ECOLOGY OF ENERGY AND NUTRIENT FLUXES IN HEMLOCK FORESTS INVADDED BY HEMLOCK WOOLLY ADELGID

BERNHARD STADLER,<sup>1,3,4</sup> THOMAS MÜLLER,<sup>2</sup> AND DAVID ORWIG<sup>3</sup>

<sup>1</sup>Bayreuth Institute for Terrestrial Ecosystem Research, University of Bayreuth, 95440 Bayreuth, Germany

<sup>2</sup>Leibnitz Centre for Agricultural Landscape and Land Use Research Müncheberg, Institute of Landscape Matter Dynamics, Gutshof 7, D-14641 Paulinenaue, Germany

<sup>3</sup>Harvard University, Harvard Forest, P.O. Box 68, Petersham, Massachusetts 01366 USA

**Abstract.** The hemlock woolly adelgid (HWA, *Adelges tsugae* Annand) is currently causing a severe decline in vitality and survival of eastern hemlock in North American forests. We analyzed the effects of light HWA infestation on vertical energy and nutrient fluxes from the canopy to the forest floor. Canopy throughfall, litter lysimeters, and laboratory litter microcosms were used to examine the effects of HWA-affected and unaffected throughfall on litter type, leachate, and litter chemistry. Early in the season adelgid infestation caused higher dissolved organic carbon (DOC; +24.6%), dissolved organic nitrogen (DON; +28.5%), and K (+39.3%) fluxes and lower inorganic nitrogen fluxes (−39.8%) in throughfall and in adjacent litter solutions collected beneath infested compared to uninfested trees. Needle litter collected beneath uninfested hemlock had significantly lower N concentrations compared to needles collected beneath infested trees, while no difference in N concentrations was found in birch litter. Bacteria were significantly more abundant on hemlock and birch litter beneath infested trees, while yeasts and filamentous fungi showed no consistent response to HWA throughfall. Litter microcosms showed that less DOC was leaching from birch than from hemlock needles when exposed to HWA throughfall. Overall, NH<sub>4</sub>-N and DON leachate concentrations were higher from birch than from hemlock litter. Thus, HWA-affected throughfall leads to qualitative and quantitative differences in nitrogen export from the litter layer. The N concentration of hemlock litter did not change with time, but the N concentration in birch litter increased significantly during the course of the experiment, especially when HWA-affected throughfall was applied. We suggest a nonlinear conceptual model for the temporal and vertical transition of energy and nutrient fluxes relative to progressing HWA infestation from a pure hemlock to a birch/maple-dominated forest. Progressive needle loss and changes in needle chemistry are likely to produce a humped-shaped DOC curve, while N fluxes initially decrease as infestation continues but rise eventually with hemlock decline and immigration of hardwood species. These findings suggest that it is necessary to understand the biology and specific physiological/trophic effects of exotic pests on their hosts and associated ecosystem processes in order to decipher the temporal dynamics, direction of change, and functional consequences.

**Key words:** *Adelges tsugae*; carbon–nitrogen cycling; hemlock woolly adelgid; litter; litter decomposition; nonlinear ecosystem processes; throughfall fluxes.

### INTRODUCTION

According to Vitousek (1990) three principal effects of exotic species on ecosystems should be recognized: changes in (1) nutrient availability in biogeochemical cycles, (2) trophic relationships within food webs, and (3) physical (structural) alterations of the biotic and abiotic environment. This classification readily captures the direct and indirect effects of exotic species on other biota and their environment, and it has been used as a framework for many studies aiming to identify the ecological consequences of invasions. An impressive

amount of information is now available on the effects of invasive species on their physical and biological environment. Reviews and special issues include exotic plants (Daehler 2003), fungi (Palm 2001), aquatic animals (Carlsson et al. 2004), and to a lesser extent exotic terrestrial vertebrates (Forsy and Allen 1999), earthworms (Bohlen et al. 2004), or insects (Holway et al. 2002, Goulson 2003). Surprisingly, even though the effects of exotic insects such as the gypsy moth (*Lymantria dispar*) can be enormously destructive in the eastern United States, these three Vitousek categories are typically studied in isolation and nutrient flux effects are underappreciated.

Insect herbivores can impact foliage, nutrient cycling in the canopy, and decomposition through manipulation of plant tissue and alteration of the chemical properties of litter produced by infested plants. For example, they

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<sup>4</sup> E-mail: bernhard.stadler@bitock.uni-bayreuth.de

can affect carbon, nitrogen, and phosphorous concentrations in living foliage and induce the production of secondary compounds such as polyphenols and tannins (Choudhury 1988, Karban and Baldwin 1997, Belovsky and Slade 2000, Hättenschwiler and Vitousek 2000, Chapman et al. 2003). In addition, the production of excreta or protective structures like wax wool changes the quantities of energy and nutrients available in the canopy (Seastedt and Crossley 1984, Schowalter et al. 1986, Lovett and Ruesink 1995, Stadler et al. 1998, Schowalter 2000, Christenson et al. 2002). For example, the sugar-rich excreta of aphids (honeydew) has significant effects on nutrient cycling in the canopies of coniferous trees with lower amounts of nitrogen leaching out of the canopies both at low (Stadler et al. 2001b) and high aphid densities (Carlisle et al. 1966, Stadler and Michalzik 1998). These energy-driven biotic effects are very robust and in terms of throughfall chemistry even more pronounced than the effects of pollutants (Stadler et al. 2001a). Less clear is how energy and nutrient fluxes are affected and whether this changing chemical environment (e.g., throughfall) carries over to the forest floor via litter quality parameters (e.g., C:N ratios) and subsequent nutrient transformation and export from the litter layer. In addition, energy and nutrient fluxes are conventionally described after filtering the solutions (standardized pore size 0.45  $\mu\text{m}$ ), potentially introducing a methodological bias. This barrier could lead to erroneous conclusions on nutrient cycling, especially when insect-mediated processes involve trophic links with microorganisms and when easily degradable compounds are involved. To reduce this potential source of error, we measured the particulate organic matter (POM) in throughfall of infested and reference trees.

Hemlock woolly adelgid (HWA, *Adelges tsugae* Annand) was introduced from Asia into the eastern United States in the 1950s, where it occurs mainly on eastern hemlock (*Tsuga canadensis* (L.); Souto et al. 1996). The ecology of this exotic species in its new environment is well documented (McClure 1989b, 1991, McClure and Cheah 1999, 2002). Its life cycle includes two annual generations with large temporal overlap among all life stages. Adult sistens of the overwintering generation deposit eggs into wax-rich woolly ovisacs from late February to March/April. Hatching commences in April, and first instar nymphs (crawlers) begin searching for suitable sites within the canopy of their host tree or through dispersal by wind, birds, or human activity (McClure 1989a). Adelgids insert their stylet at the base of a needle where they start feeding on the xylem ray parenchyma cells (Young et al. 1995). Typically, a single adelgid feeds at the base of a single needle. The progrediens initiate a second generation on hemlock by laying their eggs soon after reaching maturity in June. The hatching nymphs then enter summer aestivation, which lasts until October. This second generation feeds and develops through late autumn and matures in late February (McClure and

Cheah 1999). Trees of any age or size can be infested and damaged by HWA, resulting in progressive decline in vitality and eventual mortality within 5–15 years (Orwig and Foster 1998, Bonneau et al. 1999). Hemlock woolly adelgid is currently reported from 15 states in the eastern United States. Previous studies showed that hemlock decline initiates microenvironmental changes such as increased light reaching the forest floor and higher soil temperatures and is associated with accelerated nitrate exports (Jenkins et al. 1999). Landscape effects include the widespread and selective elimination of hemlock, eventually generating a more homogeneous landscape dominated by broad-leaved deciduous species, particularly black birch (*Betula lenta*; Orwig and Foster 1998, Orwig et al. 2002).

A widely held assumption of the effects of invaders is that they affect ecosystem functions in a linear way, e.g., with progressive infestation and increases in population size. However, alternative scenarios are possible, especially if complex food web relationships between plants, herbivores, and microorganisms are involved, and more recent models suggest the possibility of rapid regime shifts (van Nes and Scheffer 2004), especially for aquatic ecosystems (Steele 1998, Scheffer et al. 2001, Carpenter 2003). Here we build on our initial work on the effects of HWA on hemlock ecosystems (Stadler et al. 2005) in which we studied different degrees of HWA infestation and the spatial variability of HWA-mediated processes in the canopy of hemlock at different sites from central Massachusetts to southern Connecticut. Those trees were infested for several years, with heavily infested trees showing an advanced stage of needle loss and decline in vitality.

In 2004 we took advantage of the low winter temperatures in New England that reduced HWA survival by 80–90% (A. Paradis and J. Elkinton, *unpublished data*). This high mortality rate reflects a setback to a lighter stage of infestation and provided an opportunity to study infested and uninfested trees at the same location. In this study we performed a field experiment in which we collected throughfall beneath uninfested and lightly infested hemlock trees at the same site and followed HWA-mediated processes on litter solution and microbial populations beneath the sampled trees. Because there is a mixture of hemlock and birch litter in the field, we also conducted a microcosm experiment under more standardized conditions separating the effects of HWA-affected and unaffected throughfall on birch and hemlock litter.

In particular we ask: (1) What is the difference in throughfall fluxes/chemistry beneath uninfested trees and trees with low levels of HWA infestation? (2) How is POM affected in throughfall depending on infestation? (3) Are litter chemistry, microbial colonization, and litter leachate chemistry affected during a light stage of HWA infestation? (4) Do hemlock litter and birch litter respond differently to HWA throughfall application? We focus on vertical energy and ion and nutrient fluxes in the periphery

of the hemlock canopy and develop a conceptual model on fluxes summarizing our findings on nutrient cycling in eastern hemlock forests that are in a state of transition from pure hemlock to birch/maple stands.

#### MATERIAL AND METHODS

##### *Field site and HWA abundance*

Field experiments were carried out at Mount Tom State Reservation, located in the town of Holyoke, Hampden County, in south-central Massachusetts, USA (42°26' N, 72°63' W). The reservation lies on a traprock ridge consisting of basaltic volcanic rock in the Connecticut River Valley Ecoregion (Griffith et al. 1994). Mean January temperature is -2.9°C, mean July temperature is 23.1°C, and mean annual precipitation is 112 cm, with a mean of 110 cm of snow (Mott and Swenson 1978). Soils at these sites are comprised of sandy and silty loams of the Holyoke and related rock outcrop series and are generally shallow and somewhat excessively drained (Mott and Swenson 1978). Study sites contained patches of infested and uninfested reference hemlock trees at an elevation of 170 m above sea level. The experimental trees were 4–5 m tall and selected randomly on the basis that no mature trees were overshadowing their canopies to avoid interference with throughfall quantity and quality. Forest composition in the central portion of the Reservation is dominated by hemlock (54% relative importance value) and contains red oak (22%), red maple (13%), and black birch (5%; D. Orwig, N. Povak, M. Manner, D. Niebyl, and D. Foster, *unpublished data*). Hemlock woolly adelgid have been present in the Reservation since the early 1990s and have resulted in tree decline and areas of overstory mortality. Adelgid populations have fluctuated over time, based on hemlock health and winter temperatures. For example, during the relatively mild winter of 1998 adelgid mortality at Mt. Tom was approximately 20% (Skinner et al. 2003) and following the cold winter of 2004 mortality exceeded 95% (A. Paradis and J. Elkinton, *unpublished data*). Although we do not know the exact infestation history of the experimental trees, which could affect the results, we observed no visible symptoms of foliar loss, branch dieback, or gray foliage that is commonly associated with several years of HWA infestation (D. Orwig, *personal observation*). To reduce this uncertainty we restricted our experiments to the periphery of trees where most new growth occurs (see Appendix A).

Infestation of the experimental trees was determined in mid-April when the sistens have fully developed ovisacs. In this way we were able to accurately identify adelgids that were alive. We only determined the number of adelgids on the current year shoots to facilitate comparison with previous studies. HWA is fairly evenly distributed in the canopy of hemlock, probably due to crawler dispersal (McClure et al. 2001).

The uninfested reference site was a section of the Prospect Hill (PH) tract of the Harvard Forest, located in north-central Massachusetts at an elevation of 335 m above sea level. Soils are predominantly acidic, sandy

loams that developed in glacial till overlying gneiss and schist. Vegetation is typical of the transition hardwoods–white pine–hemlock region (Westveld et al. 1956).

##### *Field and laboratory throughfall and litter solution analyses*

Canopy throughfall and adjacent litter leachates were collected beneath four HWA-infested and -uninfested trees at Mt. Tom every 1–2 weeks after rain events from 12 May until 13 September 2004 (Appendix A). Hemlock and birch litter from infested trees at Mt. Tom and uninfested trees at Harvard Forest was analyzed for C and N content and abundance of yeasts, filamentous fungi, and bacteria. In addition, subsamples of uninfested hemlock and birch litter were rinsed every second week for nine weeks with either HWA-affected or unaffected throughfall in the laboratory (Appendix A). Throughfall and litter leachates were analyzed for dissolved organic carbon (DOC), ammonium-N ( $\text{NH}_4\text{-N}$ ), nitrate-N ( $\text{NO}_3\text{-N}$ ), potassium ( $\text{K}^+$ ), dissolved organic nitrogen (DON), total nitrogen ( $\text{N}_{\text{total}}$ ), and particulate organic matter (POM) (Appendix A).

##### *Data analyses*

Throughfall and litter solution fluxes were converted to milligrams per square meter per sampling interval. Fluxes for all ions and nutrients were analyzed using a repeated-measures MANOVA for the effects of HWA infestation and solution type (throughfall, litter solution) (between-subject factors). Sampling dates were used as repeated measures (within-subject factors). The response variables were log(10)- or square-root-transformed to meet assumptions of variance homogeneity (Sokal and Rohlf 1995), but untransformed data are presented in the figures to facilitate viewing and interpretation. Fluxes of different compounds collected beneath infested and uninfested trees were examined to see whether they differ over time and whether throughfall fluxes affect litter fluxes. Because HWA enters summer aestivation in late June, become inactive, and show no growth or production of wax wool, we decided to analyze fluxes beneath infested trees in two steps to better filter out HWA-related effects. The first time interval comprised the period from the beginning of the experiment to the time of summer aestivation at the end of June. The second interval comprised the period from aestivation to the end of the experiment. Because the second interval produced mostly nonsignificant main and interaction effects we do not present a detailed table on the statistical output. Fluxes of particulate organic matter and C and N concentrations of Mt. Tom litter were analyzed with one-way repeated-measures ANOVAs using infestation and litter type as the main effects. Normality assumptions of the data were checked prior to analyses and log( $x + 1$ )-transformed when necessary to normalize variances across treatments. Differences in microbial growth on infested and unin-

fested litter and differences in leachate concentrations of the litter leaching experiment were analysed with *t* tests. All statistical analyses were conducted with the SPSS statistical package (version 10.0.5; SPSS, Chicago, Illinois, USA).

## RESULTS

### *Throughfall and litter solution in the field*

After heavy mortality during the winter of 2003–2004 sistens density declined to  $2.7 \pm 1.1$  individuals/shoot (mean  $\pm$  SE). In the following we refer to differences in solution chemistry between these lightly infested and uninfested hemlock trees. The DOC fluxes in throughfall were significantly higher beneath HWA-infested trees early in the season, when the first adelgid generation was actively producing wax wool. After entering summer diapause, throughfall fluxes did not differ beneath infested and uninfested hemlock (Fig. 1a; Appendix B contains full MANOVA table). This pattern is mirrored in the DOC litter solution, with higher DOC fluxes in the HWA-affected litter, especially early in the season. Overall, DOC fluxes were higher in litter than in throughfall (Fig. 1b; Appendix B, significant solution effect). Inorganic nitrogen fluxes were somewhat higher early in the season (Fig. 1c, e) and significantly lower during the active period of the adelgids beneath infested compared to uninfested hemlock. These differences were less consistent in the litter fluxes, which also were lower compared to the throughfall fluxes (Fig. 1d, f; Appendix B, significant solution effects). In contrast, DON fluxes were higher beneath infested trees early in the season, both in throughfall and litter solution (Fig. 1g, h; Appendix B), and differences disappeared later in the season. Total nitrogen fluxes were lower beneath infested trees early in the season in throughfall (Fig. 1i) but higher in litter solution (Fig. 1j; Appendix B, significant solution  $\times$  infestation interactions). Potassium fluxes were also significantly higher in throughfall beneath infested trees and declined with time/adelgid activity (Fig. 1k). Fluxes did not differ between throughfall and litter (Fig. 1l, solution type not significant), indicating the unimpeded vertical passage of K through the system. Except for  $\text{NH}_4\text{-N}$  and  $\text{N}_{\text{total}}$ , the solution  $\times$  infestation interactions did not differ significantly, indicating that the direction of change in fluxes due to HWA infestation was similar in throughfall and litter solutions. This also suggests that throughfall fluxes strongly affect litter fluxes and that a disturbance in the canopy cascades down to the forest floor. After the adelgids entered summer aestivation, differences in matter fluxes often became less pronounced and main effects and interaction effects were mostly not significant (statistics not shown).

Particulate organic matter fluxes in throughfall showed a similar decline over time to the filtered solutions (Fig. 2, Appendix C), and total organic carbon (TOC) fluxes were significantly higher in throughfall beneath infested hemlock, especially during the early

season. Although the trend for particulate nitrogen was similar, the strong temporal change in fluxes made it less likely to detect an overall significant infestation effect (marginally nonsignificant main effect and significant time  $\times$  infestation interaction). Nevertheless, compared to the filtered solutions (Fig. 1i), the unfiltered N fluxes were much higher beneath infested trees early in the season. This indicates that HWA enhances those biological processes that reduce the availability of inorganic nitrogen compounds and promotes processes that convert energy and nutrients into larger particles (e.g., microbial growth).

### *Litter C, N content and abundance of epiphytic microorganisms*

Birch and hemlock litter collected at Mt. Tom during three sampling dates showed a significant increase in the N concentrations over time. The main effect of litter type was significant ( $F_{1,12} = 21.935$ ,  $P < 0.001$ ), with hemlock litter collected beneath uninfested trees at PH showing significantly lower N concentrations. Percentage of N was also significantly increasing with time ( $F_{2,11} = 24.252$ ,  $P < 0.001$ ) and time  $\times$  infestation interactions were not significant ( $F_{2,22} = 6.000$ ,  $P = 0.281$ ). The seasonal change in percentage of C was less consistent in the different types of litter, but hemlock litter from PH had the highest C concentrations (main effect, litter type:  $F_{1,12} = 42.322$ ,  $P < 0.001$ ), which resulted in the highest C:N ratio compared to birch and hemlock litter receiving HWA-affected throughfall (main effect, litter type:  $F_{1,12} = 21.865$ ,  $P < 0.001$ ). The seasonal changes in C:N ratios were also significant ( $F_{2,11} = 9.693$ ,  $P = 0.004$ ) but interaction terms were not ( $F_{2,22} = 0.840$ ,  $P = 0.552$ ).

Bacteria, numerically the largest group of microorganisms in the samples, had significantly larger colony-forming units (CFUs) on HWA-infested hemlock and on birch litter (Fig. 3). This is also true for filamentous fungi on hemlock, but less pronounced for birch litter. The microbial growth was also increased during the aestivation period of HWA, indicating a lasting effect of wax wool as a source of energy. Hemlock woolly adelgid had no consistent effects on the abundance of yeasts on both litter types. Yeasts are likely suppressed by a prolific growth of filamentous fungi.

### *Litter leaching experiment*

Separating the effects of HWA-affected and uninfested throughfall on litter leachates provides an indication of the functional consequences associated with changes in species composition, which subsequently follow the demise of infested hemlock. The relative litter masses of hemlock and birch in the lysimeters represent the situation in the field. Though the amount of rainfall varied substantially in the field, we provide the mean concentrations for each compound (plus and minus signs in Fig. 4) in the litter solution collected in the field during the complete experimental period as a point of reference. In addition, each figure contains the mean

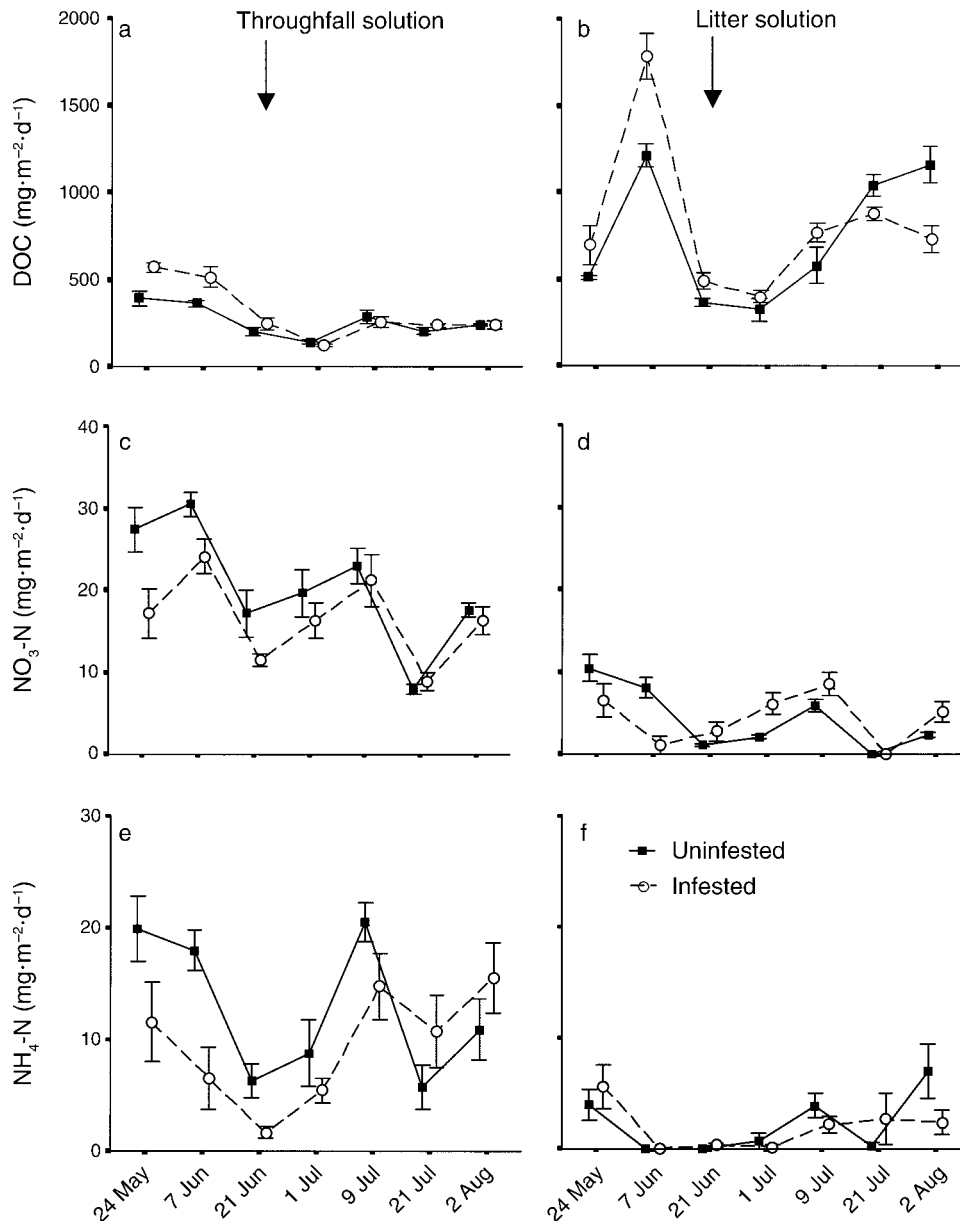


FIG. 1. Seasonal change in the fluxes of energy, nutrients, and ions (means  $\pm$  SE) in throughfall and litter solutions collected beneath hemlock woolly adelgid (HWA)-infested and uninfested trees at Mt. Tom State Reservation in south-central Massachusetts, USA, in 2004. Fluxes were calculated for different periods of time (per day) because of the variable sampling regime. Arrows indicate the time of HWA summer aestivation. Abbreviations are: DOC, dissolved organic carbon; DON, dissolved organic nitrogen.

concentration of a particular compound in the throughfall solution (arrows in Fig. 4) collected beneath infested hemlock (in 2002) and beneath uninfested hemlock (in early 2004). For example, HWA-affected throughfall contained higher concentrations of organic compounds (DOC, DON) and lower inorganic nitrogen compounds ( $\text{NO}_3\text{-N}$ ,  $\text{NH}_4\text{-N}$ ). Leachates from hemlock litter contained significantly higher DOC concentrations than from birch when HWA throughfall was added (Fig. 4a), indicating immobilization processes in birch litter. In

both cases, though, flushing with HWA throughfall led to an increased efflux of DOC from both litter types (hemlock, +42.8%; birch, +8.0%) relative to what one would expect on the basis of the concentrations added with throughfall. Similarly, for DON the application of HWA throughfall increased the leachate concentrations and more so in hemlock than in birch (Fig. 4b; hemlock, +16.2%; birch, -21.6%, relative to what was added). That is, overall more nitrogen is leaching from birch litter, but the addition of HWA throughfall reduced the

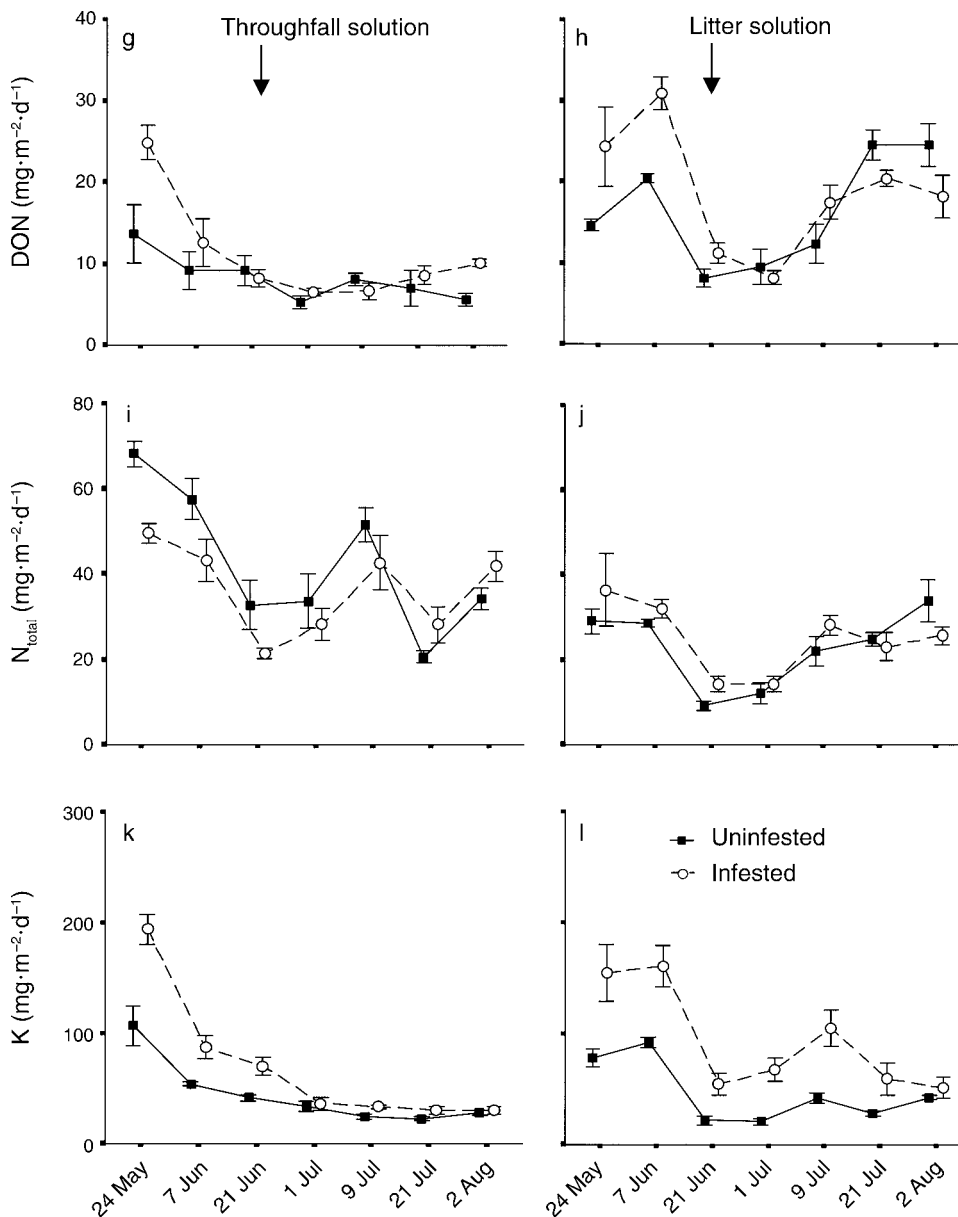


FIG. 1. Continued.

relative output of DON. Nitrate-N concentrations did not significantly differ in leachates between hemlock and birch when HWA-affected or unaffected throughfall was applied (Fig. 4c). Ammonium-N concentrations were significantly lower in leachates compared to the concentrations in throughfall, again indicating immobilization processes. However, concentrations significantly increased in birch relative to hemlock litter when HWA throughfall was applied (Fig. 4d). Concentrations of total nitrogen in leachates were significantly higher in birch than in hemlock and increased only in hemlock leachates with the addition of HWA throughfall (Fig. 4e; hemlock, +50%; birch, -100%). Potassium concen-

trations did not differ in leachates between hemlock and birch and the addition of potassium with HWA throughfall leached from the litter unimpeded (Fig. 4f).

Percentage of N of HWA-affected and unaffected litter did not differ between treatments nor between the start and the end of the experiment for hemlock needles ( $F_{2,11} = 0.639$ ,  $P = 0.550$ ), but was significantly higher in birch litter, especially in birch leaves receiving HWA throughfall ( $F_{2,11} = 40.357$ ,  $P < 0.001$ ). Percentage of carbon concentrations did not differ between litter type receiving HWA-affected or unaffected throughfall or between the beginning and end of the experiment (hemlock,  $F_{2,11} = 0.729$ ,  $P = 0.509$ ; birch,  $F_{2,11} = 1.148$ ,

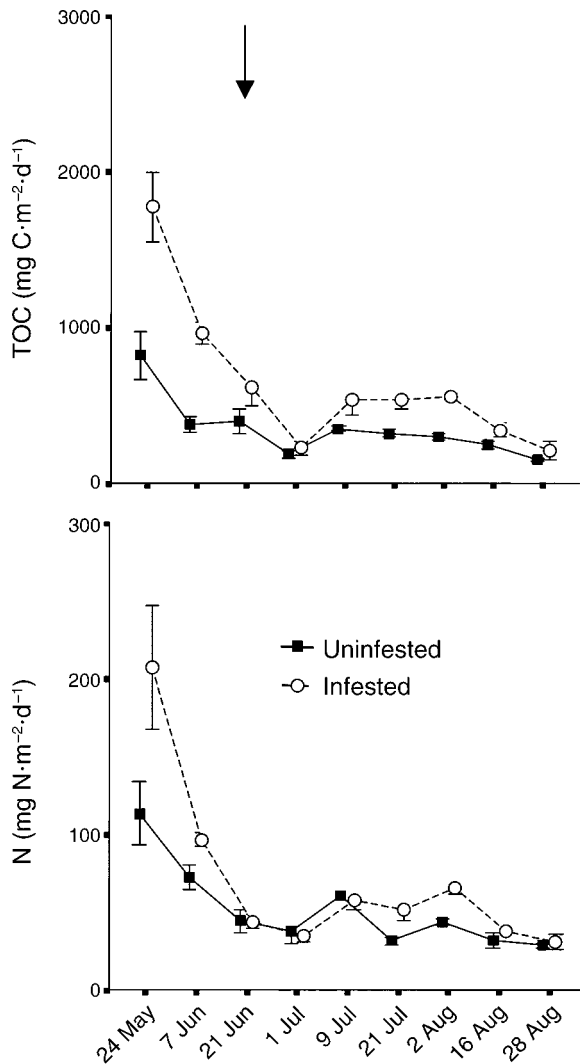


FIG. 2. Seasonal change in the flow of unfiltered compounds (total organic carbon [TOC] and total nitrogen; means  $\pm$  SE) beneath hemlock woolly adelgid (HWA)-infested and uninfested trees at Mt. Tom State Reservation in 2004. Fluxes were calculated for different periods of time (per day) because of the variable sampling regime. The arrow indicates the time of HWA summer aestivation.

$P = 0.360$ ). As a consequence, the C:N ratio differed significantly with treatment in birch ( $F_{2,11} = 24.306$ ,  $P < 0.001$ ), but not in hemlock ( $F_{2,11} = 0.836$ ,  $P = 0.464$ ). That is, the birch litter response to the addition of HWA-affected throughfall was more pronounced than that of hemlock litter.

## DISCUSSION

### Field experiments

Understanding the ecosystem-level effects of invaders requires a comprehensive, cross-disciplinary approach because of the multitude of effects they exert on ecosystem structure and function (Schowalter et al.

1991). Exotic insect pests might serve as good examples to decipher the manner in which the life cycles of insects, activity patterns, and impacts on their host plants affect the flow and availability of nutrients, trophic relationships with microorganisms, and the physical environment. This is because their effects are not diluted by a host of buffering processes, which make it less likely to identify cause and effects. In this way they might function as a paradigm when studying the impact of insects on ecosystem processes (Chapin et al. 1997, Crooks 2002) because they may cover the whole range from a light stage of infestation to outbreak levels and ecosystem reorganization after the extinction of a core species (in this case hemlock; cf. Ellison et al. 2005). In particular, the HWA is a good example to explore Vitousek's (1990) principles.

Low winter temperatures in 2003–2004 caused very low densities in adult sistens, which provided the opportunity to follow processes at the very dispersal frontier of exotic pest species infestation. The presence of HWA is mirrored in throughfall chemistry with higher DOC fluxes beneath infested trees up to early July. During that period wax wool is breaking down and washing out of the canopy (Fig. 1a), leading to 24.6% higher DOC fluxes in throughfall. The availability of feeding residues and energy caused an immobilization of inorganic nitrogen ( $-39.8\%$ ) and increased fluxes of organic nitrogen ( $+28.5\%$ ) in throughfall beneath infested trees (Fig. 1c, e, g). That is, there is a qualitative and quantitative change in nitrogen compounds entering the forest floor beneath infested trees even at quite low densities of HWA. Overall, 25.8% less nitrogen was leaching from the canopy beneath infested hemlock during that period of time in which HWA was actively growing. Once the progeny of progrediens (sistens) entered summer aestivation, fluxes of most compounds were similar beneath infested and uninfested trees. Litter solutions usually showed less pronounced differences, but the direction of change was similar to the throughfall fluxes. Overall, even the low degree of infestation in the periphery of the canopy, with only 2–3 egg masses per shoot, clearly reflected the HWA life cycle and revealed the effect on ecosystem processes early in the season. The most pronounced positive response to HWA infestation was shown in the  $K^+$  fluxes, which increased by 39.3% in throughfall and 51.5% in litter solution. A significant increase in potassium fluxes/concentrations due to herbivory was also reported for other temperate forest ecosystems (Seastedt et al. 1983, Seastedt and Crossley 1984, Stadler et al. 2001a), which might indicate the usefulness of this mobile ion to evaluate the impact of sap- and leaf-feeding herbivores on forest ecosystems.

The unfiltered nutrient fluxes for TOC and total N showed an identical seasonal effect, with differences in fluxes between infested and uninfested trees gradually declining. However, compared to the filtered solutions, the particulate fraction of throughfall showed higher

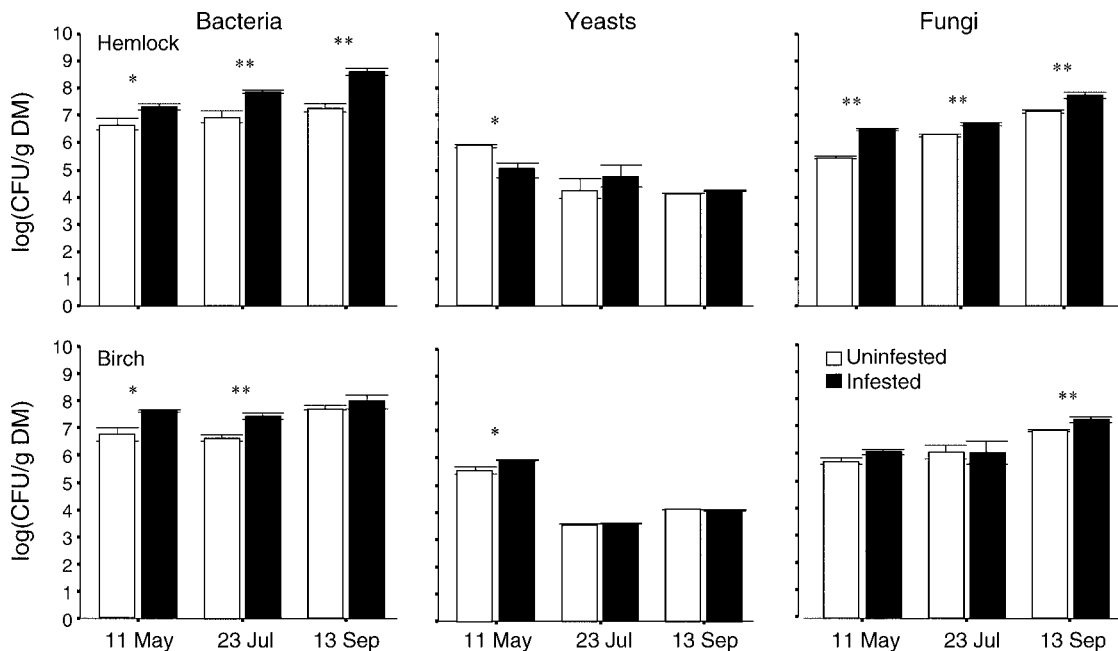


FIG. 3. Log(number of colony-forming units [CFUs] per gram dry mass [DM]) (means + SE) for bacteria, yeasts, and filamentous fungi on hemlock and birch litter collected in 2004 beneath hemlock woolly adelgid (HWA)-infested trees (black bars, Mt. Tom) and uninfested trees (open bars, Prospect Hill). Data are separated for different sampling dates showing the beginning, middle, and end of the experiments. Asterisks indicate significant differences: \* $P < 0.05$ ; \*\* $P < 0.01$ .

TOC and N fluxes, which suggests trophic links with epiphytic microorganisms, which were found in higher abundances on needles of infested trees (Stadler et al. 2005). This result could partly explain the relatively higher DON fluxes in litter leachates beneath infested trees early in the season, and it might also account for the greater N availability in soils found in HWA-infested mature forest using the resin bag technique (Kizlinski et al. 2002). Infested hemlock and birch litter sampled in the field had similar percentage of N concentrations and C:N ratios, while uninfested hemlock litter had significantly lower percentage of N values resulting in higher C:N ratios. Higher litter N concentrations of infested hemlock might provide a better substrate for microorganisms. In addition, litter receiving HWA-affected throughfall in the field is a better environment for bacteria because of the higher throughput of carbon and nitrogen (Fig. 3), suggesting that the breakdown of the carbon-rich wax wool provided the energy for better growth. The results for yeasts and filamentous fungi showed higher fluctuations and might mirror their higher sensitivity to other environmental conditions, such as humidity (Andrews and Harris 2000). These trophic relationships between HWA and microorganisms provide the mechanism that links aboveground and belowground processes and determines changes in organic and inorganic nutrient fluxes.

#### Litter leaching experiment

In the laboratory, litter experienced no direct physical damage and was only affected indirectly by altered

throughfall. It is also noteworthy that we used senescent litter in our experiment in which decomposition processes are usually slower compared to fresh litter because most of the readily decomposable compounds have already broken down (Norden and Berg 1990). Therefore, adding energy and nutrients with throughfall could be expected to speed up decomposition and the leaching process again. The HWA-affected throughfall contained higher concentrations of DOC, DON, and lower concentrations of inorganic N compared to unaffected throughfall. Throughfall of uninfested hemlock contained relatively high amounts of N, because we collected throughfall early in the season of 2004 when the trees were actively growing. It also must be kept in mind that the biomass of needles used in this experiment was eight times as high as the biomass of birch leaves in order to mirror field conditions. In spite of these mass differences, less DOC is leaching from birch than from hemlock litter when HWA throughfall is added. The nitrogen fraction (especially DON) leaching from litter is much higher in birch than in hemlock, and the addition of HWA throughfall usually reduces N losses from litter (e.g., Fig. 4b, d), most likely because the added energy leads to the immobilization of  $\text{NH}_4\text{-N}$  by microorganisms.

Changes in litter diversity have been demonstrated to affect carbon and nitrogen fluxes during litter decomposition, and even losses in intraspecific genetic diversity of litter affected soil respiration and nitrogen leaching from forest soils (Madritch and Hunter 2002, 2003). Given the substantial change in litter input with declining hemlock vitality and the subsequent establish-



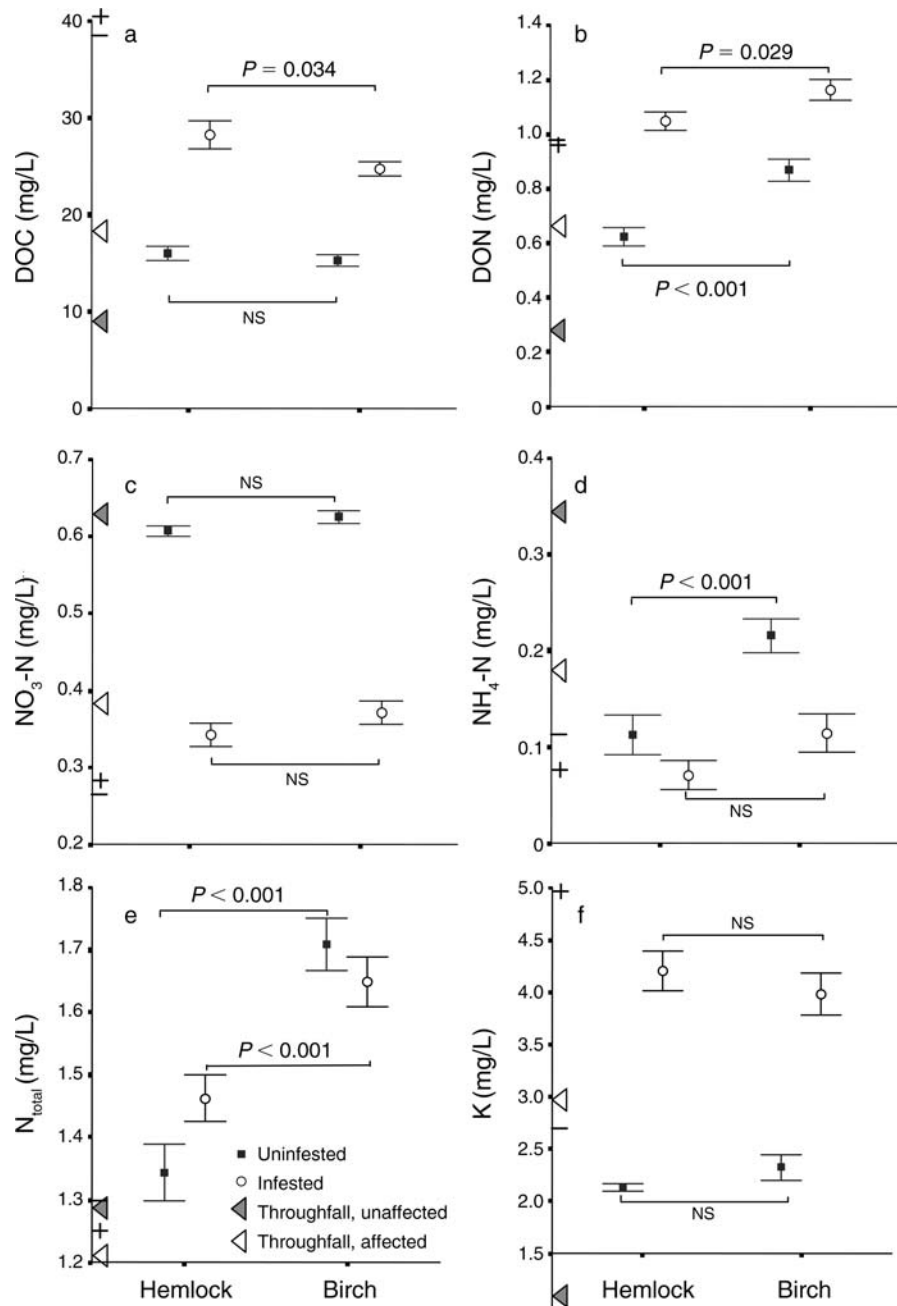


FIG. 4. Leachate concentrations of different compounds (means  $\pm$  SE) collected from hemlock and birch litter during a 16-wk experimental period. Samples were taken once every two weeks, and litter was flushed with either hemlock woolly adelgid (HWA)-affected or unaffected throughfall collected before the start of the experiment. Arrowheads along the y-axis indicate the concentration of a particular compound in the throughfall applied to hemlock and birch litter. Plus and minus signs indicate the mean concentrations of a particular compound in the litter solutions of the field experiment. This provides some indication of the range of concentrations found in the field with a mixture of hemlock and birch litter. We used *t* tests to compare the mean leachate concentrations from hemlock and birch litter receiving either HWA-affected throughfall or pure hemlock throughfall. Abbreviations are: DOC, dissolved organic carbon; DON, dissolved organic nitrogen.

ment of deciduous species, less needle litter may provide less substrate and eventually increase DON losses through leaching. Additionally, inputs from canopy herbivores such as the gypsy moth significantly increased soil respiration and nutrient cycling (Reynolds

and Hunter 2001, Hunter et al. 2003). Whether this input during outbreak periods increases rates of soil nitrogen losses (Swank et al. 1981, Eshleman et al. 1998) or decreases N export (Lovett et al. 2002) is strongly debated. As we describe below, potential explanations

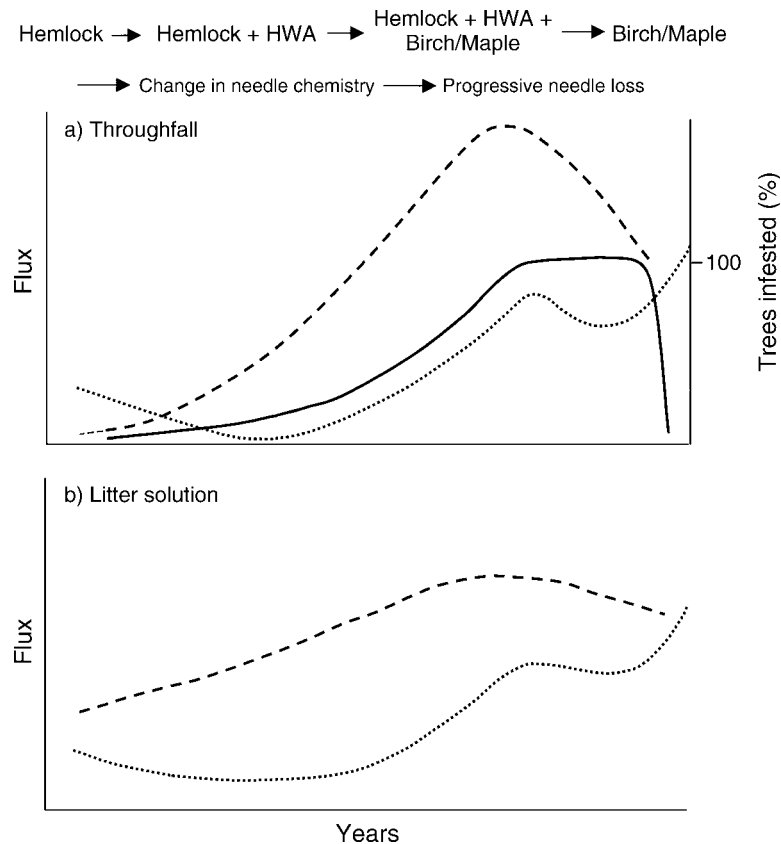


FIG. 5. Conceptual model for the transition in energy and nutrient fluxes relative to hemlock woolly adelgid (HWA) infestation in a forest stand that is eventually converted from a pure hemlock into a birch/maple stand because of enduring HWA infestation. Hemlock woolly adelgid infestation is characterized by progressive needle loss, changes in needle chemistry, increased growth of epiphytic microorganisms, and changes in abiotic conditions (higher temperatures, greater precipitation, and light intercepting the canopy). The dashed line represents dissolved organic carbon, and the dotted line represents N dynamics. The solid line represents the level of infestation.

for the different results are the temporal changes in abiotic and biotic perturbation, extent of tree mortality, buffering capacity of litter, and changes in N species in both litter and leachates. For example, it has been suggested that DON plays an important role in terrestrial N cycling (Neff et al. 2003). Due to its heterogeneous composition DON might play a dual role in N loss from ecosystems and uptake by plants. Even at low infestation rates exotic pests like HWA significantly alter the quality of nutrient fluxes by increasing the organic C and N pool in throughfall. This could affect either the direct uptake of organic N forms by plants or the leaching from ecosystems. In addition, the long-term behavior of larger quantities of POM is not clear but it might lead to different interpretations (see, e.g.,  $N_{\text{total}}$  fluxes Fig. 1).

#### CONCLUSIONS

Based on the results of this study and our previous results on nutrient cycling in hemlock stands showing different degrees of HWA infestation, we provide evidence that varying levels of HWA abundance lead

to opposing effects on energy and nutrient flows in these systems. The transition in species composition will follow a trajectory including: hemlock, hemlock + initial HWA infestation, hemlock + HWA + birch, hemlock decline, and eventually pure birch/maple stands (Orwig et al. 2002). This transition in species is accompanied by progressive needle loss and changes in needle chemistry, such as increased nitrogen concentrations (Stadler et al. 2005). Relative to the infestation profile that shows a steady to exponential increase in the number of infested needles/trees up to complete infestation and eventual death of hemlock, DOC fluxes in throughfall will show a similar initial increase, but level off with progressive infestation (Fig. 5a). The reason is that for trees of identical age and/or size moderately infested trees hold a higher needle biomass and also have egg masses/wax wool twice as large as heavily infested trees (Stadler et al. 2005). As a consequence, the eventual breakdown of wax wool provides the energy for epiphytic microbes, which thrive better on needles of infested trees. This transition in infestation/tree vitality also has consequences for the fluxes of nitrogen, both in the canopy and

litter. As our results in 2004 showed, there is an initial decline in nitrogen fluxes with increasing infestation because of microbial-N immobilization processes. Nevertheless, the quality of the nitrogen compounds in throughfall changes significantly (Fig. 2, 3). The turning point at which nitrogen fluxes eventually start to increase in throughfall of hemlock will occur when the HWA population is large enough to affect needle chemistry and mortality. Our previous results also showed that beneath heavily infested trees nitrogen throughfall concentrations will decline again, possibly because of the declining needle biomass and therefore less overall N leaching from the canopy of hemlock. As hemlock continues to deteriorate, there will be an increase in both the quantity and quality of deciduous litter, which will eventually increase N throughfall fluxes again, at least during the summer months (Tukey 1970, Aerts 1996, Michalzik et al. 2001).

Similar effects can be expected for litter solutions (Fig. 5b) because changing nutrient fluxes in the canopy will eventually affect the forest floor. However, temporal changes in nutrient fluxes associated with the shift in tree species following HWA infestation are probably less pronounced for DOC because leachate concentrations (Fig. 4a) and percentage of C were similar for hemlock and birch litter. The nitrogen flux from litter is likely to increase with time in these stands because hardwood litter will increase in abundance (Orwig and Foster 1998), has higher percentage of N, and leaches more nitrogen (Fig. 4b, e). Therefore, we suggest that nutrient fluxes in forest stands, which are in transition from pure hemlock to pure hardwood stands, are likely to show nonlinear trajectories (cf. Hunter 2001). These nonlinear effects of exotic pest species on ecosystem processes are currently not sufficiently represented in ecosystem models (but see de Mazancourt and Loreau 2000), and it will be interesting to explore how mechanistic models on nitrogen losses from forested ecosystems are able to incorporate biotic disturbance to make regional-scale predictions (Aber et al. 2002, Rastetter et al. 2003). In addition, matter fluxes are often analyzed without knowledge of the ecology of the organisms that influence them. We feel there is a need to not only examine the magnitude and direction of matter and energy flows in forest ecosystems associated with forest insects, but to also incorporate knowledge of the activity patterns (life cycle traits), physiological impacts at varying insect densities, and trophic relationships to better understand the ecology driving fluxes.

An ecological approach that combines nutrient and energy flows may eventually be combined with population/community ecological processes to understand the spatial patterns of energy and nutrient flows at the landscape scale (Vitousek 1990, Loreau 1995, Loreau and Holt 2004).

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#### APPENDIX A

A description of throughfall and leachate sampling methods and analyses (*Ecological Archives* E087-106-A1).

#### APPENDIX B

A table showing repeated-measures MANOVA on the fluxes of different compounds collected in throughfall and litter solutions under HWA-infested and uninfested hemlock trees (*Ecological Archives* E087-106-A2).

#### APPENDIX C

A table showing repeated-measures ANOVA on the fluxes of particulate organic matter collected in throughfall under HWA-infested and uninfested hemlock trees (*Ecological Archives* E087-106-A3).