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Modeling nitrogen flux by larval insect herbivores from a temperate hardwood forest

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Abstract Herbivorous insects flux considerable amounts of nitrogen from the forest canopy to the soil in the form of frass. The amount of nitrogen fluxed varies depending on the characteristics of the herbivores, their food resources, and their physical environment. We used concepts from metabolic ecology and ecological stoichiometry to develop a general model of individual nitrogen flux via frass fall for moth and sawfly larvae from a temperate hardwood forest in northern Wisconsin, USA. We found that individual nitrogen flux (Q_N, mg N/day) was related to larval body mass (M_B, mg dry), short-term variation in environmental temperature (T, K), and larval nitrogen concentration (N_B, proportion dry mass) as $Q_N = e^{25.75} M_B^{0.77}\, e^{-0.83/kT} N_B^{1.56}$, where k is Boltzmann's constant (8.62×10^{-5} eV/K). We also found that larval nitrogen flux did not vary with the nitrogen concentration of food, and suggest that this was due to compensatory feeding by larvae living on low-quality leaves. With further work, models of individual N flux could be used to scale individual fluxes to population and community levels, and thus link the characteristics of insect herbivore communities with the flow of nitrogen through forested ecosystems.

Keywords Body mass · Consumer-driven nutrient cycling · Ecological stoichiometry · Environmental temperature · Forest insects · Hymenoptera · Lepidoptera · Metabolic theory of ecology

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Introduction

Herbivores play important roles in nutrient cycling in both aquatic and terrestrial ecosystems (Mattson and Addy 1975; Carpenter and Kitchell 1988; McNaughton et al. 1988; Belovsky and Slade 2000; Vanni 2002). In forested biomes, in particular, larval insect herbivores are responsible for transforming and translocating (sensu Vanni 2002) considerable amounts of nitrogen (N) from the canopy to the soil in the form of frass (Fogal and Slansky 1985; Hollinger 1986; Reynolds and Hunter 2001; Lovett et al. 2002; Hunter et al. 2003). Frass-derived N typically falls at the peak of the growing season and is in a highly labile form (Lovett and Ruesink 1995). As a result, it is rapidly transformed by microbes, absorbed by plants, or flushed from the local system during precipitation events (Swank et al. 1981; Webb et al. 1995; Eshleman et al. 1998; Frost and Hunter 2007).

Nitrogen inputs from insect frass are typically quantified by collecting frass in trays placed on the forest floor, weighing and analyzing the N concentration of the frass, and calculating the amount of N deposited per unit area and time (Fogal and Slansky 1985; Hunter et al. 2003). A complementary approach to estimating frass N inputs is to scale individual N flux to the community level using general models of individual flux and information about community structure. This strategy has been used to study N flux by a variety of aquatic (Peters and Rigler 1973; Ejsmont-Karabin 1984; Grimm 1988; Wen and Peters 1994; Vanni et al. 2002) and mammalian herbivores (Clark et al. 2005), but this approach has not been used with herbivorous insects.

Our primary objective in the present study was to develop a general model of individual N flux via frass production for larval insect herbivores using concepts from

ecological energetics and metabolic ecology (Grodzinski et al. 1975; Peters 1983; Gillooly et al. 2001, 2005; Enquist et al. 2003; Brown et al. 2004; Allen et al. 2005) and nutritional ecology and ecological stoichiometry (Sterner et al. 1992; Elser et al. 1996; Elser and Urabe 1999; Sterner and Elser 2002). The scaling of individual fluxes to the community level will be addressed elsewhere.

Model

The quantity of N fluxed via frassfall by an individual insect herbivore per unit time (Q_N, mg N/day) should be related to the individual frass production rate (M_F, mg dry frass/day) and the N concentration of frass (N_F, proportion of frass dry mass) as:

$$Q_N = M_F N_F \quad (1)$$

From metabolic ecology, we expect individual frass production to be proportional to the rate of ingestion, which, in turn, should be proportional to whole organism metabolic rate when animals are not using internal stores of energy (Lavigne 1982; Peters 1983; Peters et al. 1996; Brown et al. 2004). If frass production and metabolic rate are approximately proportional to one another, then frass production should be related to larval body mass (M_B, mg dry) as a power function (Kleiber 1932; Hemmingsen 1960; Peters 1983; Gillooly et al. 2001) and to short-term variation in environmental temperature (from hours to days, where minimal temperature acclimation occurs; T, K) as an exponential function (Crozier 1924; Robinson et al. 1983; Clarke and Johnston 1999; Gillooly et al. 2001). The combined effects of body mass and temperature on frass production can thus be modeled using an equation similar to the metabolic rate equation of Gillooly et al. (2001):

$$M_F \propto M_B^b e^{-c/kT} \quad (2)$$

Here, b is a mass-scaling exponent, c is a coefficient describing the temperature dependence of frass production, sometimes called the "critical thermal increment" or "apparent activation energy" for a complex biological process (Withers 1992), and k is Boltzmann's constant (8.62×10^{-5} eV/K) (Gillooly et al. 2001). Given the proportionality of metabolic rate and frass production, values for b and c should fall within ranges generally observed for metabolic rate, and thus $0.65 < b < 0.85$ (Peters 1983; Glazier 2005) and $0.25 < c < 0.80$ eV (Vasseur and McCann 2005; Meehan 2006). Metabolic scaling theory predicts that values for b and c should be 0.75 and 0.65 eV, specifically (West et al. 1997; Gillooly et al. 2001; Banavar et al. 2002; Gillooly et al. 2006).

The N concentration of frass is influenced by a complex suite of physiological factors (Nation 2002). It can be approximated, however, using abstractions provided by ecological stoichiometry (Sterner et al. 1992; Elser and Urabe 1999; Sterner and Elser 2002). First, the N concentration of frass is expected to be a positive function of the N concentration of food (N_L, proportion of leaf dry mass), simply because a large fraction of N in food is not absorbed by larvae. Second, ecological stoichiometry predicts that consumers showing elemental homeostasis should excrete absorbed N above their physiological demands. Most insect herbivores studied have demonstrated partial to complete N homeostasis (Fox and Macauley 1977; Slansky and Feeny 1977; Raubenheimer and Simpson 2004; Kagata and Ohgushi 2006). Thus, N excretion should reinforce the positive relationship between frass and leaf N concentration that is due to lack of absorption. Third, according to ecological stoichiometry, the physiological demands for N are proportional to the N concentration of an organism's body (N_B, proportion of body dry mass). Thus, frass N concentration should be inversely related to body N concentration. These relationships can be formalized simply as:

$$N_F \propto N_B^{-d} N_L^g \quad (3)$$

We approximate the relationships between the N concentration of frass, food, and larvae using power functions because they are simple and flexible mathematical forms, i.e., depending on the values of d and g, the functions can fit relationships that are positive or negative, accelerating or decelerating.

Substituting Eqs. 2, 3 into Eq. 1 gives:

$$Q_N = a M_B^b e^{-c/kT} N_B^{-d} N_L^g \quad (4)$$

Here, a is a normalization constant with units of mg N $\times$ day^{-1} $\times$ mg dry body mass^{-b}. Equation 4 is a general model for individual N flux via frass fall by a larval insect herbivore. The model is an intentional simplification of many complex physiological processes that vary across age, sex, and taxonomic groups. This simplification, admittedly, reduces the precision of the model when predicting N flux for any particular group. However, by creating a general model, our intention is to trade precision for applicability, and to provide a means to approximate frass-derived N inputs across a diverse community of larval insect herbivores. Equation 4 is based on principles from metabolic ecology and ecological stoichiometry. In the process of testing this model, we hoped to simultaneously: (1) evaluate a new tool for studying insect-derived N inputs, and (2) assess the generality of several expectations from ecological theory.

Materials and methods

To evaluate the individual N flux model described above, we assembled a dataset that included information on frass production, frass N concentration, larval body mass, environmental temperature, larval N concentration, and leaf N concentration for a variety of larval insect herbivores common to the hardwood forests of the Great Lakes region. The dataset was compiled from two different studies of individual N flux. One study was of moth and sawfly larvae collected from the field (hereafter, "field animals") and a second study was of moth larvae that were reared in the laboratory (hereafter, "lab animals").

Field animals

Field animals included 87 larvae, from 22 species of moths, butterflies, and sawflies (Table 1). Larvae were collected opportunistically from the lower branches of eight dominant tree species (Table 1) as they were encountered during walks through forest stands in Onieda County, Wisconsin, USA. We collected larvae, along with corresponding host plant foliage, placed them into plastic bags, and stored them in a cooler for 1–3 h until they were transported to the laboratory.

At the lab, larvae were transferred, along with their food and a moist piece of tissue paper, into 20-ml polyethylene vials for 24-h feeding trials. In all, 60 feeding trials were conducted using the 87 field animals. The number of animals was greater than the number of trials because, on ten occasions, 2–7 similarly sized animals were placed into one vial to increase the quantity of frass produced during the trial. Before each trial, we weighed larvae and divided the total mass by the number of larvae to estimate the average pre-trial wet mass. During trials, animals were kept at room temperature, 22 °C, under a natural light cycle of 15:9 light:dark hours. After the feeding trial, we collected frass from the bottom of the vial for frass production and N concentration estimates, reweighed larvae, calculated a post-trial wet mass, calculated a midpoint wet mass as the average of pre- and post-trial wet masses, and transferred larvae and leaves to a new vial for an additional 24-h period so that additional frass could be collected for chemical analysis. Afterwards, we reweighed larvae and promptly placed frass, larvae, and foliage into a freezer.

We dried frass, larvae, and foliage in an oven (55 °C) and weighed frass and larvae. We converted midpoint wet mass for each trial to midpoint dry mass using the following conversion equations: lepidopteran dry mass = 0.15 × wet mass$^{1.05}$ (R^2 = 0.99); hymenopteran dry mass = 0.16 × wet mass$^{1.05}$ (R^2 = 0.98). Midpoint dry mass was then converted to a final larval mass per trial by multiplying midpoint dry mass by a factor of 0.90 to account for the mass of gut contents (Bowers et al. 1991). Per capita frass production rate was calculated as the dry mass of frass produced over the one-day trial divided by the number of animals in the trial.

Frass, foliage, and larvae were then homogenized using a mortar and pestle and 2–10 mg samples were packed into tin capsules for N analysis on either a Carlo Erba (Milan, Italy) NV 2100 or a Thermo Finnigan (San Jose, CA, USA) Flash 1112 elemental analyzer. Larval N concentration was corrected for that of gut contents using the equation: larval concentration = (measured concentration – (0.10 × average concentration of leaf and frass))/0.90, after Fagan et al. (2002). The coefficient, 0.10, represented the approximate fraction of larval dry mass that is gut contents (Bowers et al. 1991), and was multiplied by the average concentration of the leaf and frass because that was our best estimate of the N concentration of the total gut contents. Larval N flux per feeding trial was calculated as the per capita frass production rate multiplied by frass N concentration.

On six occasions, larvae, frass, or leaf samples from a given feeding trial were too small for N analysis. As a result, materials from 2–3 feeding trials were pooled before N analysis and the same larval, frass, and leaf N concentration was used to represent the two or three trials included in that pool (Table 1). This caused a minor lack of independence in our N concentration data. The N flux data from pooled trials were not entirely correlated, however, because N flux was the product of both N concentration and frass production, and all trials produced independent frass production measurements. Our decision to use a common set of N concentrations across 2–3 trials on six occasions had no effect on the conclusions of this study.

Lab animals

Lab animals used in this study were whitemarked tussock moth (*Orygia leucostigma*) larvae. Larvae were raised from eggs purchased from the Canadian Forest Service (Sault St. Marie, ON, Canada). Egg masses were divided into two groups and put into two rearing dishes in a growth chamber set to 22 °C and a 14:10 light:dark hour cycle. Eggs hatched after two weeks of incubation and half of the larvae were fed aspen leaves with a high nitrogen concentration, while half were fed aspen leaves with a low nitrogen concentration. Leaves came from ten potted trees propagated from a single aspen clone; five of the ten trees were given 4.5 g/L soil of slow release fertilizer (18:6:12, N:P:K without micronutrients) in May 2004 and 2006 to increase nitrogen content of foliage. At the time of this study, the trees were in their fourth growing season.

As above, N flux was measured during 24-h feeding trials in 20-ml vials. Trials were conducted at various

Table 1 Data used in this analysis

Larva				Leaf		Frass		Flux
Species	*n*	Mean body mass (mg)	N	Species	N	Per capita frass production (mg/day)	N	Per capita N flux (mg/day)
Field animals								
Hymenoptera								
Arge pectoralis	7	0.18	0.106	*Corylus cornuta*	0.023	0.91	0.019	0.02
Arge pectoralis	3	1.33	0.100	*Corylus cornuta*	0.025	4.13	0.019	0.08
Arge pectoralis	3	1.65	0.105	*Corylus cornuta*	0.027	4.44	0.021	0.09
Arge pectoralis	3	1.78	0.093	*Corylus cornuta*	0.022	4.72	0.021	0.10
Cimbex americana	1	204.49	0.077	*Betula papyrifera*	0.020	219.39	0.017	3.79
Cimbex americana	1	268.52	0.075	*Betula papyrifera*	0.025	322.61	0.016	5.23
Cimbex americana	1	75.06	0.082	*Tilia americana*	0.026	43.30	0.020	0.86
Lepidoptera								
Achatia distincta	1	53.84	0.089	*Populus tremuloides*	0.034	30.94	0.025	0.78
Acronicta leporine	1	76.77	0.082	*Populus tremuloides*	0.022	96.12	0.024	2.33
Archips cerasivorana	1	6.63	0.081	*Quercus rubra*	0.024	7.09	0.023	0.16
Bucculatrix ainseliella	3	0.65	**0.096**	*Quercus rubra*	**0.029**	1.10	**0.028**	0.03
Bucculatrix ainseliella	4	0.66	**0.096**	*Quercus rubra*	**0.029**	1.33	**0.028**	0.04
Bucculatrix ainseliella	1	1.17	**0.096**	*Quercus rubra*	**0.029**	4.80	**0.028**	0.13
Bucculatrix ainseliella	1	1.60	**0.100**	*Quercus rubra*	**0.025**	3.85	**0.020**	0.08
Bucculatrix ainseliella	2	1.09	**0.102**	*Quercus rubra*	**0.027**	2.70	**0.024**	0.06
Bucculatrix ainseliella	1	1.36	**0.102**	*Quercus rubra*	**0.027**	3.39	**0.024**	0.08
Bucculatrix ainseliella	3	1.43	**0.102**	*Quercus rubra*	**0.027**	3.67	**0.024**	0.09
Ellida caniplaga	1	14.39	0.106	*Tilia americana*	0.024	27.00	0.021	0.57
Erranis tiliaria	1	37.22	0.081	*Acer rubrum*	0.016	28.62	0.020	0.57
Erranis tiliaria	1	31.76	0.086	*Betula papyrifera*	0.024	25.98	0.020	0.52
Erranis tiliaria	1	20.90	0.088	*Betula papyrifera*	0.022	25.67	0.020	0.51
Erranis tiliaria	1	46.44	0.101	*Quercus rubra*	0.021	23.83	0.025	0.60
Erranis tiliaria	1	42.40	0.101	*Populus tremuloides*	0.024	34.32	0.020	0.70
Erranis tiliaria	1	43.52	0.103	*Betula papyrifera*	0.029	10.70	0.038	0.41
Erranis tiliaria	1	43.06	0.107	*Betula papyrifera*	0.026	22.49	0.025	0.55
Erranis tiliaria	1	53.26	0.107	*Betula papyrifera*	0.027	22.46	0.024	0.54
Erranis tiliaria	1	45.75	0.108	*Betula papyrifera*	0.028	27.35	0.019	0.51
Erranis tiliaria	1	12.33	0.112	*Betula papyrifera*	0.023	7.38	0.021	0.15
Erranis tiliaria	1	53.23	0.117	*Betula papyrifera*	0.028	28.31	0.028	0.80
Erranis tiliaria	1	42.44	0.130	*Acer rubrum*	0.020	12.72	0.029	0.36
Heterocampa guttivitta	1	113.16	0.091	*Betula papyrifera*	0.018	228.91	0.023	5.34
Hyphantria cunea	1	2.26	0.117	*Prunus virginiana*	0.025	2.96	0.013	0.04
Hyphantria cunea	1	1.81	**0.128**	*Prunus virginiana*	**0.026**	1.28	**0.015**	0.02
Hyphantria cunea	2	2.39	**0.128**	*Prunus virginiana*	**0.026**	1.40	**0.015**	0.02
Lambdina fiscellaria	1	4.22	0.095	*Betula papyrifera*	0.024	3.14	0.016	0.05
Nadata gibbosa	1	105.73	0.091	*Betula papyrifera*	0.024	130.93	0.017	2.25
Orgyia leucostigma	1	18.43	0.090	*Corylus cornuta*	0.024	33.40	0.018	0.59
Orgyia leucostigma	1	45.60	0.093	*Betula papyrifera*	0.019	65.34	0.020	1.30
Orgyia leucostigma	1	1.52	0.107	*Acer rubrum*	0.012	2.79	0.013	0.04
Orgyia leucostigma	1	1.18	0.111	*Alnus incana*	0.019	2.85	0.012	0.03
Orgyia leucostigma	2	0.76	0.116	*Alnus incana*	0.022	2.06	0.015	0.03
Orgyia leucostigma	1	0.96	0.121	*Acer rubrum*	0.016	1.15	0.016	0.02
Polyphemus sp.	1	23.11	0.103	*Quercus rubra*	0.025	15.04	0.020	0.30

Table 1 continued

Larva				Leaf		Frass		Flux
Species	*n*	Mean body mass (mg)	N	Species	N	Per capita frass production (mg/day)	N	Per capita N flux (mg/day)
Unknown Lepidoptera A	1	2.55	0.089	*Tilia americana*	0.027	6.40	0.019	0.12
Unknown Lepidoptera B	1	1.04	**0.105**	*Tilia americana*	**0.030**	2.70	**0.018**	0.05
Unknown Lepidoptera C	1	0.50	**0.105**	*Tilia americana*	**0.030**	0.76	**0.018**	0.01
Unknown Lepidoptera D	1	9.84	0.105	*Populus tremuloides*	0.028	9.80	0.012	0.11
Unknown Lepidoptera D	1	1.93	0.097	*Populus tremuloides*	0.026	2.09	0.010	0.02
Unknown Lepidoptera E	1	19.32	0.130	*Betula papyrifera*	0.028	9.06	0.018	0.16
Unknown Lepidoptera E	1	19.79	0.084	*Betula papyrifera*	0.023	8.70	0.030	0.26
Unknown Lepidoptera E	1	20.33	0.111	*Betula papyrifera*	0.027	8.41	0.030	0.25
Unknown Lepidoptera E	1	65.44	0.078	*Betula papyrifera*	0.019	52.70	0.021	1.08
Unknown Lepidoptera F	1	7.40	0.076	*Acer rubrum*	0.019	6.63	0.017	0.12
Unknown Lepidoptera F	1	8.94	0.078	*Acer rubrum*	0.020	9.00	0.015	0.13
Unknown Lepidoptera G	1	2.36	**0.085**	*Betula papyrifera*	**0.034**	2.58	**0.031**	0.08
Unknown Lepidoptera G	1	4.94	**0.085**	*Betula papyrifera*	**0.034**	6.78	**0.031**	0.21
Unknown Lepidoptera G	1	7.01	0.116	*Betula papyrifera*	0.026	6.30	0.014	0.09
Unknown Lepidoptera H	1	3.02	0.080	*Quercus rubra*	0.024	5.43	0.015	0.08
Unknown Lepidoptera H	1	3.52	**0.100**	*Quercus rubra*	**0.025**	5.22	**0.020**	0.10
Unknown Lepidoptera H	1	5.48	0.093	*Quercus rubra*	0.030	4.47	0.024	0.10
Lab animals								
Lepidoptera								
Orgyia leucostigma[a]	11	0.47	0.116	*Populus tremuloides*	0.014	2.58	0.007	0.02
Orgyia leucostigma[b]	10	0.57	0.111	*Populus tremuloides*	0.011	1.37	0.006	0.01
Orgyia leucostigma[a]	9	0.89	0.132	*Populus tremuloides*	0.027	4.10	0.021	0.08
Orgyia leucostigma[a]	2	7.03	0.099	*Populus tremuloides*	0.014	29.79	0.006	0.18
Orgyia leucostigma[a]	2	7.52	0.102	*Populus tremuloides*	0.013	33.39	0.007	0.24
Orgyia leucostigma[b]	1	7.58	0.097	*Populus tremuloides*	0.015	11.98	0.007	0.08
Orgyia leucostigma[b]	1	15.38	0.094	*Populus tremuloides*	0.013	21.61	0.009	0.19
Orgyia leucostigma[a]	1	23.89	0.114	*Populus tremuloides*	0.028	59.84	0.025	1.50
Orgyia leucostigma[a]	1	25.28	0.112	*Populus tremuloides*	0.025	74.45	0.021	1.57
Orgyia leucostigma[a]	1	28.11	0.104	*Populus tremuloides*	0.029	71.23	0.025	1.79
Orgyia leucostigma[b]	1	41.48	0.094	*Populus tremuloides*	0.013	43.55	0.009	0.39

Each row is a replicate feeding trial. Masses are dry mass and N concentrations are proportion dry mass

Ambient temperature for trials was 22 °C except for those denoted by [a](30 °C) and [b](15 °C)

Bolded N concentrations indicate pooled samples

masses over the course of larval development. In total, 11 trials were conducted using 39 larvae. The number of animals was greater than the number of trials because, in five cases, 2–11 similarly sized animals were placed into one vial for a feeding trial. For each trial, tussock moth larvae were weighed, an average pre-trial wet mass was calculated as described above, and larvae, fresh aspen foliage, and a moist piece of tissue paper were placed into a vial. During feeding trials, vials were placed into environmental chambers at 15 or 30 °C. After 24 h, the vials were removed from chambers and placed directly into a freezer.

Samples were then freeze-dried and larvae and frass were weighed. Post-trial dry mass per larva was calculated for each trial as the total dry mass of all larvae divided by the number of larvae in vial. A pre-trial dry mass was estimated for each trial using pre-trial wet mass and the function: $\text{larval dry mass} = 0.17 \times \text{wet mass}^{0.98}$ ($R^2 = 0.99$). A midpoint dry mass was then calculated as the average of pre- and post-trial dry masses. A final larval mass for each trial was calculated by correcting midpoint average dry mass for gut contents using the equation: $\text{gut-content-free dry mass} = 0.78 \times \text{midpoint dry mass}^{1.01}$ ($R^2 > 0.99$). The gut content correction function was pro-

duced for the tussock moths in our study following the fasting method of Bowers et al. (1991). Per capita frass production rate for each of these trials was calculated as described previously for field animals. The N concentrations of frass, foliage, and larvae were also quantified as described previously. Larval N concentration was corrected for gut contents using the equation given for field animals. Here, however, we used a gut content proportion of 0.22, which was calculated from our fasting tussock moth larvae. Finally, larval N flux per feeding trial was calculated as described previously.

Data analysis

We linearized the N flux model by taking the natural logarithm of both sides of Eq. 4 and fitted it to natural-log-transformed data using multiple regression. The full linear model used in our analysis was $\ln(Q_N) = b_0 + b_1 \ln(M_B) + b_2\ 1/kT + b_3 \ln(N_B) + b_4 \ln(N_L)$, where the regression coefficients b_0, b_1, b_2, b_3, and b_4 corresponded with $\ln(a)$, b, c, d, and g, respectively, in Eq. 4. We used ANOVA to evaluate the contribution of each term, and calculated 95% confidence intervals to assess the uncertainty around estimated model coefficients.

Results

Larval body masses of field animals ranged from 0.18 to 268.52 and averaged 28.16 mg dry, while larval N concentration ranged from 7.5 to 13 and averaged 9.9%, leaf N concentration ranged from 1.2 to 3.4 and averaged 2.5%, and N fluxes ranged from 0.01 to 5.34 and averaged 0.56 mg N/day (Table 1). Larval body mass of lab animals ranged from 0.47 to 41.48 and averaged 14.38 mg dry, while larval N concentration ranged from 9.4 to 13.2 and averaged 10.7%, leaf N concentration ranged from 1.1 to 2.9 and averaged 1.8%, and N fluxes ranged from 0.008 to 1.79 and averaged 0.55 mg N/day (Table 1).

When we combined information from studies of field and lab animals, we had data for 71 feeding trials. When we fit these data to the linear version of Eq. 4, we found that body mass, temperature, and body N concentration terms were related to N flux as:

$$\ln(Q_N) = 25.75 + 0.77 \ln(M_B) - \frac{0.83}{kT} - 1.56 \ln(N_B) \quad (5)$$

The model fit the N flux data well, with a whole model R^2 of 0.89. The coefficients for the intercept, body mass ($F_{(1,67)} = 424.23$; $P < 0.001$), temperature ($F_{(1,67)} = 28.00$; $P < 0.001$), and body N concentration ($F_{(1,67)} = 10.83$; $P = 0.002$) terms had 95% confidence intervals of 13.74–37.77, 0.69–0.84, –1.14 to –0.52, and –2.50 to –0.61, respectively. Contrary to our expectations, ANOVA indicated that the leaf N term ($F_{(1,66)} = 1.85$; $P = 0.18$) was not a significant predictor of N flux.

Figure 1 depicts the relationships described in Eq. 5. For each panel in Fig. 1, we standardized N flux rates for two of the independent variables in order to demonstrate the partial relationship between N flux and the third independent variable. In panel a, N flux was standardized for a temperature of 293 K (20 °C) and a larval N concentration of 0.10 using the equation: standardized $Q_N = Q_N\ (e^{0.83/kT}\ N_B^{1.56})\ (e^{-0.83/k293}\ 0.10^{-1.56})$. In panel b, N flux was standardized for a larval mass of 20 mg and an N concentration of 0.10 using the equation: standardized $Q_N = Q_N (M_B^{-0.77}\ N_B^{1.56})\ (20^{0.77}\ 0.10^{-1.56})$. In panel c, N flux was standardized for a larval mass of 20 mg and a temperature of 293 K using the equation: standardized $Q_N = Q_N\ (M_B^{-0.77}\ e^{0.83/kT})\ (20^{0.77}\ e^{-0.83/k293})$. Several patterns are evident in Fig. 1. First, body mass accounted for more variation (partial $R^2 = 0.86$) in individual N flux than did environmental temperature (partial $R^2 = 0.29$) or body N concentration (partial $R^2 = 0.14$). Second, the relationships between N flux and body mass and N flux and body N concentration were reasonably represented by power functions, i.e., straight lines could be fitted to the data on log–log axes. Third, the relationship between N flux and temperature was reasonably represented by an exponential function, i.e., a straight line could be fit to the data on log-linear axes.

Discussion

Our primary objective in this study was to construct a general model of individual N flux for a novel group of herbivores using concepts from metabolic ecology and ecological stoichiometry. We found that a model that included larval mass, environmental temperature, and larval N concentration explained nearly 90% of the variation in the flux of egested and excreted N. We evaluated the model using data from a wide variety of insect (22) and tree (8) species, and over a broad range in body mass (0.18–268.52 mg dry), temperature (15–30 °C), larval N concentration (7.5–13.2%), and leaf N concentration (1.1–3.4%). The model should yield reasonable N flux predictions for moth and sawfly larvae from hardwood forests of the upper Great Lakes region. However, the model should be considered a quantitative hypothesis to be tested before it is used in systems where species composition, body mass range, temperature, or leaf N concentration differs markedly.

Larval body mass

Our analysis showed that the relationship between larval N flux and larval mass was well fit by a power function with a mass-scaling exponent of 0.77 (Fig. 1a). Thus, for a given environmental temperature and larval N concentration, a 100-fold increase in body mass corresponded with a 35-fold increase in N flux. Figure 1a illustrates how this pattern appeared to hold across multiple field-collected species and within lab-reared whitemarked tussock moths. We are aware of only one previous report on the mass dependence of total N flux across terrestrial animals of varying species and sizes. Brody (1945) showed that the flux of excreted and egested N by domesticated mammals and birds scaled with body mass raised to the 0.74 power. Studies conducted on aquatic organisms have shown that N excretion, on its own, scales with body mass raised to the powers of 0.85 (Brett and Groves 1979), 0.78 (Schaus et al. 1997), and approximately 0.79 (from Fig. 2 in Vanni et al. 2002) for fish, and 0.79 for zooplankton (Wen and Peters 1994).

In developing the individual N flux model, we reasoned that N flux would be proportional to egestion rate, which, in turn, would be proportional to metabolic rate. Accordingly, the mass-scaling exponent of 0.77 was similar to scaling exponents for egestion rates from other animal studies, which have ranged from 0.59 for crabs (Cammen et al. 1980), to 0.63 for mammals (Blueweiss et al. 1978), 0.68 for insects (Peters et al. 1996), 0.79 for birds and mammals (Peters et al. 1996), 0.91 and 0.81 for benthic invertebrates (McDiffett 1970; Hargrave 1972), 0.93 for lepidopteran larvae (Smith 1972), and 1.18 for reptiles and amphibians (Peters et al. 1996). The mass-scaling exponent of 0.77 was also centered within the range of 0.65–0.85 generally observed for metabolic allometries (Peters 1983; Glazier 2005), was identical to the mass-scaling exponent of 0.77 observed for larval lepidopteran metabolic rate (Smith 1972), and was very close to and not significantly different from the value of 0.75 predicted by metabolic scaling theory (West et al. 1997; Banavar et al. 2002; West and Brown 2005).

Environmental temperature

We found that short-term variation in environmental temperature was significantly related to variation in individual N flux. The relationship between temperature and N flux was reasonably represented by the Boltzmann–Arrhenius equation with a critical thermal increment of 0.83 eV (Fig. 1b). Given this functional form and temperature coefficient, an increase in environmental temperature from 20 to 25 °C would result in a 75% increase in individual N flux. Relatively little has been published on the effects of temperature on herbivore nutrient fluxes, and all of the information available relates to the temperature dependence of N excretion by aquatic organisms. Wen and Peters (1994) assessed N excretion by zooplankton using data compiled from the literature. They found that Q_{10} values (the factorial increase in a rate with a temperature increase of 10 °C) for N excretion averaged 2.0, and reported that

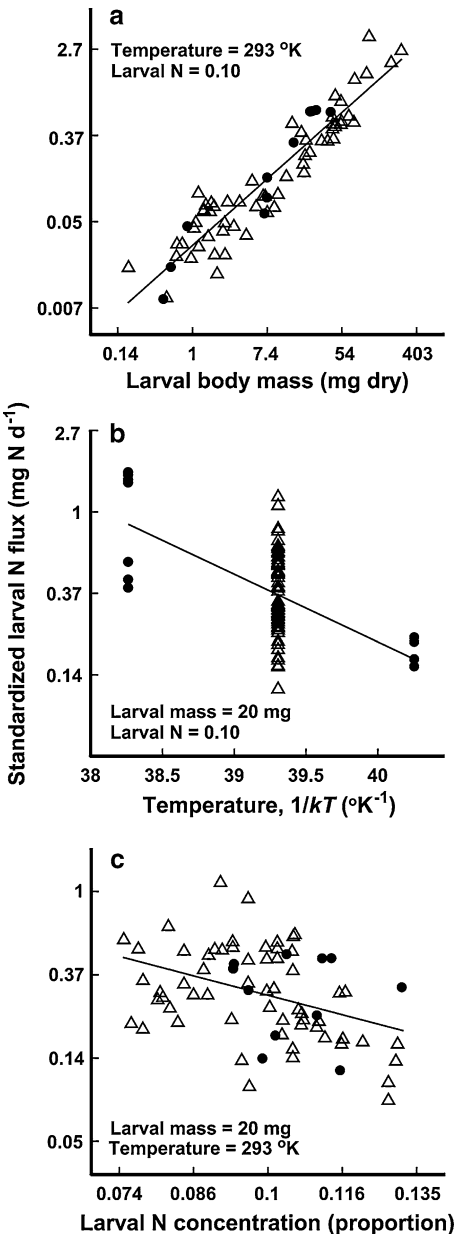

Fig. 1a–c Relationship between standardized larval nitrogen flux (excreted and egested nitrogen, mg N day^{-1}) and **a** larval body mass (mg dry), **b** environmental temperature (1/kT, where temperature, T, is in K and k is 8.62×10^{-5} eV/K), and **c** larval N concentration (proportion of dry mass) for field-collected (*open triangles*) and lab-reared (*filled circles*) larvae. All *axes* are on a logarithmic scale except for temperature. Standard larval masses, temperatures, and larval N concentrations are given per panel. See text for further details

other reviews (Ejsmont-Karabin 1984) have given Q_{10} values as high as 2.8. The critical thermal increment from our study can be converted to a Q_{10} value using the equation $Q_{10} = e^{c/0.1kT_0^2}$, where T_0 is the median of the range over which Q_{10} was measured (Gillooly et al. 2001; Vasseur and McCann 2005). Using this equation, the observed thermal increment of 0.83 gives a Q_{10} of 3.07, which is slightly higher than the value observed in other studies. However, given that the 95% confidence interval for the thermal increment extended to 0.52 (Q_{10} = 2.02), the temperature dependence observed here was not significantly different from that seen in studies of other organisms.

Regarding the proportionality of N flux, egestion rate, and metabolic rate, the temperature sensitivity observed here was similar to that noted for sawfly frass production, where Q_{10} values range from 2.43 to 2.93 and average 2.64 (Green and deFreitas 1955; Simandl 1993). The temperature sensitivity of N flux was also comparable to that of metabolic rate, where empirical Q_{10} values typically range from 2 to 3 (Withers 1992; Hill et al. 2004) and critical thermal increments typically range from 0.25 to 0.80 eV (Vasseur and McCann 2005; Meehan 2006). Concerning ecological theory, the critical thermal increment of 0.83 was not significantly different from the value of 0.65 predicted by metabolic scaling theory (Gillooly et al. 2001, 2006).

There are two additional aspects of the temperature component of this study that are worth noting. First, the temperature coefficient in Eq. 5 was estimated mainly from the data on whitemarked tussock moth larvae. We recognize the shortcomings of this approach, and are conducting additional studies on other species to assess the generality of the temperature effect. Second, larvae were not acclimated to experimental temperatures before onset of the feeding trials. This method was consistent with our intention to assess larval responses to temperature changes that occur at diurnal time scales. Temperature variations over larger time scales (e.g., months to years) could lead to temperature acclimation that might alter the apparent relationship between temperature and N flux.

Larval N concentration

We found that larval N flux scaled with larval N concentration as $N_B^{1.56}$ (Fig. 1c). In quantitative terms, this indicated that a larva that was 8% N fluxed N at twice the rate of a larva that was 12% N. The dependence of nutrient release on body composition was expected from ecological stoichiometry, and has been previously observed for aquatic herbivores (Elser and Urabe 1999; Vanni et al. 2002; Evans-White and Lamberti 2006). To our knowledge, however, it has not been documented for terrestrial herbivores.

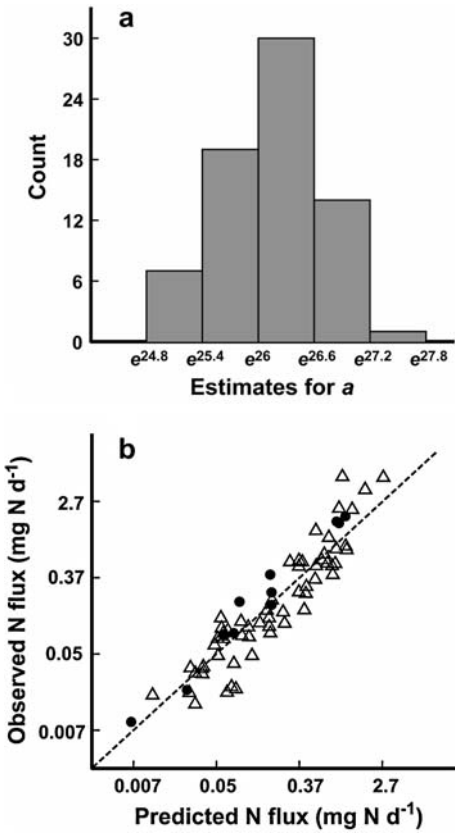

Fig. 2a–b **a** Distribution of values for the normalization constant, a, from Eq. 6. The mean of this distribution was $e^{26.16}$. **b** Relationship between observed larval nitrogen flux (mg N day^{-1}) and that predicted by Eq. 6 with $a = e^{26.16}$ for field-collected (*open triangles*) and lab-reared (*filled circles*) larvae. The *dashed line* is the line of equality and axes are on a logarithmic scale

Leaf N and compensatory feeding

Ecological stoichiometry predicted a positive relationship between larval N flux and leaf N concentration (Sterner et al. 1992; Elser and Urabe 1999). A similar pattern has been found for N excretion by aquatic herbivores (Sterner and Elser 2002) and for total N flux by locusts (Raubenheimer and Simpson 2004). Given the theoretical prediction and previous findings, we were surprised that leaf N was not included in the final model of individual N flux. This result was likely due to a combination of factors related to the relationships between leaf N concentration, frass N concentration, and frass production rate.

For example, when we looked at the relationship between leaf N and frass N concentration, we found that, as expected, the two were positively related ($N_F \propto N_L^{1.10}$). However, increases in leaf N concentration were also accompanied by decreases in frass production ($M_F \propto M_B^{0.76}\, e^{-0.69/kT}\, N_L^{-0.79}$). The inverse relationship between leaf N concentration and frass production was (1) observed

across multiple field-collected species and within laboratory-reared whitemarked tussock moths, and (2) indirect evidence for compensatory feeding, which has been demonstrated for terrestrial (Slansky and Feeny 1977; Raubenheimer 1992; Kingsolver and Woods 1998; Lavoie and Oberhauser 2004) and aquatic (Cruz-Rivera and Hay 2000; Fink and Von Elert 2006) herbivores. Given these relationships, an increase in leaf N concentration from 1.3 to 2.5% resulted in an approximate doubling of frass N concentration and an approximate halving of frass production. This finding suggests that compensatory feeding should have a role in the development of future stoichiometric theory.

Other theoretical considerations

In developing the N flux model, we borrowed functional forms from metabolic ecology for the mass and temperature terms and used flexible power function forms to represent qualitative relationships suggested by ecological stoichiometry. The coefficients associated with the functional forms were left as free parameters that were estimated using standard regression techniques. As noted previously, we found that estimated coefficients for the mass, temperature, and stoichiometric terms were similar to those quantitatively or qualitatively predicted by theory. A different way to assess the value of these theories would be to test the explanatory power of a model where coefficients were forced to hold theoretical values. We attempted this using the model:

$$Q_{\mathrm{N}} = a\, M_{\mathrm{B}}^{3/4} \mathrm{e}^{-0.65/kT} N_{\mathrm{B}}^{-1} N_{\mathrm{L}}. \quad (6)$$

Here, the mass-scaling exponent was fixed at a theoretical value of 0.75 (West et al. 1997; Gillooly et al. 2001; West and Brown 2005), the temperature coefficient was fixed at 0.65 eV (Gillooly et al. 2001, 2006), and stoichiometric terms were linear functions, which might be expected for organisms that are not nutrient-stressed, have constant assimilation efficiencies, and are strictly homeostatic. The only free parameter in this model was the normalization constant, a. We calculated values for a using our data by rearranging the equation such that $a = Q_{\mathrm{N}}/(M_{\mathrm{B}}^{3/4}\ \mathrm{e}^{-0.65/kT} N_{\mathrm{B}}^{-1}\ N_{\mathrm{L}})$. When this was done, we obtained the distribution shown in Fig. 2a. The mean of this distribution was $\mathrm{e}^{26.16}$; the exponent, 26.16, was close to and not significantly different from the value of 25.75 from Eq. 5. When $\mathrm{e}^{26.16}$ was placed into Eq. 6 and N flux was predicted for the larvae in our study, we found that the regression of observed $\ln(Q_{\mathrm{N}})$ against predicted $\ln(Q_{\mathrm{N}})$ had a slope not significantly different from 1, an intercept not different from 0, and an R^2 of 0.87 (Fig. 2b). Thus, with the addition of an empirical normalization constant, a theoretical model predicted larval N flux nearly as well as our empirical model. Future work could involve use of the framework proposed by Gillooly et al. (2005) to derive normalization constants for N flux models from first principles.

Future work

The next step in this research will be to explore the scaling of larval N flux models from the individual level to population and community levels. This exercise will have its own set of challenges, such as developing valid, spatially and temporally-integrated estimates of herbivore body mass, temperature, stoichiometry, and abundance. The reward for this effort will be a new set of tools for exploring the contribution of insect larvae to N cycling in forested ecosystems. These tools may also be useful for forecasting the role of insects in N cycling under different scenarios of environmental change. For example, human introduction of invasive species (Lovett et al. 2006) and alteration of forest structure (Cunningham and Murray 2007) can affect the abundances, body mass distributions, and elemental profiles of canopy herbivore communities. Additionally, increases in atmospheric carbon dioxide concentrations are expected to alter environmental temperatures (IPCC 2001) and the elemental ratios of foliage (Throop and Lerdau 2004). Nutrient flux models that incorporate these key variables may provide a means to predict the impact of anthropogenic changes on the role of herbivorous insects in future ecosystem function.

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