Effects of Climate-induced Distributional Shifts in Caddisfly Larvae on Detritus Processing and Ecosystem Function in High-elevation Ponds and Wetlands



By:
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Pledge

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ABSTRACT

Climate-change induced shifts in the abiotic environment have altered the hydrology and temperature of high elevation ponds and wetlands, and consequently altered the distribution of aquatic invertebrates. The purpose of this study was to determine how shifts in the distribution of caddisfly species along elevational and permanence gradients could affect ecosystem processes including overall detritus processing rates and the mobilization of detritus-bound nutrients.

In the first part of this study, I quantified species-specific excretion rates of ammonium-nitrogen (N) and total soluble phosphorus (P) in pond-side microcosms for nine species of caddisflies. For all species, I found no variation in N and P excretion at different times of day or at different elevations, but did find considerable variation among species.

I used these data to parameterize generalized linear models to predict how new species combinations resulting from climate change should affect ecosystem processes in high elevation ponds. The models predict that species replacements will not always be functional replacements in terms of their effects on nutrient regeneration or detritus processing. My research demonstrates that the degree to which species range shifts and replacements will alter ecosystem processes depends on the identity of both the invading and resident species.

INTRODUCTION

In a recent synthesis report for policymakers, the Intergovernmental Panel on Climate Change (IPCC) concluded that the reality of climate change is "unequivocal" (Pachauri et al. 2014). The report details numerous empirically supported consequences of climate change, including increasing mean atmospheric and oceanic temperatures, increasing mean sea levels, increasing atmospheric greenhouse gas concentrations, changes in timing and volume of precipitation, and shrinking polar ice caps. In producing these environmental changes, climate change subsequently constitutes a dynamic stressor to living organisms, prompting many changes in the phenology (the timing of species' life events), distribution (species' ranges), and abundance (species' quantity/sample) of Earth's biota (Parmesan & Yohe 2003).

Many of these biotic changes have been empirically studied across a wide range of ecosystems. Changes in phenology are typically marked by advances in the timing of springtime events, including earlier deciduous leaf unfolding, earlier breeding and migration in birds and amphibians, and earlier emergence of butterflies (Walther et al. 2002; Parmesan 2006). Changes in distribution and abundance are typified by gradual movements towards higher altitudes and/or latitudes, as species pursue the climactic window to which they are best adapted. Examples include North American butterflies' ranges moving northward, treeline shifting upslope, lowland birds extending their ranges to the uplands, and an overall increase in the abundance of warm-water phytoplankton, invertebrates, and fish (Walther et al. 2002; Parmesan 2006). Such shifts are reported almost daily in the scientific literature (Davis & Shaw 2001; Parmesan & Yohe 2003; Thuiller 2004; Hickling et al. 2006). Furthermore, these shifts often result in species replacements along many environmental gradients (Loarie et al. 2009; Chen et al. 2011).

Subsequently, shifts in the diversity and relative abundance of species are documented to impact a variety of ecosystem processes and functions (Naeem and Wright 2003; Giller et al. 2004; Bracken et al. 2008). Ecosystem processes are fundamentally driven by the ecosystem's unique assemblage of co-adapted species in food webs (Tilman et al. 1997; Primack 2014). However, in many cases, the extent to which new combinations of species affect the rates of various ecosystem functions remains unstudied.

One of the most foundational ecosystem functions is the processing and decomposition of dead plant material (hereafter called "detritus"). In most ecosystems, a significant proportion of energy and chemical nutrients contained in vascular plants is not eaten alive, but rather, re-enters food webs as detritus (Wetzel 1995; Cebrian & Lartigue 2004; Moore et al. 2004). To visualize this, consider that relatively few living leaves on a deciduous tree are consumed by herbivores, but rather, the nutrients in those leaves re-enter soil when they are shed (as detritus) in the fall.

In aquatic ecosystems, algae are also important primary producers, which are consumed by herbivores while living and by detritivores when dead (Lemke and Benke 2007). Thus, there are two pathways by which the energy and chemical nutrients from primary production enter food webs in aquatic ecosystems. The energy and nutrients contained in vascular plant detritus enters the food web through detritivores – the "brown side" of the food web; while that contained in algae enters through herbivores – the "green side" of the food web (Figure 1). Although these two pathways are assumed to be isolated, nutrients released during detritus processing could potentially stimulate the growth of algae, especially in oligotrophic (nutrient-poor) systems such as alpine ponds and lakes (Klemmer et al. 2012; Figure 1).

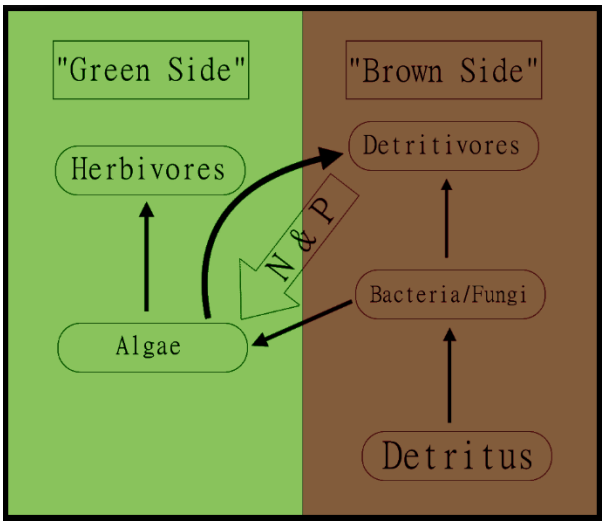

Figure 1: Summary of brown (detrital) and green (algal) trophic pathways and the nutrient linkages (Nitrogen and Phosphorus) between them in ponds. Figure adapted from Klemmer (2012).

Cased caddisfly larvae (Trichoptera: Limnephilidae) are aquatic detritivores found in alpine ponds and lakes, notable for the charismatic cases they build with silk using detritus or other benthic substrate (Figure 2). A recent study by Klemmer et al. (2012) examining the effects of caddisfly density on detritus breakdown suggests that multiple ecosystem processes (i.e. primary and secondary productivity, energy flow, nutrient cycling) are regulated through detritus processing by caddisflies. Moreover, there is evidence that different species break down detritus at different rates (Vlah 2013).

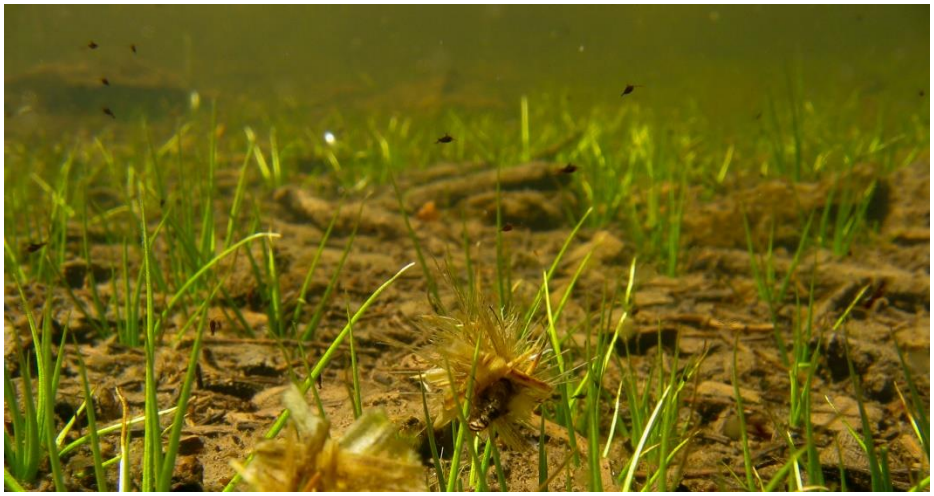

Figure 2: *L. externus* grazing, photo courtesy of Nixie Boddy.

Previous research has established that ponds at different elevations and drying regimes (temporary vs. permanent) have different species of caddisflies as a consequence of tradeoffs between traits that facilitate coexistence with predators and those that facilitate emergence before drying (Wissinger et al. 1999; 2003; 2006; Figure 3). This work also demonstrates that within those habitats, caddisfly larvae are both the biomass-dominant processors of coarse detritus and prey resource for the top predators (salamanders or fish). Furthermore, long-term data in the central Rocky Mountains indicate that snowmelt is occurring sooner and summer droughts are more severe (Ozgul et al. 2010; Boggs & Inouye 2012; Barr 2015), resulting in earlier pond drying (Balik & Wissinger unpublished data), as predicted by climate change literature (Seager et al. 2007). Given these altered pond permanence gradients, caddisfly species historically found in permanent ponds could be replaced by species that typically inhabit temporary vernal ponds (Schneider and Frost 1996; Wissinger et al. 1999), and in actuality, long-term survey data indicates that such shifts are already occurring throughout this system (Table 1).

Table 1: Distributions of detritivorous caddisflies in central Colorado. L = *Limnephilus*; A = *Asynarchus*; G = *Grammotaulis*. **Bold** indicates dominance. * indicates recent upslope range shift in elevation. Dates show first occurrence. (*Table adapted from Wissinger NSF Proposal)*

Montane-Elevation Basins			**Subalpine-Elevation Basins**		
Temporary	Semi-permanent	Permanent w/ Predators	Temporary	Semi-permanent	Permanent w/ Predators
	L. externus	***L. externus***		***L. externus***	***L. externus***
	**L. sublunatus*	**L. sublunatus* (2000)			
	L. picturatus	***L. picturatus***		**L. picturatus* (1998)	**L. picturatus* (1998)
	G. lorretae	*G. lorretae*		**G. lorretae* (2009)	*** G.lorretae* (2009)
L. tarsalis					
L. secludens					
A. nigriculus			***A. nigriculus***	***A. nigriculus***	

Given the importance of this guild to detritus processing, and given that different species appear to process at different rates (Vlah 2013), one might predict that new combinations of species should change overall nutrient recycling that can in turn stimulate algal productivity, thus influencing the strength of the connectivity between the green and brown tropic paths in aquatic systems (Wissinger et al. ms).

In the first part of this study, I conducted a series of field experiments using organisms from the ponds and wetlands near the Rocky Mountain Biological Laboratory (38°6'N, 106°6'W; Figure 3). These experiments allowed me to quantify species-specific areal excretion rates of ammonium-nitrogen (N) and total soluble phosphorus (P) following a microcosm-scale incubation technique adapted from Taylor et al. (2016). I hypothesized that**:**

1. **Different species of caddisflies generate different levels of algal nutrients [ammonium-nitrogen and phosphate-phosphorus]**.
2. **Within a species, different levels of N&P will be generated throughout the day.** This hypothesis was informed by previous studies that found diel variation in nitrogen excretion (Brett & Zala 1975; Checkley et al. 1992).
3. **Within a species, different levels of N&P will be generated at different elevations**. This hypothesis was based on the differing tradeoffs across elevations among maintenance, growth, and reproduction (Porter 1989).

In the second part of this study, I combined these data with those from previous studies on species-specific rates of detritus breakdown to parameterize generalized linear models to predict how these species range and distributional shifts and species-specific excretion rates

will affect ecosystem processes. Despite the recent emphasis in ecology on understanding how differences in species' traits translate into outcomes at the ecosystem level, few previous studies have done so for aquatic detritivores (Poff 1997). These models allow us to make predictions regarding whether climate change-induced shifts in species composition will affect the linkage between detritus processing, algal productivity, and the overall metabolism in ponds. By extension, this research aims to determine whether species replacements in similar habitats at different altitudes or changing hydroperiods can translate to functional replacements with regard to their role(s) in various ecosystem functions.

METHODS

Site Selection:

This study was conducted in ponds near the Rocky Mountain Biological Laboratory in central Colorado (Figure 3; 38°6'N, 106°6'W) (Figure 3). Using historical distributional data (Wissinger et al. 2003), I selected ponds and wetlands distributed across an elevational gradient ranging from montane (~2900m, Figure 4) to upper montane (~3200m, Figure 5) to subalpine (~3500m, Figure 6). The subalpine sites were located in the Mexican Cut Nature Preserve (39°1'N, 107°4'W). At montane elevations, the ponds should have higher levels of nutrients because of cattle grazing, whereas at subalpine elevations they are oligotrophic (nutrient-poor) and co-limited by phosphorus and nitrogen (Elser et al. 2009). At all elevations, pond permanence ranges from ephemeral (temporary) to semi-permanent to permanent (Wissinger et al. 1999; 2003).

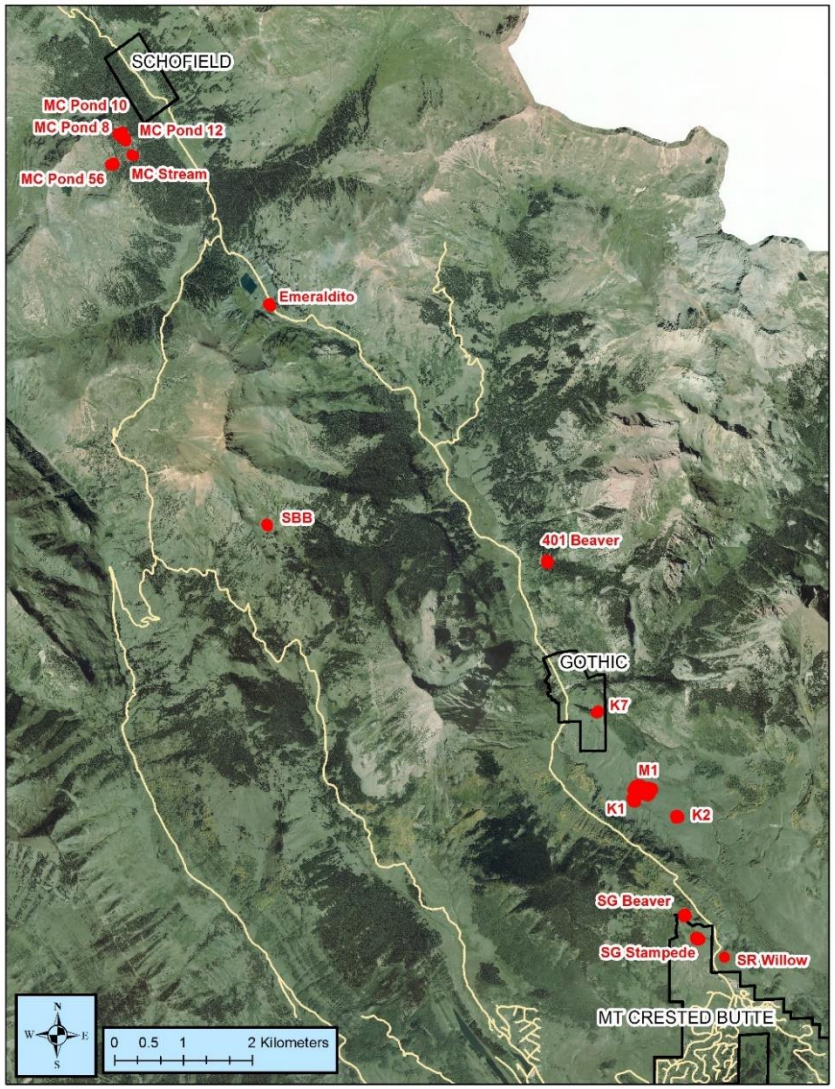

Figure 3: Vicinity map of my study sites near the Rocky Mountain Biological Laboratory (depicted as town of "Gothic"). Ponds are indicated in red.

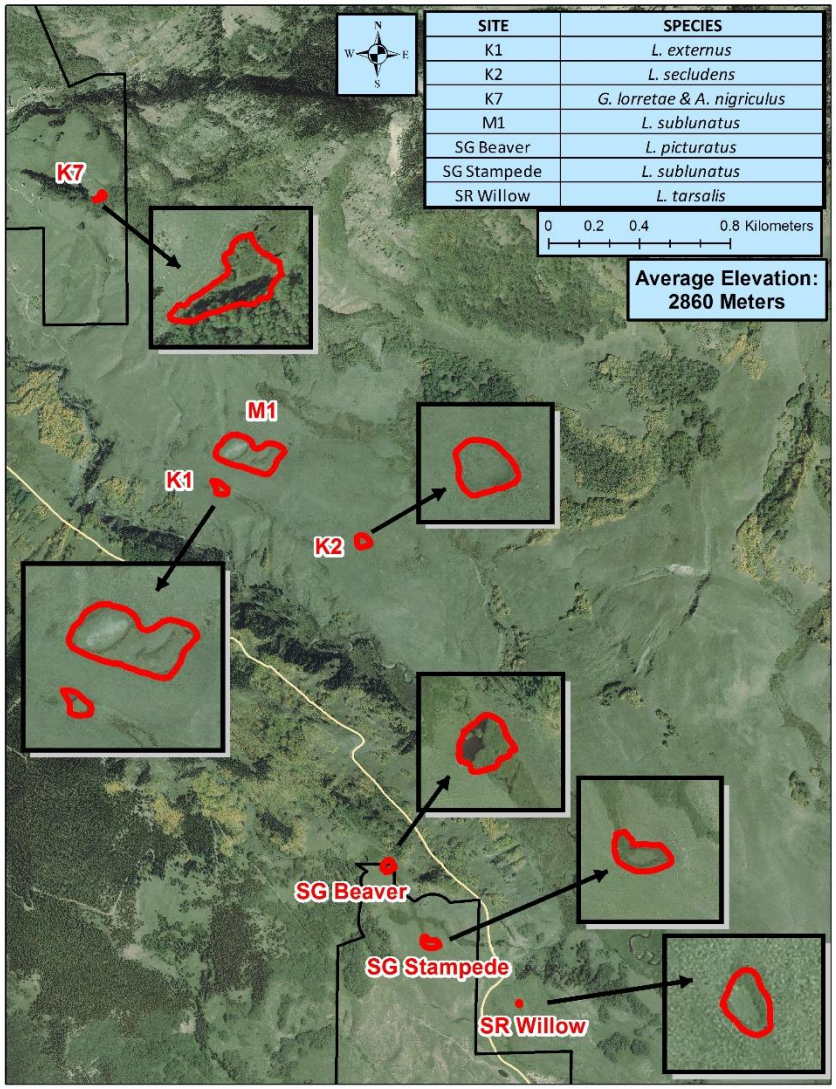

Figure 4: Map of my montane study sites. Ponds are indicated in red. Legend indicates which species were studied in each pond.

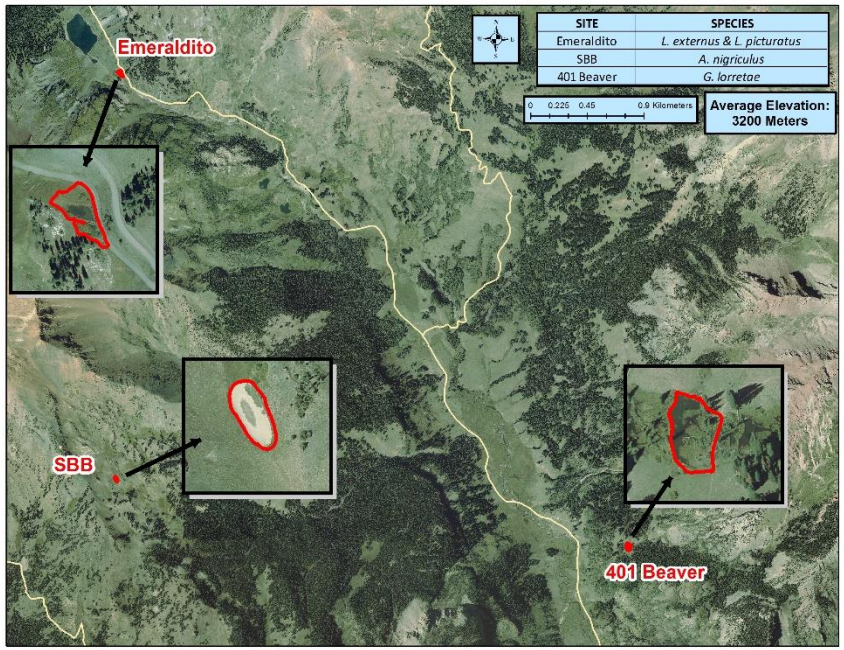

Figure 5: Map of my upper-montane study sites. Ponds are indicated in red. Legend indicates which species were studied in each pond.

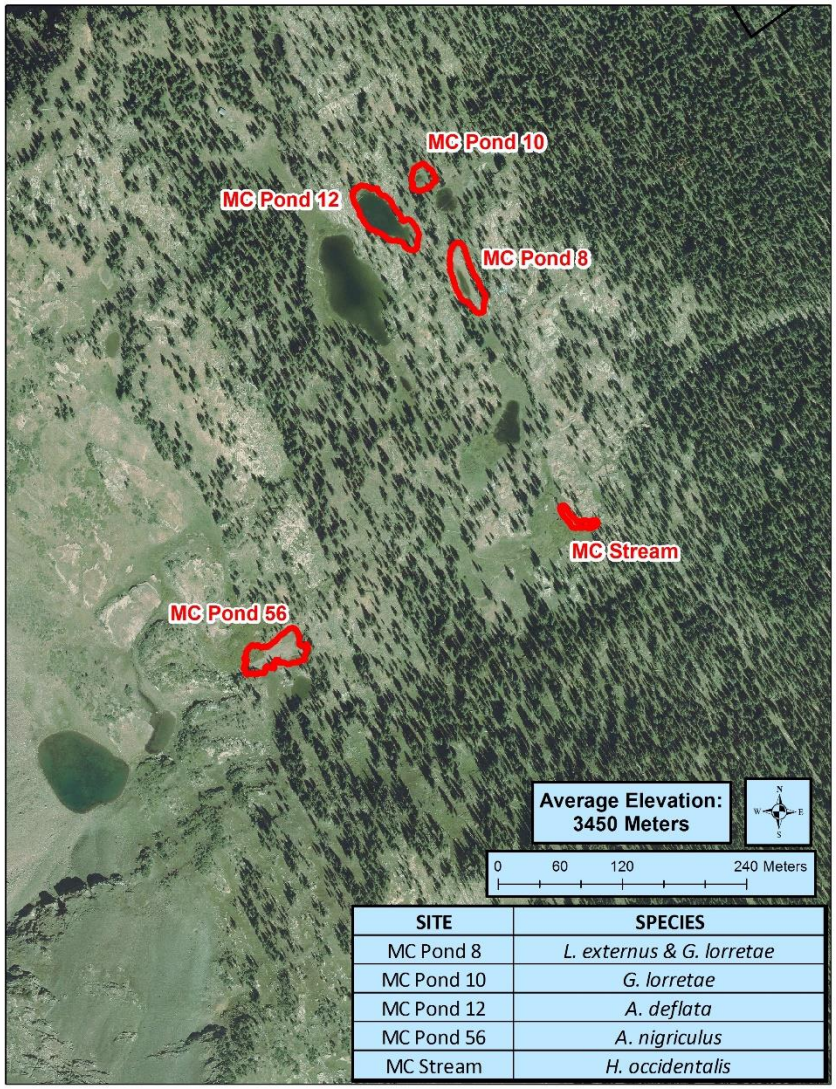

Figure 6: Map of my subalpine study sites. Ponds are indicated in red. Legend indicates which species were studied in each pond.

Study Species:

I studied the excretion rates of nine species of cased caddisflies – one in the family Phyrganeideae, *Agrypnia deflata*, and eight in the family Limnephilidae, including *Asynarchus nigriculus*, *Grammotaulius lorettae, Hesperophylax occidentalis*, *Limnephilus externus*, *Limnephilus picturatus*, *Limnephilus secludens*, *Limnephilus sublunatus*, and *Limnephilus tarsalis*. These animals are native to Gunnison County (Herrmann et al. 1986) and are the biomass-dominant detritivores in ponds and wetlands throughout the study region (Wissinger et al. 1999). The detritus they consume predominantly consists of wetland sedges (*Carex* spp.) and grasses, willow leaves (*Salix* spp.), and in some species (e.g., *A. nigriculus*) conifer needles (*Abies lasiocarpa*, *Picea engelmannii*) depending on elevation.

Experimental Design

For each excretion experiment, triplicate sets of five caddisflies of the same species in the predominant instar at that time were placed into Ziploc bags pre-filled with 315ml of filtered pond water. The incubations were conducted for one hour in the shade to maintain ambient temperature. The duration was selected as a compromise between wanting to capture their ambient excretion rate and minimizing stress or starvation effects on metabolic rates. Three time blocks were conducted during morning, midday, and early afternoon (n=9 for total incubations for each species at each pond). At the beginning of each experimental block, water and air temperature were recorded. With four of the study species that have broad elevational ranges (*A. nigriculus*, *G. lorettae*, *L. externus*, and *L. picturatus*) this experiment was replicated at three elevations; montane, upper montane, and subalpine (for each species n=27).

To estimate species-specific excretion, I compared ammonium-nitrogen (NH_4^+-N) and total soluble phosphate-phosphorus (PO_4^{3-}) in filtered water samples drawn at the beginning

and end of each one hour excretion experiment. This technique has been used in previous studies on macroinvertebrates (e.g. Grimm 1988; Hall et al. 2003; Taylor et al. 2016) as well as with fish (e.g. Brabrand & Faafeng 1990; Wheeler et al. 2015) and even amphibians (Whiles et al. 2009). Water samples were collected and filtered using a Gelman AE brand syringe and Swinnex brand filter head with a 25mm glass fiber filter.

NH_4^+ Analysis

For each experiment, quadruplicate 40ml filtered water samples were collected in amber Nalgene bottles (60ml capacity), chilled in the field, and then frozen upon returning to the laboratory. The opacity of the bottles and the cooler temperatures were intended to help preserve the samples (Klemmer et al. 2012). Samples were later thawed and measured following a standard fluorometric method established by Holmes et al. (1999) and revised by Taylor et al. (2007) using a Turner Trilogy Fluorometer (Sunnyvale CA, USA). The method uses a linear regression to calculate the unknown concentration of NH_4^+ in ug/L^{-1}. For my analysis, two water samples from each replicate were spiked with 5ug NH_4^+ L^{-1} and 25ug NH_4^+ L^{-1} to create the regression, with the third sample being unadulterated, while the final sample was used to correct for both background fluorescence and matrix effects.

TSP Analysis

For each experiment, a 50ml filtered water sample was collected in a glass test tube and stored in the laboratory. Each sample was treated with 0.4g $K_2S_2O_8$ and immersed in a pressure cooker for one hour to oxidize all reactive phosphorus. Samples were then measured following a standard colorimetric light spectroscopy assay known as the "molybdenum blue technique"

(Strickland & Parsons 1968; Ostrofsky & Rigler 1987) using a Thermo Scientific GENESYS 10S VIS Spectrophotomer (Waltham MA, USA).

Caddisfly Body Mass

Average caddisfly larvae body mass was estimated by collecting 15 similar-size larvae of each species at each site. Larvae were preserved in 95% EtOH. Body lengths and head widths were measured and larvae were oven dried for 48 hours at 600°C to obtain dry mass. I calculated mean larval body mass values for each species using those dry masses. Through comparison with historical data provided by Wissinger et al. (2003), I verified the instar used in each experiment.

GIS Mapping

The perimeter of each study site (14 ponds and water marshes, 1 outflow stream) was mapped in the field using a Trimble GEOXT handheld GPS in July of 2015. Maps were then generated using ArcGIS 10.3.1 (Environmental Systems Research Institute, Redlands CA, USA) with orthoimagery obtained from the United States Geological Survey's (USGS) National Map. In some locations, the only available orthoimagery depicts semi-permanent or temporary ponds when they are dry.

Statistical Methods

Analysis of Variance (ANOVA) was used to compare differences in excreted NH_4^+ and TSP between experimental replicates based on bag, time of day and location (proxy of elevation). Simple linear regression was used to test for a water or air temperature effect. These analyses allowed me to generate mean areal excretion rates (with n=9 or n=27) by collapsing experimental replicates across temperature, time, and location. ANOVA was used

again to compare body mass-specific excretion rates across species. Simple linear regression was used to determine if there was any relationship between a species' ratio of N:P regeneration and diet. All statistical analysis was completed using Statview 5.01. (SAS Institute, Cary NC, USA).

Calculation of Biomass-specific Species-specific Areal Excretion Rates

Rates of NH_4^+ or PO_4^{3-} excretion with units of ug mg^{-1} d^{-1} were calculated by the following general equation:

$$\frac{\left[\frac{\left(\text{Experimental ug } NH_4^+ \text{ or } PO_4^{3-}\right) - \left(\text{Ambient ug } NH_4^+ \text{ or } PO_4^{3-}\right)}{(Total\ mass\ of\ Caddisflies\ per\ bag\ in\ mg)}\right]}{1 \text{ hour}} * \frac{24 \text{ hours}}{1 \text{ day}}$$

Where "*Total mass of Caddisflies per bag in mg*" is 5x the mean caddisfly mass used in the experiment.

Modeling

I used generalized linear models to make predictions about how the new species combinations that are likely to result from range shifts along elevational and permanence gradients will affect overall levels of nutrient regeneration and detritus processing. The nutrient regeneration models were parameterized with my nutrient excretion data, life history and density data for each species in natural populations (e.g., time spent in the larval stage; Wissinger et al. 2003; unpublished data) to predict the contribution of each species to overall levels of mobilized N & P. The detritus processing (hereafter "DP") models were parameterized using the results of a series of microcosm experiments conducted over the past six years (Krejsa 2011; Burns 2012; Vlah 2013; Washko unpublished data; Wissinger et al. ms). In each model, *L. externus* at a density of 100ind/m^2 was used as a baseline for comparing the DP rates of other

species. The standardized per-unit body mass DP rates used in the models were calculated by dividing each species' relative DP rate by that of *L. externus* in the microcosm experiments then multiplying by the field experiment DP rate for *L. externus* at a density of 100ind/m^2 from Klemmer et al. (2012). For example:

$$\left(\frac{\text{X mg detritus by } other\ species\ (\mathbf{microcosm})}{\text{Z mg detritus by } L.\ externus\ (\mathbf{microcosm})}\right) * \left(\frac{\frac{0.5672 \text{ mg detritus}}{\text{mg } L.\ externus \text{ body mass } \mathbf{in\ field\ at\ 100ind/m^2}}}{\text{Day}}\right)$$

Where "X" and "Z" are from the same microcosm study. All models show 95% confidence intervals (error bars) around these projections, based on lowest and highest possible values for each variable.

In competition-extinction models, invasions are simulated by incrementally increasing biomass of the invading species while simultaneously reducing biomass of the resident species and subsequently recalculating individual contributions to overall summer nutrient regeneration and detritus breakdown until each resident biomass falls to 0 mg/m^2. Thus, this class of model assumes that the invading species outcompetes the resident species, or that the resident species is unable to persist in the changing habitat. The model allows the invading species biomass to rise to the sum of the initial resident species biomass and the initial invading species biomass.

In partial replacement models, invasions are simulated by incrementally increasing biomass of the invading species while gradually dropping biomass of the resident species and subsequently recalculating individual contributions to overall summer nutrient regeneration and detritus breakdown. Thus, this class of model assumes partial niche overlap – i.e. that the invading species reduces the biomass of the resident species, but the two species coexist at

1.5x the initial biomass of the resident species. The model allows the invading species to rise to 75% of the sum of the initial resident species biomass, while the biomass of each resident species falls to 75% of its initial value.

In niche-splitting models, invasions are simulated by incrementally increasing biomass of the invading species while maintaining biomass of the resident species and subsequently recalculating individual contributions to overall summer nutrient regeneration and detritus breakdown. Thus, this class of model assumes that the invaders are filling a vacant niche. The model allows invading species to rise to the sum of the initial resident species biomass and the initial invading species biomass.

In all three model classes, the algorithm could generate models that depict true invasions (invading species biomass initially = 0 mg/m^2) as well as models where a native species usurps dominance because it is favored by changing climate conditions (e.g., increased temperature, increased ephemerality; thus, invading species biomass initially > 0 mg/m^2). However, in all scenarios modeled here, the invading species biomass always began at 0 mg/m^2.

RESULTS

Pond Ambient Nutrient Levels

Phosphorus levels differed at all three elevations (Figure 7A, $p<0.01$). Ammonium levels at the montane and upper montane elevations differed from those at the subalpine elevation (Figure 7B, $p<0.01$). Both ambient phosphorus and ammonium levels were constant from morning to midday to early afternoon. (PO_4^{3-} $p=0.99$; NH_4^+ $p=0.76$).

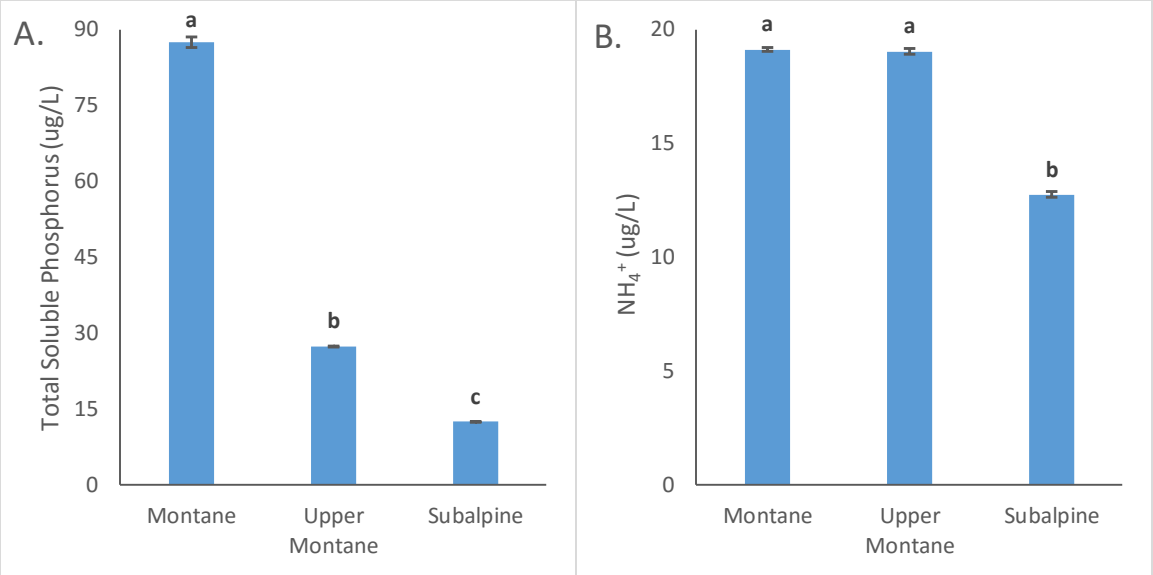

Figure 7: Ambient nutrient levels at the three study elevations. Panel A shows PO_4^{3-}; panel B shows NH_4^+. Montane data are from seven sites, upper montane data from three sites, and subalpine from five sites. All data are pooled from summer 2014 and summer 2015. Error bars represent +/- 1 SE. Groupings are from Fisher's PSLD.

Excretion Rates

For each species, replicates were not statistically different (Table 2). For species studied at all three elevations (*A. nigriculus*, *L. externus*, *L. picturatus*, *G. lorretae*), replicates across all three elevations were not statistically different (Table 2).

Table 2. Statistical summary table for the ANOVAs of each species' replicates and elevations (where applicable). Within each species, none of the replicates or elevations are significantly different. The regression coefficient of temperature versus body mass specific excretion rates are also presented; the corresponding p values are not significant.

Species	PO_4^{3-}			NH_4^+		
	Replicate (p=)	**Elevation (p=)**	**Temperature (R^2=)**	**Replicate (p=)**	**Elevation (p=)**	**Temperature (R^2=)**
Broad Distributions (n=27)						
A. nigriculus	0.7551	0.0745	0.022	0.7993	0.6976	0.018
L. externus	0.837	0.072	0.415	0.5967	0.3067	0.133
L. picturatus	0.0789	0.9098	0.623	0.6701	0.2872	0.242
G. lorretae	0.845	0.006	0.052	0.3244	0.5349	0.173
Montane Only (n=9)						
L. tarsalis	0.905	--	--	0.5297	--	--
L. sublunatus	0.5327	--	--	0.4938	--	--
L. secludens	0.5546	--	--	0.8297	--	--
Subalpine Only (n=9)						
H. occidentalis	0.0534	--	--	0.2939	--	--
A. deflata	0.7721	--	--	0.956	--	--

Per-unit Body Mass excretion rates

Since there were no significant differences among replicates for any species, standardized species-specific per-unit body mass excretion rates (ug of NH_4^+ or PO_4^{3-} mg^{-1} d^{-1}) were calculated by collapsing replicate means across experiments. These standardized rates are significantly different for phosphorus (Figure 8A, $p<0.01$) and ammonium (Figure 8B, $p<0.01$).

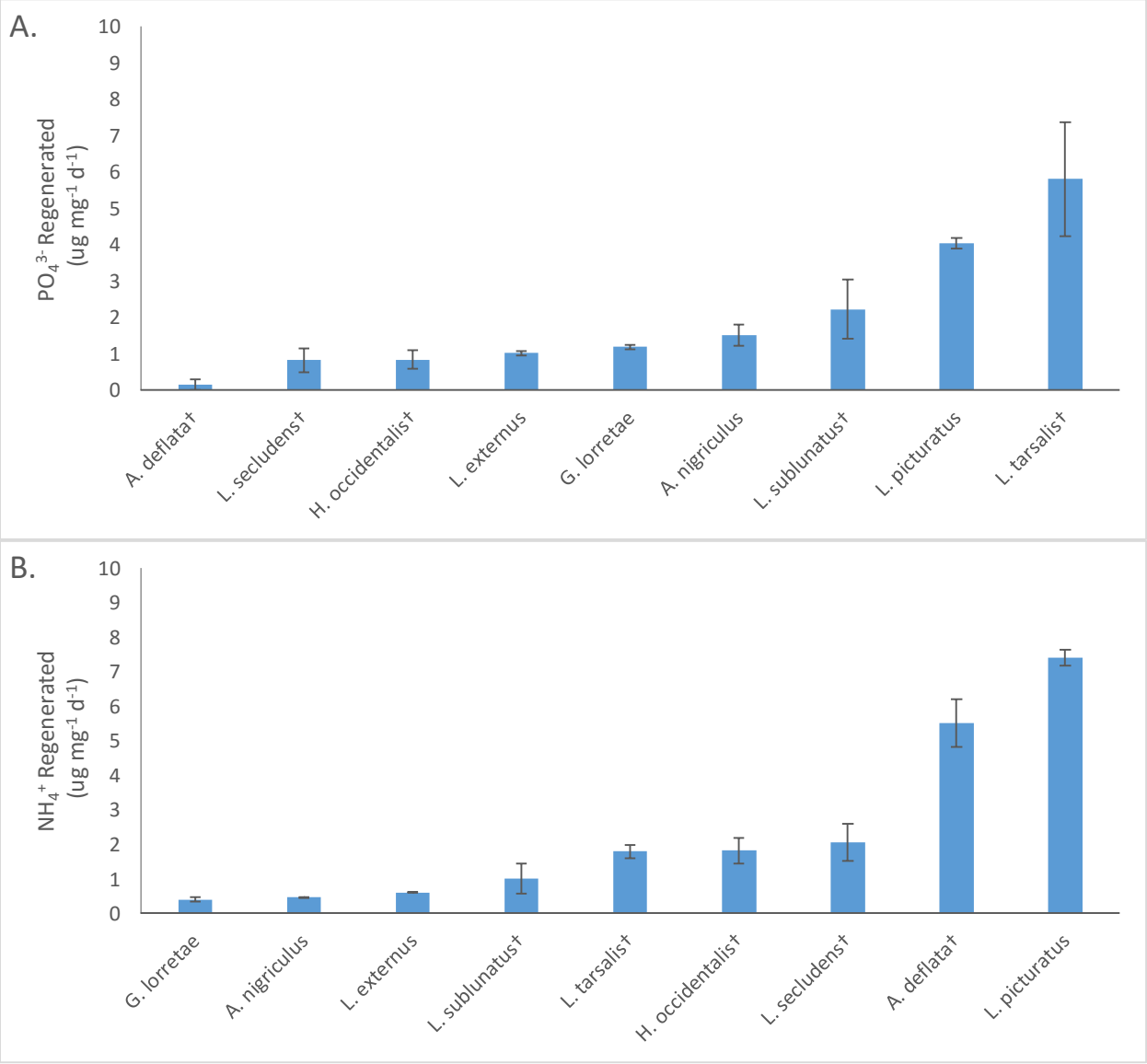

Figure 8: Amount of each nutrient regenerated (ug) per unit body mass (mg) per day (d) of each species. Panel A shows PO_4^{3-}; panel B shows NH_4^+. Data are pooled from summer 2014 and summer 2015 for L.p. and G.l.. Data for L.e. and A.n. are from 2014. Data for L.sub., L.sec., L.t., H.o., and A.d. are from 2015. For species studied at all three elevations, n=27, whereas for species studied at only one elevation (denoted by "†") n=9. Error bars represent +/- 1 SE.

Using these standardized species-specific per-unit body mass excretion rates, N:P ratios were calculated to compare the rates at which the two nutrients are regenerated by each species (Figure 9).

Standardized species-specific per-unit body mass detritus processing rates, calculated from past studies, are also presented for comparison (Figure 10).

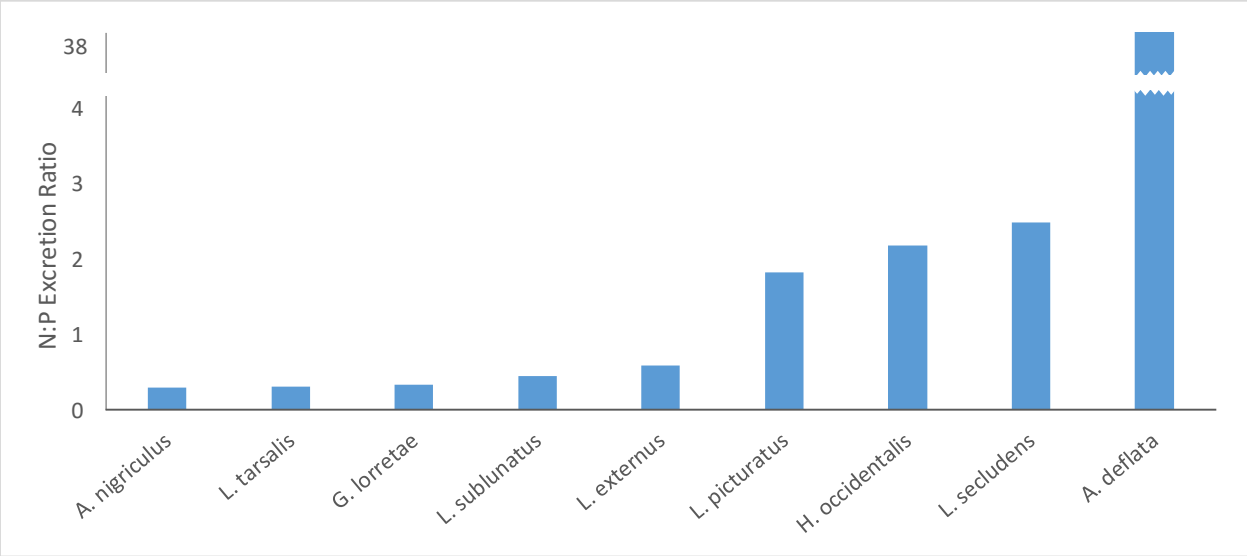

Figure 9: Ratio of N:P (NH_4^+ to TSP) regenerated when each is expressed as (ug) per unit body mass (mg) per day (d) for each species.

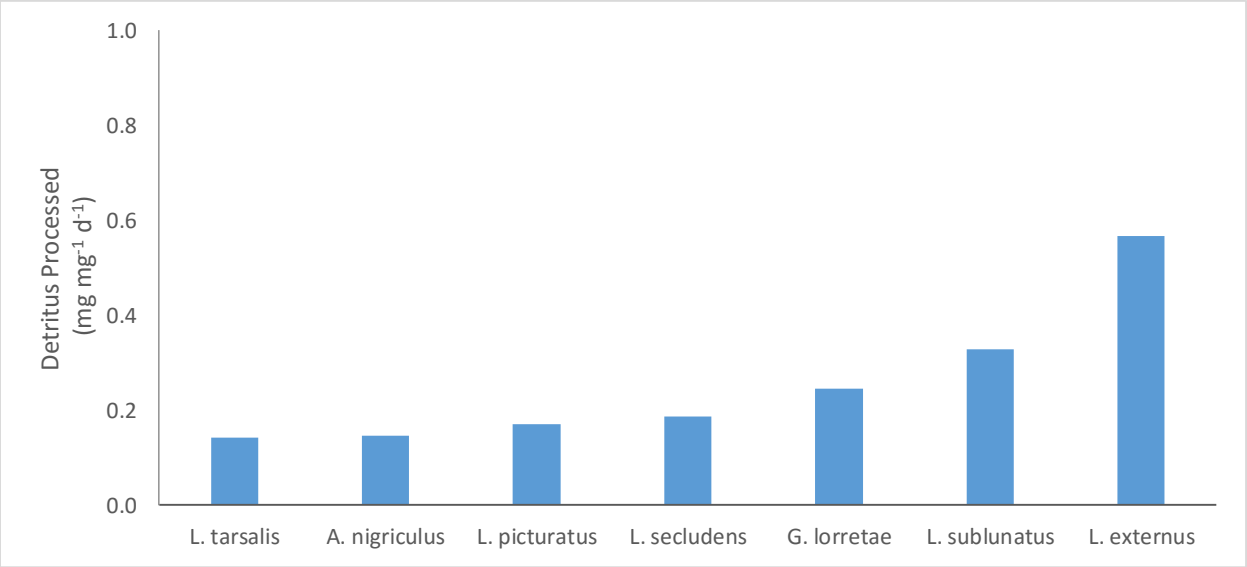

Figure 10: Standardized per-unit body mass DP rates, calculated by dividing each species' relative DP rate from microcosm experiments (Krejsa 2011; Burns 2012; Vlah 2013; Washko unpublished data; Wissinger et al. ms) by that of *L. externus*, multiplied by the in-situ DP rate for *L. externus* at a density of 100ind/m^2 from Klemmer et al. (2012). No data for A. deflata or H. occidentalis.

Temperature Regressions

Ambient water temperature did not explain any of the variation in N or P excretion rates for *A. nigriculus*, *L. externus*, *L. picturatus*, or *G. lorretae* (all $p>0.05$). Because I only had three temperature datapoints for excretion experiments with *H. occidentalis*, *A. deflata, L. tarsalis*, *L. secludens*, and *L. sublunatus,* I could not test for an effect of temperature.

Dietary Regression

Several dietary components (Wissinger unpublished data; Figure 11) significantly explained excretion rates, N:P ratios, and detritus breakdown rates. The percent of filamentous algae in a species' diet predicted the P excretion rates (Figure 12; $p<0.01$, $R^2=0.77$). The total percent of detritus in a species' diet predicted the N:P excretion ratios (Figure 13; $p = 0.01$, $R^2=0.61$) , as did the percent of chitin (Figure 14; $p<0.01$, $R^2=0.66$). Finally, the percent of herbaceous CPOM predicted the detritus processing rates (Figure 15; $p<0.01$, $R^2=0.94$).

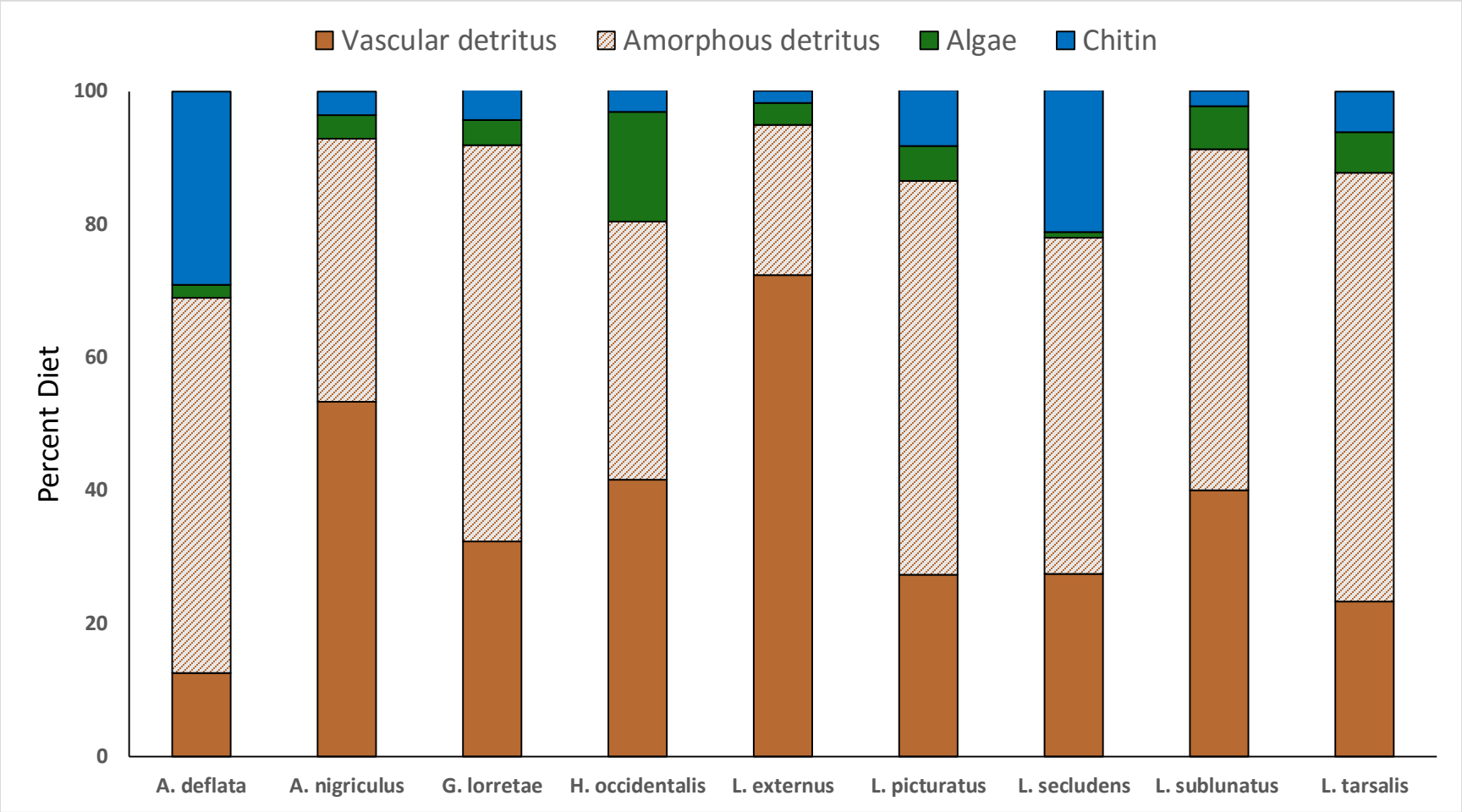

Figure 11: Stacked diet breakdowns for several species, collected by percent of microscope field area in an unpublished study. Vascular detritus (solid brown) includes herbaceous and woody detritus. Amorphous detritus (brown hatch) includes all 0.5um-1mm FPOM particles. Algae (green) includes diatoms, filamentous algae, and other algae. Chitin (blue) is a proxy for animal tissue. Figure adapted by Amanda Klemmer from Wissinger unpublished data.

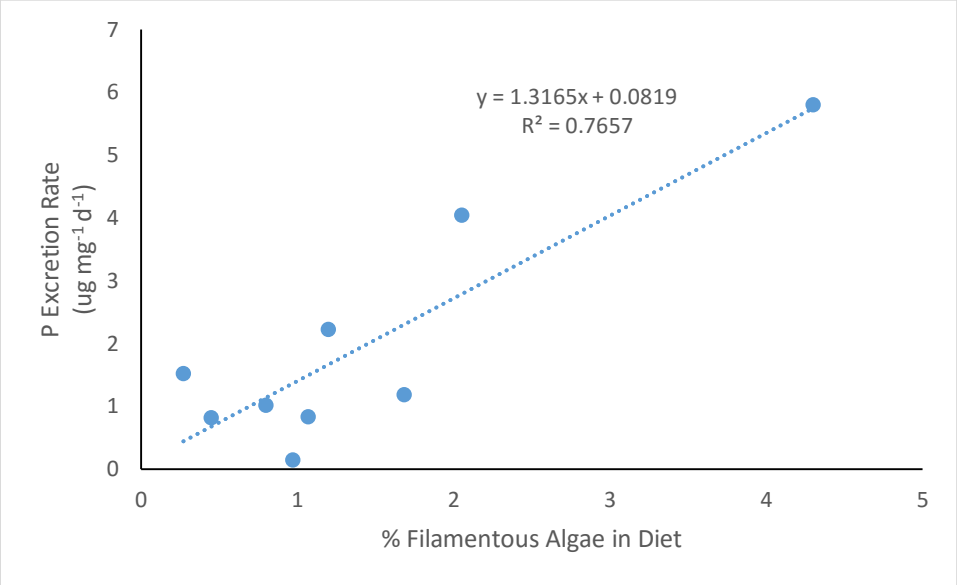

Figure 12: Regression of percent filamentous algae in several species' diets against their phosphorus excretion rates, expressed in ug mg^{-1} d^{-1}. Dietary data are for *H. occidentalis, A. deflata, L. picturatus, G. lorretae, L. secludens, L. tarsalis, A. nigriculus*, and *L. externus*. ($p<0.01$, $R^2 = 0.77$).

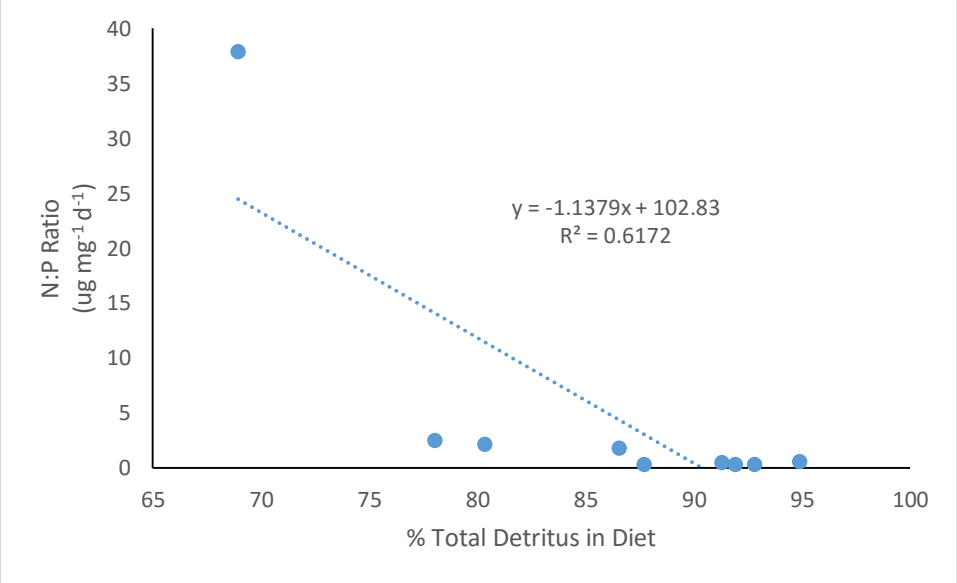

Figure 13: Regression of percent total detritus in several species' diets against their N:P excretion ratios, expressed in ug mg^{-1} d^{-1}. Dietary data are for *H. occidentalis, A. deflata, L. picturatus, G. lorretae, L. secludens, L. tarsalis, A. nigriculus*, and *L. externus*. ($p=0.02$, $R^2=0.61$).

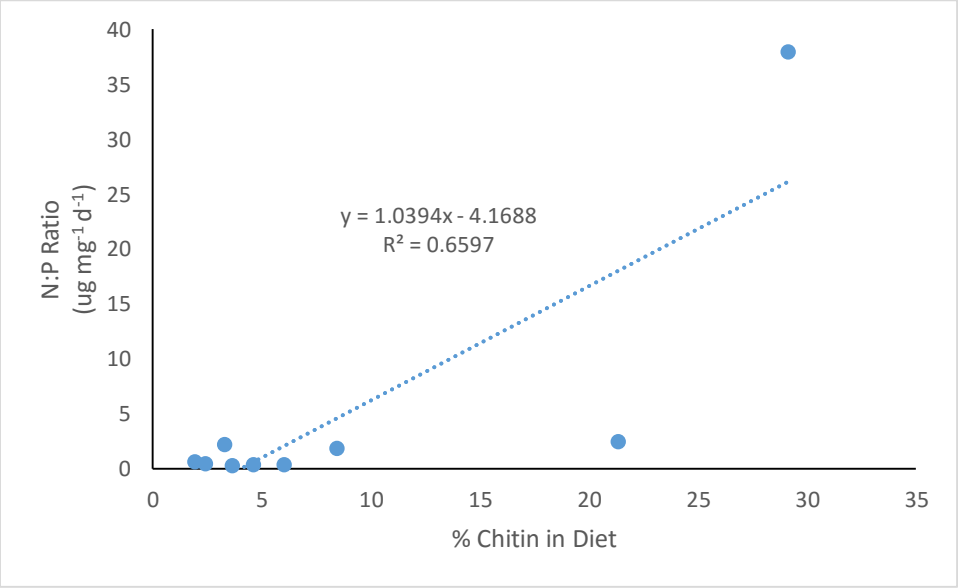

Figure 14: Regression of percent chitin in several species' diets against their N:P excretion ratios, expressed in ug mg^{-1} d^{-1}. Dietary data are for *H. occidentalis, A. deflata, L. picturatus, G. lorretae, L. secludens, L. tarsalis, A. nigriculus*, and *L. externus*. ($p=0.01$, $R^2=0.65$).

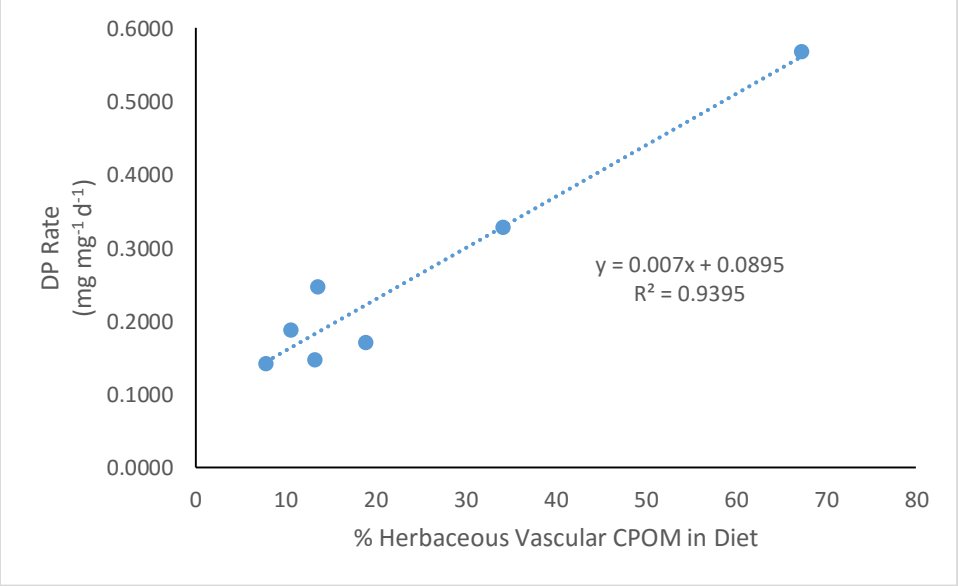

Figure 15: Regression percent of herbaceous vascular CPOM in several species' diets against their detritus processing rates, expressed in ug mg^{-1} d^{-1}. Dietary data are for *L. picturatus, G. lorretae, L. secludens, L. tarsalis, A. nigriculus*, and *L. externus*. ($p<0.01$, $R^2=0.93$).

Model Analysis

Twelve invasions were tested, resulting in thirty-three unique models. These invasions were split into three groups: *Upslope Invasions* (Table 3), *Permanence Invasions* (Table 4), and *Combination of Upslope and Permanence Invasions* (Table 5). All models are presented in the appendices.

Table 3. Upslope invasions. Percent changes are calculated by subtracting each parameters' initial output from its final output. Each output is the aggregate of all modeled species' biomasses, in-pond durations, and rates (N, P, or DP).

					% Change				
	Pond Type	**Resident Species**	**Invading Species**	**Scenario**	**N Regeneration**	**P Regeneration**	**N:P**	**Detritus Processing**	**Appendix; Figure#**
1)	Subalpine Permanent	*L. externus*	*L. picturatus*	Competition-Extinction	795	189	210	-78	Appendix A; Fig. 1
				Partial Replacement	646	192	156	-9	Appendix B; Fig. 1
				Niche Split	895	289	156	22	Appendix C; Fig. 1
2)	Subalpine Permanent	*L. externus*	*G. lorretae*	Competition-Extinction	-46	-4	-44	-64	Appendix A; Fig. 2
				Partial Replacement	16	47	-21	2	Appendix B; Fig. 2
				Niche Split	54	96	-21	36	Appendix C; Fig. 2
3)	Subalpine Semi-Permanent	*A. nigriculus*	*L. picturatus*	Competition-Extinction	1518	166	509	16	Appendix A; Fig. 3
				Partial Replacement	1189	174	370	62	Appendix B; Fig. 3
				Niche Split	1618	266	370	116	Appendix C; Fig. 3
4)	Subalpine Semi-Permanent	*A. nigriculus*	*L. secludens*	Competition-Extinction	348	-46	726	28	Appendix A; Fig. 4
				Partial Replacement	311	16	255	71	Appendix B; Fig. 4
				Niche Split	448	54	255	128	Appendix C; Fig. 4
5)	Subalpine Temporary	*A. nigriculus*	*L. tarsalis*	Competition-Extinction	291	281	2	-3	Appendix A; Fig. 5
				Partial Replacement	268	261	2	48	Appendix B; Fig. 5
				Niche Split	391	381	2	97	Appendix C; Fig. 5
6)	Montane Permanent	*L. externus* *L. picturatus*	*L. sublunatus*	Competition-Extinction	-76	-18	-70	-31	Appendix A; Fig. 6
				Partial Replacement	-7	36	-32	27	Appendix B; Fig. 6
				Niche Split	24	82	-32	69	Appendix C; Fig. 6
7)	Montane Permanent	*L. externus* *G. lorretae*	*L. sublunatus*	Competition-Extinction	57	63	-3	-38	Appendix A; Fig. 7
				Partial Replacement	93	97	-2	21	Appendix B; Fig. 7
				Niche Split	157	163	-2	62	Appendix C; Fig. 7

Table 4. Permanence invasions. Percent changes are calculated by subtracting each parameters' initial output from its final output. Each output is the aggregate of all modeled species' biomasses, in-pond durations, and rates (N, P, or DP).

					% Change				
	Pond Type	**Resident Species**	**Invading Species**	**Scenario**	**N Regeneration**	**P Regeneration**	**N:P**	**Detritus Processing**	**Appendix Figure**
1)	Subalpine Semi-Permanent	*L. externus*	*A. nigriculus*	Competition-Extinction	-45	9	-49	-81	Appendix A; Fig. 8
				Partial Replacement	16	57	-26	-11	Appendix B; Fig. 8
				Niche Split	55	109	-26	19	Appendix C; Fig. 8
2)	Montane Semi-Permanent	*L. secludens*	*L. tarsalis*	Competition-Extinction	-13	604	-88	-24	Appendix A; Fig. 9
				Partial Replacement	40	503	-77	32	Appendix B; Fig. 9
				Niche Split	87	704	-77	76	Appendix C; Fig. 9
3)	Montane Semi-Permanent	*L. externus*	*L. picturatus*	Competition-Extinction	795	189	210	-78	Appendix A; Fig. 1
				Partial Replacement	646	192	156	-9	Appendix B; Fig. 1
				Niche Split	895	289	156	22	Appendix C; Fig. 1

Table 5. Combination of permanence and upslope invasions. Percent changes are calculated by subtracting each parameters' initial output from its final output. Each output is the aggregate of all modeled species' biomasses, in-pond durations, and rates (N, P, or DP).

					% Change				
	Pond Type	**Resident Species**	**Invading Species**	**Scenario**	**N Regeneration**	**P Regeneration**	**N:P**	**Detritus Processing**	**Appendix Figure**
1)	Subalpine Semi-Permanent	*L. externus*	*A. nigriculus* *G. lorretae*	Competition-Extinction	-45	2	-47	-73	Appendix A; Fig. 10
				Partial Replacement	5	52	-31	-23	Appendix B; Fig. 10
				Niche Split	109	205	-31	54	Appendix C; Fig. 10
2)	Montane Semi-Permanent	*L. externus*	*L. picturatus* *L. sublunatus*	Competition-Extinction	408	124	127	-68	Appendix A; Fig. 11
				Partial Replacement	458	174	104	-18	Appendix B; Fig. 11
				Niche Split	1016	448	104	64	Appendix C; Fig. 11

DISCUSSION

Climate change prompts many taxa to adjust their distributions, and thus influences the trophic and resource dynamics of ecosystems as well as their functions (Chapin et al. 1997). These types of shifts are occurring globally across all ecosystems (e.g. Davis & Shaw 2001; Parmesan & Yohe 2003; Thuiller 2004; Hickling et al. 2006). In my study region, these shifts were observed by Scott Wissinger (unpublished data; Table 1) in 1998 when *L. picturatus* first invaded subalpine semi-permanent and permanent basins. In 2000, *L. sublunatus* appeared in montane permanent basins for the first time. Most recently, *G. lorettae* invaded in subalpine semi-permanent and permanent basins in 2009. Given the functional role of these animals as biomass-dominant detritivores (Wissinger et al. 2003) and the literature linking species identity and ecosystem processes (e.g. Chapin et al. 1997; Vanni et al. 2002; Taylor et al. 2006; Estes et al. 2011), I wanted to quantify the ecosystem-level functional impacts of these invasions.

A previous study concluded that two species in this guild (*L. externus* and *A. nigriculus*) process detritus and recycle nutrients at different rates (Vlah 2013). One interpretation of this finding was that there is little dietary overlap between the two species. Still, the extended duration of larval development in *L. externus* (about 2 weeks longer than other species) restricts it to permanent and semi-permanent ponds, so it is being replaced by *A. nigriculus* as those habitats are becoming increasingly temporary due to climate change. Vlah (2013) suggests that the climate-induced shift in pond-permanence and the subsequent replacement of *L. externus* by *A. nigriculus* could result in reduced detritus processing and nutrient regeneration at the ecosystem level, which translates to a change in overall ecosystem function.

However, upslope migration and shifts in pond permanence could initiate many other species replacements within this guild. Because Vlah (2013) attributed different algal chlorophyll-a levels across *L. externus* and *A. nigriculus* treatments to species-specific nutrient excretion rates, I quantified the body mass-specific N and P regeneration rates of nine species, along with their detritus processing capacity (from Klemmer et al. 2012; Krejsa 2011; Burns 2012; Vlah 2013; Washko unpublished data; Wissinger et al. ms). Using these data, I parameterized models that estimate the functional impact of new species combinations and replacements in these montane and subalpine ecosystems.

Species-specific excretion rates

There were clear differences in the N and P excretion rates among species (Figure 8 A&B), but not between replicates (time of day) or populations (different elevations) of each species (Table 2). Previous studies demonstrated that invertebrate communities can supply a significant proportion of an aquatic ecosystem's nutrient demand via excretion (e.g. Grimm 1988; Hall et al. 2003; Taylor et al. 2016). Vanni (2002) argues that of all the direct (excretion, ingestion, egestion, production) and indirect (competition and physical modification of the environment) effects that animals can have on nutrient cycling, excretion is the most important because these inorganic forms of nutrients are readily assimilated by producers. This particular guild has been shown to strongly modulate detritus decay rates and ambient water-column N and P concentrations (e.g. Klemmer et al. 2012; Wissinger et al. ms), which has been theorized to subsequently fuel increased algal productivity (Vlah 2013). Because my data indicate that both excretion (Figure 8A&B) and detritus processing rates (Figure 10) vary by species,

community reassembly could change the rate at which a pond's nutrients are regenerated during a growing season, and consequently affect ecosystem productivity.

Ambient water temperature did not affect excretion rates in this study (Table 2). In my experiments, ambient water temperatures varied by less than 3 degrees within each taxon except for *G. lorretae*, which varied by less than 5 degrees. Temperature variation was small within each taxon because all experiments spanned the same six hour period from morning to early afternoon. This finding is similar to Taylor et al. (2016), where temperature ranges of less than 4 degrees had a very weak positive effect on the N excretion rate for only two of the 34 stream macroinvertebrate taxa studied. Still, temperature influences metabolism (Gillooly et al. 2001), which could in turn influence excretion (Sterner & Elser 2002). A previous study in another system found that detritus processing rates are positively correlated with temperature, which theoretically could expedite nutrient recycling (Mas-Martí et al. 2015). However, I intentionally minimized the effect of temperature by running all of my experiments in the morning-early afternoon.

Across experiments for all taxa, ambient water temperatures did vary by almost 18 degrees, but this range does not explain the taxonomic variation in excretion of N ($p=0.53$) or P ($p=0.63$). The large variation in temperature across all experiments can be attributed to differences in elevation and sampling season (i.e., early June vs late July). Within a given species, thermal adjustment could explain consistent excretion rates among populations along an elevational gradient. A recent study (Stoks et al. 2014) found that such thermal adjustment could be explained by either genetic changes or phenotypic plasticity, or both. Still, transplanting individuals across elevational (therefore thermal) gradients has never been

attempted with this guild of caddisflies, so the degree to which thermal adjustments affect the ecosystem-level consequences of range shifts is unclear. An understanding of the degree to which such thermal adjustments are present among caddisfly populations at different elevations will be important when selecting source populations for future experimental studies.

Why might N:P excretion stoichiometry differ across species?

Some species recycle one nutrient quickly and another slowly (e.g. *A. deflata* has an extremely high N:P excretion ratio of 38, while *L. tarsalis* has a low N:P excretion ratio of 0.3; Figure 9). Whereas, *L. picturatus* recycles a large quantity of both nutrients (Figure 8A&B). Extricating the trait-level influences on these functional traits was not the express purpose of this study, but data collected through previous experiments (e.g. Wissinger unpublished data) and basic stoichiometric theory from the literature has allowed me to begin linking species-specific functional differences back to individual traits.

Differences in diet have been suggested as a possible explanation for the difference in *C. aquatilis* decomposition rates between experiments with *L. externus* (Klemmer et al. 2012) and *A. nigriculus* (Vlah 2013). While mass-specific DP rates did not explain mass-specific excretion rates for N ($p=0.46$) or P ($p=0.32$), my analysis indicated that certain dietary components might begin to explain nutrient excretion. Excretion of phosphorus could increase with the amount of algae consumed (Figure 12) if excess P is mineralized from the algae. I do not have N:P data for the algae from the study region, but Halvorson et al. (2016) suggest that biofilm grazing caddisflies consume microbes to acquire mineral P because detrital substrates tend to have very low P content (Bärlocher 1985; e.g. *Carex* N:P = 19 from Klemmer 2012). Likewise, N:P excretion ratios could be inversely related to the amount of detritus consumed (Figure 13), if

detritus is consumed because of a metabolic demand for its high N content. The N:P excretion ratios could also be positively related to the amount of chitin consumed (Figure 14), because taxa that consume more animal protein are consuming less detritus, which might suggest that their metabolic demands are not being met by the N-rich detritus. Halvorson et al. (2015) found that when caddisflies consume P-rich detritus, they excrete more P, which they argue is a function of consuming excess P. Here, animal protein (chitin) consumed could cause the same trend. Finally, it follows that DP rate increases with the amount of herbaceous vascular CPOM consumed (Figure 15) because those species that process the most detritus might be doing so simply because they prefer to eat it over algae.

Body size can exert a strong control on metabolism, which is closely related to excretion (Kleiber 1947). Because smaller animals have faster metabolisms, smaller species should generally have higher mass-specific excretion rates (Sterner and Elser 2002; Hall et al. 2007). However, when the 5th instar body masses of these animals are regressed against excretion rates, there was no relationship for N ($p=0.67$), while P ($p=0.07$) borders statistical significance.

Still, given these ambiguous dietary speculations, comparing the body stoichiometry of different species would be a fruitful line of future research for this system. Larval tissue C:N:P ratios could help explain why species with similar diets incorporate and excrete different quantities of nutrients (Sterner and Elser 2002). Differences in body elemental composition can predict differences in nutrient requirements (Frost et al. 2006). Bärlocher and Porter (1986) found that functional differences in feeding strategies and digestion among aquatic detritivores result in the differential incorporation of nutrients from detrital-microbial substrates. However, the species-level digestive function, metabolic demands, and body elemental composition of

this guild have not been studied. Broadly, Sterner and Elser (2002) warn that species-specific excretion rates are likely controlled by aggregates of taxon-unique traits and ecosystem-unique factors.

Modeling implications of species specific excretion using microcosm data

All of the model scenarios summarized in Tables 3-5 are included in the appendices. The following three scenarios demonstrate several emergent points.

The first scenario characterizes both an upslope invasion in a subalpine permanent pond (Table 3 Scenario #1) and a permanence invasion in a montane semi-permanent pond (Table 4 Scenario #3) where *L. picturatus* replaces *L. externus* (Appendices A, B, and C Figure 1). The upslope invasion was first observed in 1998 (Table 1). Long-term yearly pond censuses have historically characterized *L. externus* as the biomass-dominant detritivore in both of these habitats (e.g. Wissinger et al. 2003; unpublished data). These animals are comparable in body size at their final instar, but differ in their phenology – *L. picturatus* has a much faster lifecycle, pupating almost two weeks earlier (Wissinger et al. 2003). This gives *L. picturatus* a slight advantage in more ephemeral habitats, potentially allowing it to invade due to shifts in pond permanence. Given that *L. picturatus* excretes nearly seven times more N and four times more P (Figure 8A&B) despite processing one third of the detritus (Figure 10), the competition-extinction model predicts massive increases in the amount of N (+794%, Appendix A Figure 1A) and P (+189%, Appendix A Figure 1B) regenerated in a given summer along with a considerable decrease in the amount of detritus processed (-78%, Appendix A Figure 1C). Since *L. externus* primarily consumes CPOM while *L. picturatus* primarily consumes FPOM (Figure 11), local extinctions of *L. externus* are unlikely without considerable permanence shifts, and therefore

the partial replacement model is most appropriate for this scenario. Here, we still see massive increases in the amount of N (+646%, Appendix B Figure 1A) and P (+191%, Appendix B Figure 1B) regenerated due to the addition of *L. picturatus*, while the amount of detritus processed only drops slightly (-8%, Appendix B Figure 1C) due to the decreased abundance of *L. externus.*

These models exemplify how *L. picturatus* is extremely influential in nutrient recycling while *L. externus* plays a major role in detritus processing. Typically, biodiversity and ecosystem function are assumed to be positively correlated, but in some instances the loss of a dominant species can actually trigger a decline in ecosystem function (Creed et al. 2009). Here, the competition-extinction model demonstrates how the loss of the dominant *L. externus* could cause a massive decrease in detritus processing. However, the partial replacement model implies that the combination of *L. externus* and *L. picturatus* is efficient in terms of differing patterns of resource use and contributions to ecosystem function. This resonates with the idea that shifts in community composition can differentially affect the overall rates of various ecosystem processes, whereas certain combinations of species can be very beneficial to overall ecosystem function (Hooper et al. 2005).

The second scenario is an upslope invasion in a subalpine temporary pond where *L. tarsalis* invades *A. nigriculus* (Table 3 Scenario #5; Appendices A, B, &C Figure 5). Long-term yearly pond censuses have never documented *L. tarsalis* above the upper montane (Table 1). In montane temporary ponds, *L. tarsalis* is the one of the dominant species while *A. nigriculus* is present but in very low numbers. This modest coexistence could be because *A. nigriculus* is simply more adapted to subalpine habitats (Wissinger et al. 2003). The two species have some dietary overlap, though *A. nigriculus* favors vascular detritus while *L. tarsalis* consumes more

amorphous detritus (Figure 11). While the two ultimately have similar N:P excretion ratios, *L. tarsalis* excretes almost four times more P, the most of any species (Figure 8A), and over four times the amount of N (Figure 8B). This means that nitrogen and phosphorus regeneration more than double in all of the models for this scenario (Appendices A, B, &C Figures 5A&B). Meanwhile, the two species process nearly the same amount of detritus (Figure 10), so DP only drops slightly in competition-extinction (-3%, Appendix A Figure 5C) and rises by nearly half in partial replacement (+48%, Appendix B Figure 5C) and almost doubles in niche-splitting (+98%, Appendix C Figure 5C). Because the reason for *L. tarsalis*'s domination at montane elevations is unclear, it is impossible to speculate which of these three model outcomes is most likely after a subalpine invasion.

This scenario may best demonstrate that diversity could indeed build functional redundancy (Hooper et al. 2005, Primack et al. 2014). However, some of the models make the opposite prediction, as whenever *L. externus* is lost in a competition-extinction scenario, DP rates plummet (Table 3 Scenarios 1, 2, and 6; Table 4 Scenarios 1 and 3; Table 5 Scenarios 1 and 2). This reinforces the assertion that species-specific contributions to a particular ecosystem process and the degree of functional redundancy are absolutely paramount when considering the impact of species loss (e.g., Tilman et al. 1997; Hall et al. 2003; Creed et al. 2009) and community rearrangements.

The third is a combination of upslope and permanence invasions in a subalpine semi-permanent pond where *A. nigriculus* and *G. lorettae* both invade *L. externus* (Table 5 Scenario #1, Appendices A, B, &C Figure 10). Long term censuses indicate that the upslope component of this invasion may already be beginning, as *G. lorettae* appeared at the subalpine sites in 2009

(Table 1; Wissinger unpublished data). Due to local advances in spring snowmelt (Barr 2015), ponds in the region are opening earlier, and thus have greater potential to dry during the summer (Balik & Wissinger unpublished data), which could eliminate predators and allow *A. nigriculus* to invade (Wissinger et al. 2003). Since both *A. nigriculus* and *G. lorretae* have shorter larval development (56 and 63 days respectively) than *L. externus* (77 days) and similar diets (Figure 11), a competition-extinction outcome is likely in this scenario. Interestingly, here the model predicts a drop to approximately half of the current N regeneration (-45%, Appendix A Figure 10A) and a slight increase in P regeneration (+2%, Appendix A Figure 10B) along with a substantial drop in overall detritus processing (-73%, Appendix A Figure 10C). This is because both *A. nigriculus* and *G. lorretae* excrete much less N and slightly more P than *L. externus* (Figure 8) while also processing roughly half as much detritus (Figure 10).

These models again demonstrate that different ecosystem processes could respond differentially (i.e. decrease, increase, or no change) to species replacements (Hooper et al. 2005). Moreover, this scenario exemplifies how climate change is an incredibly dynamic stressor on aquatic ecosystems (e.g. Woodward et al. 2010). Here, climate change creates the opportunity for invasion along multiple axes of niche space; the invasion of *A. nigriculus* represents a local compositional shift due to changes in hydrology, while the invasion of *G. lorretae* represents a range shift in biogeography associated with increased temperatures. However, climate change can theoretically interfere with this system in a multitude of other ways; for example, elevated atmospheric CO_2 is expected to alter the C:N:P ratios of detritus (Tuchman et al. 2002). Sterner and Elser (2002) suggest that this will force detritivores to either feed faster or shift to a different food resource to extract the same quantity of nutrients, but

either of these responses will in turn shift both biomass-specific excretion rates and detritus processing rates.

There are several important caveats for the predictive value of this kind of modeling. First and foremost, the long term census data indicates that other species rarely reach the in-pond biomass of *L. externus,* with the sole exception of *A. nigriculus* in a drying pond. It is unclear as to whether or not this is because of *L. externus*'s dominance or another factor (i.e. physiological constraints, dietary requirements). Although excretion rates were consistent across the six hour span of each experiment, variation is possible over the span of a full day. While individual taxon-specific traits (i.e. excretion rates, detritus processing rates, larval development duration, body mass) are used to parameterize the model, biomass is the largest value and therefore plays a considerable role in determining the models' projected changes. The differences among the outcomes of a given scenario's competition-extinction, partial replacement, and niche-splitting models demonstrate the extent to which the allocation of biomass determines the magnitude (and occasionally direction) of the predicted change.

Furthermore, these models assume that final instar individuals comprise the entirety of the ponds' biomass throughout the year. This could be a shortcoming of this modeling approach, as it is unclear whether or not predation, competition, or other causes of mortality could cause a population bottleneck strong enough to maintain the same in-pond biomass throughout the growing season despite the growth of individual organisms. Likewise, these models also assume that the excretion and detritus processing rates of each species are linear throughout the season. By ignoring the dietary requirements of each species, these models assume that the unique excretion and detritus processing rates will remain consistent after

species additions and replacements. However, the literature suggests that under different dietary conditions, and even under different microbial and temperature detritus conditioning regimes, excretion and egestion rates will shift (Halvorson et al. 2015, Mas-Martí et al. 2015). So, while these projections depict interesting consequences of species replacements and could theoretically translate from microcosms to the scale of a mesocosm or whole-pond, their actual utility is yet to be determined. Whether non-linear responses are similar (or not) among species might determine whether they complicate the model predictions.

CONCLUSIONS

In microcosms, different species of caddisflies generate different levels of ammonium-nitrogen and phosphate-phosphorus. Within each species, these excretion rates are constant throughout the day and along an elevational gradient. However, I cannot rule out the possibility that these rates change at night, nor can I definitively conclude that the interspecies variation in excretion rates can be attributed to differences in diet. Further stoichiometric analysis of caddisfly body tissue will be necessary to extricate the species-specific explanations for these different excretion rates. The results of this study reinforce Vlah's (2013) suggestion that species range shifts and replacements will *not* result in equivalent functional replacements in terms of species' bottom-up effects on fundamental ecosystem processes. This finding echoes the well-documented link between species identity and ecosystem processes (e.g. Chapin et al. 1997, Vanni et al. 2002, Taylor et al. 2006, Estes et al. 2011). The models generated from these data demonstrate that these replacements could cause significant changes in nutrient recycling, detritus processing, and primary production. However, my models make a wide range of predictions, from very small to very large changes, and the combinations of resident and

invading species are more important than any distinction between permanence versus upslope invasions. Therefore, I cannot speculate as to whether the impacts of shifts along permanence gradients are weaker or stronger than those of shifts along elevational gradients. That said, this modeling exercise demonstrates that species-specific rates and other taxon-unique traits collectively predict that species replacements in this guild will not always be functionally equivalent replacements.

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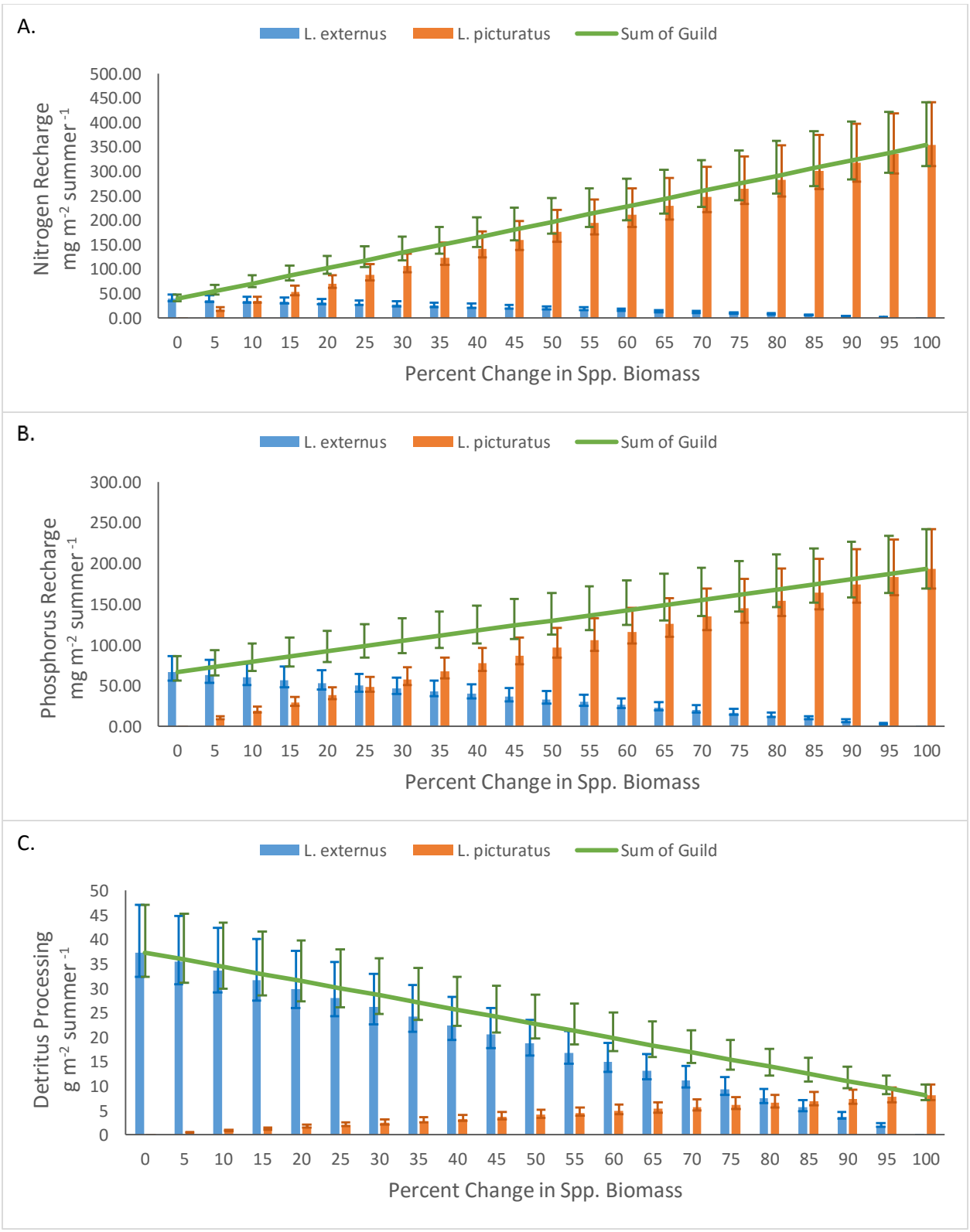
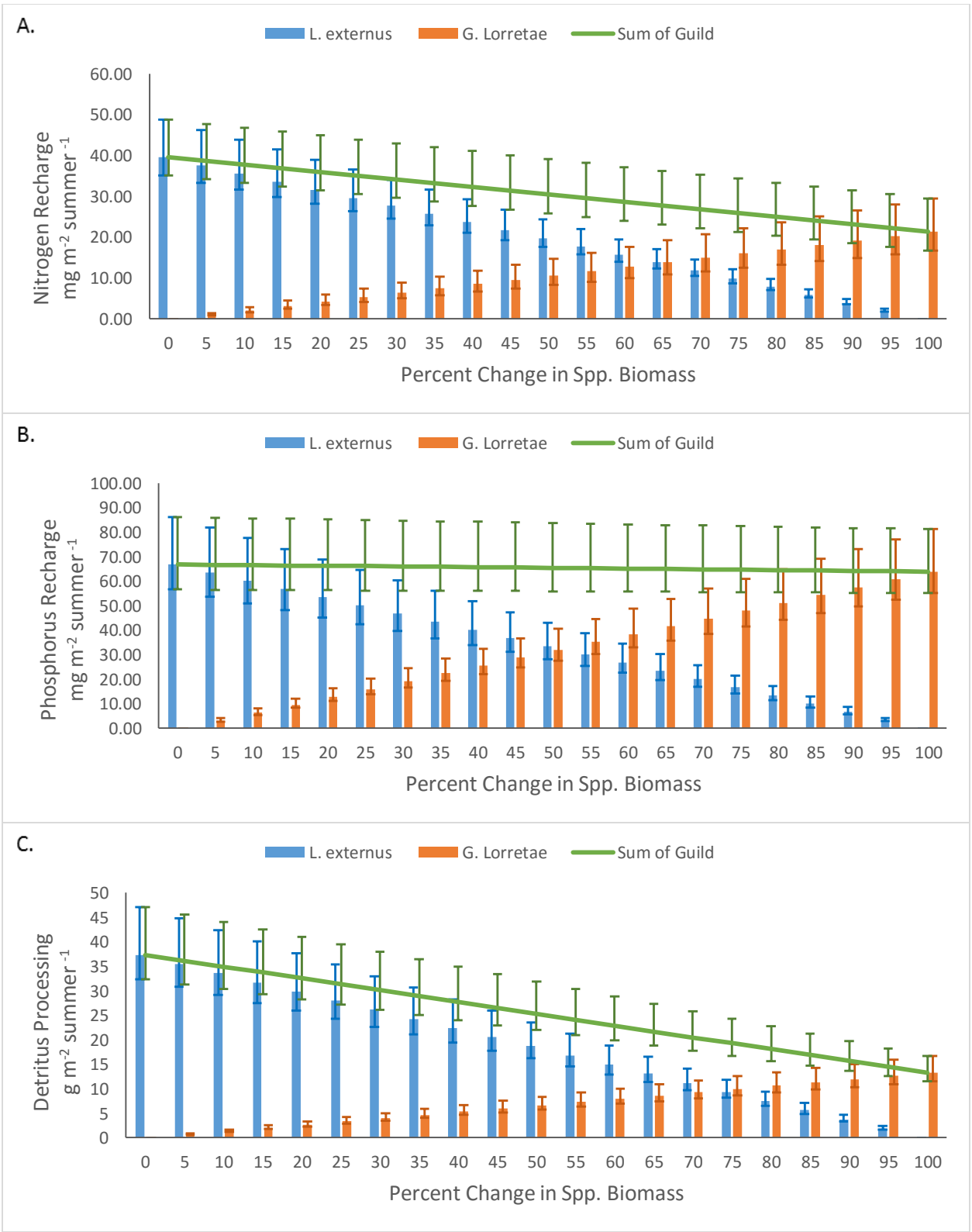
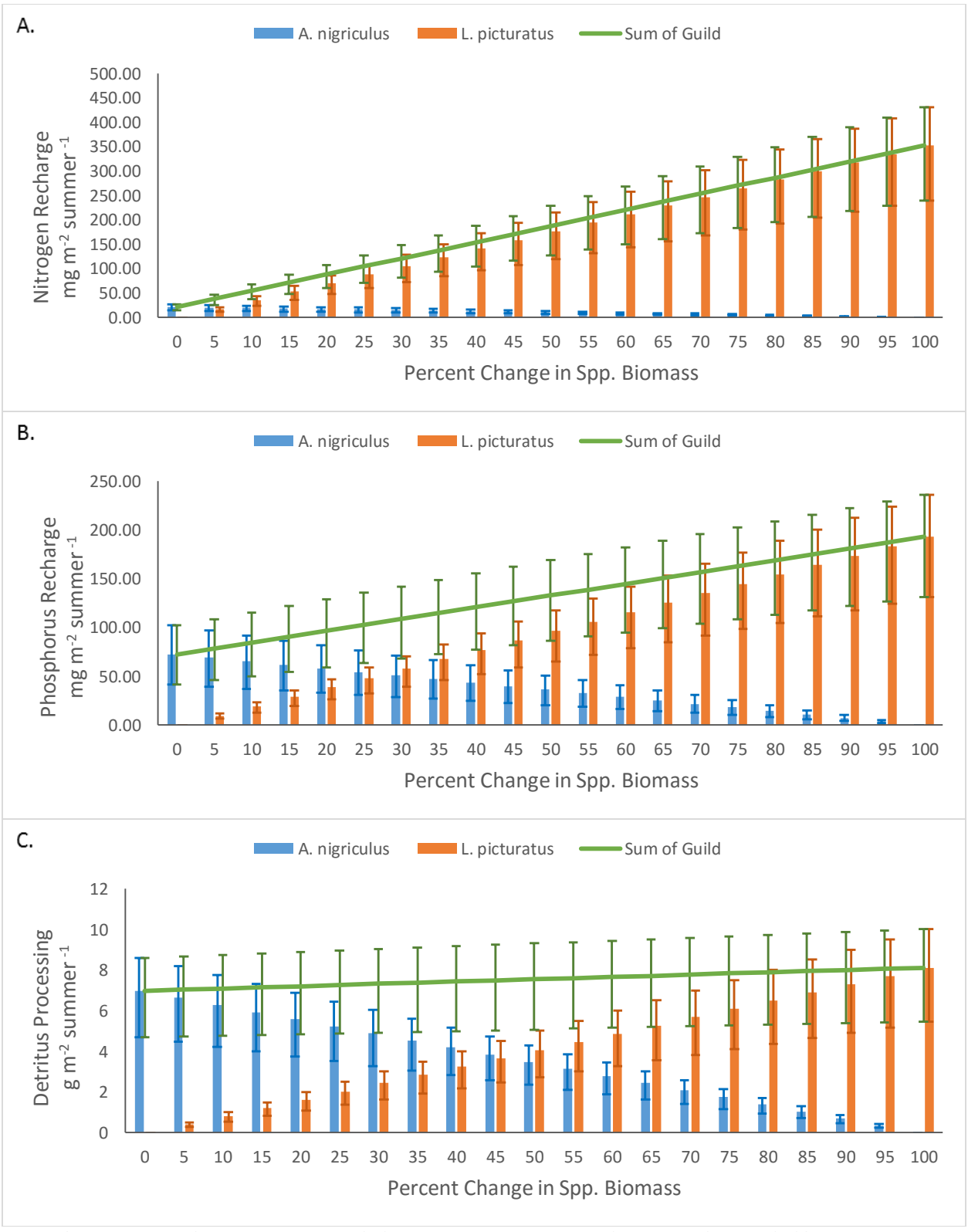


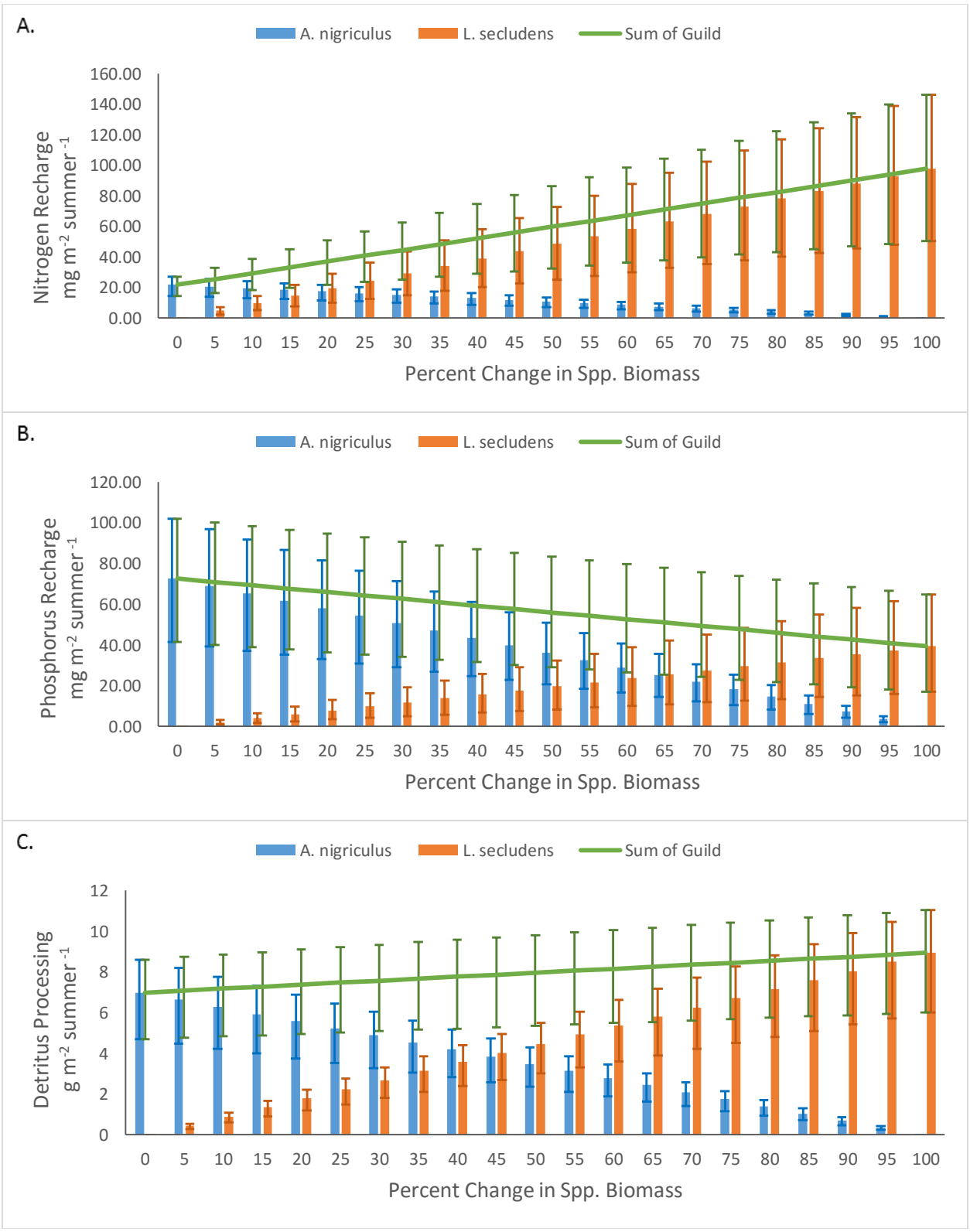
Appendix A Fig. 1: Upslope invasion in a subalpine permanent pond, or permanence invasion in a Montane Semi-Permanent Pond: *L. externus* replaced by *L. picturatus*. Competition-extinction outcome. Panel A shows nitrogen regeneration, panel B shows phosphorus regeneration, and panel C shows detritus processing.



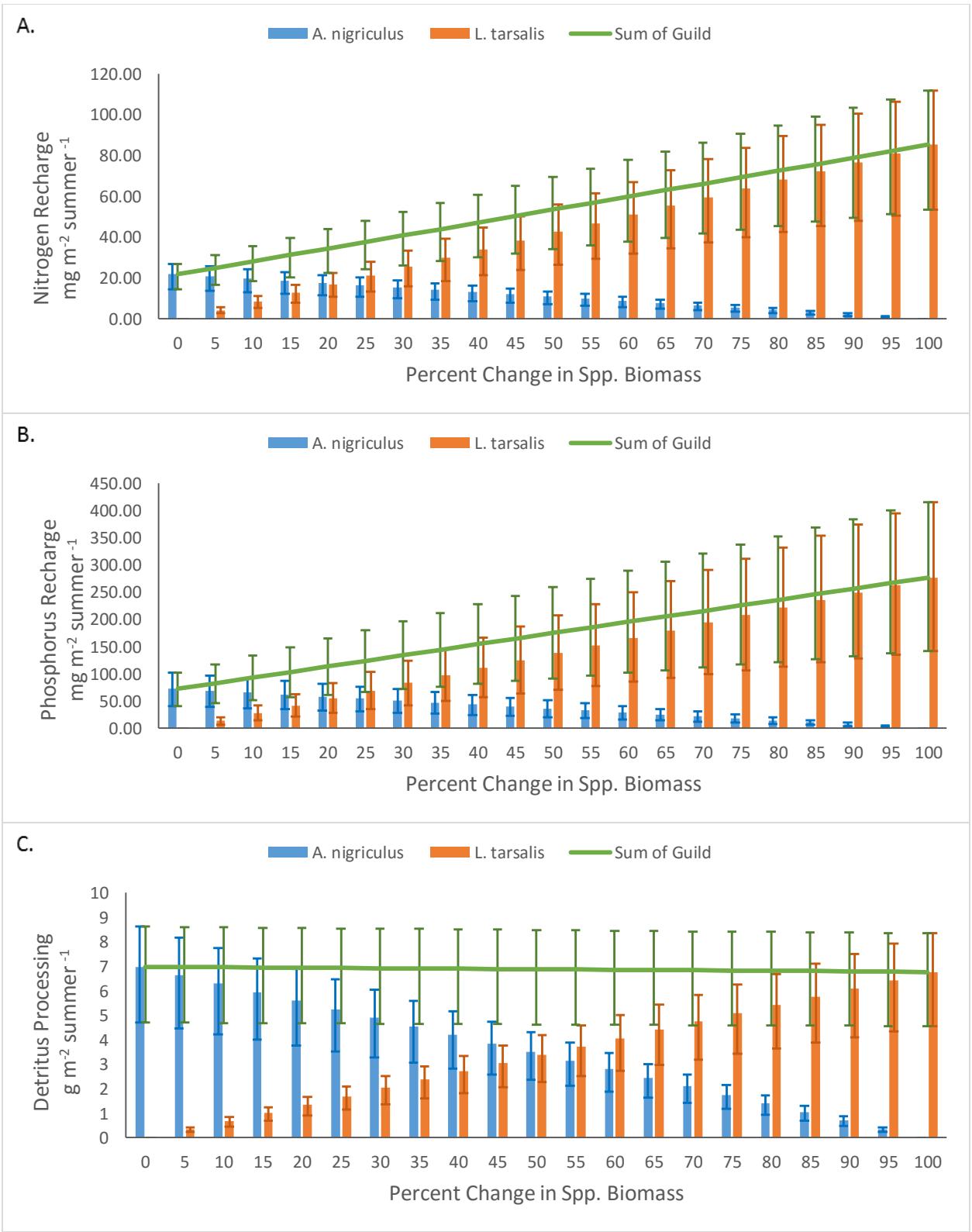
Appendix A Fig. 2: Upslope invasion in a subalpine permanent pond: *L. externus* invaded by *G. lorettae.* Competition-extinction outcome. Panel A shows nitrogen regeneration, panel B shows phosphorus regeneration, and panel C shows detritus processing.



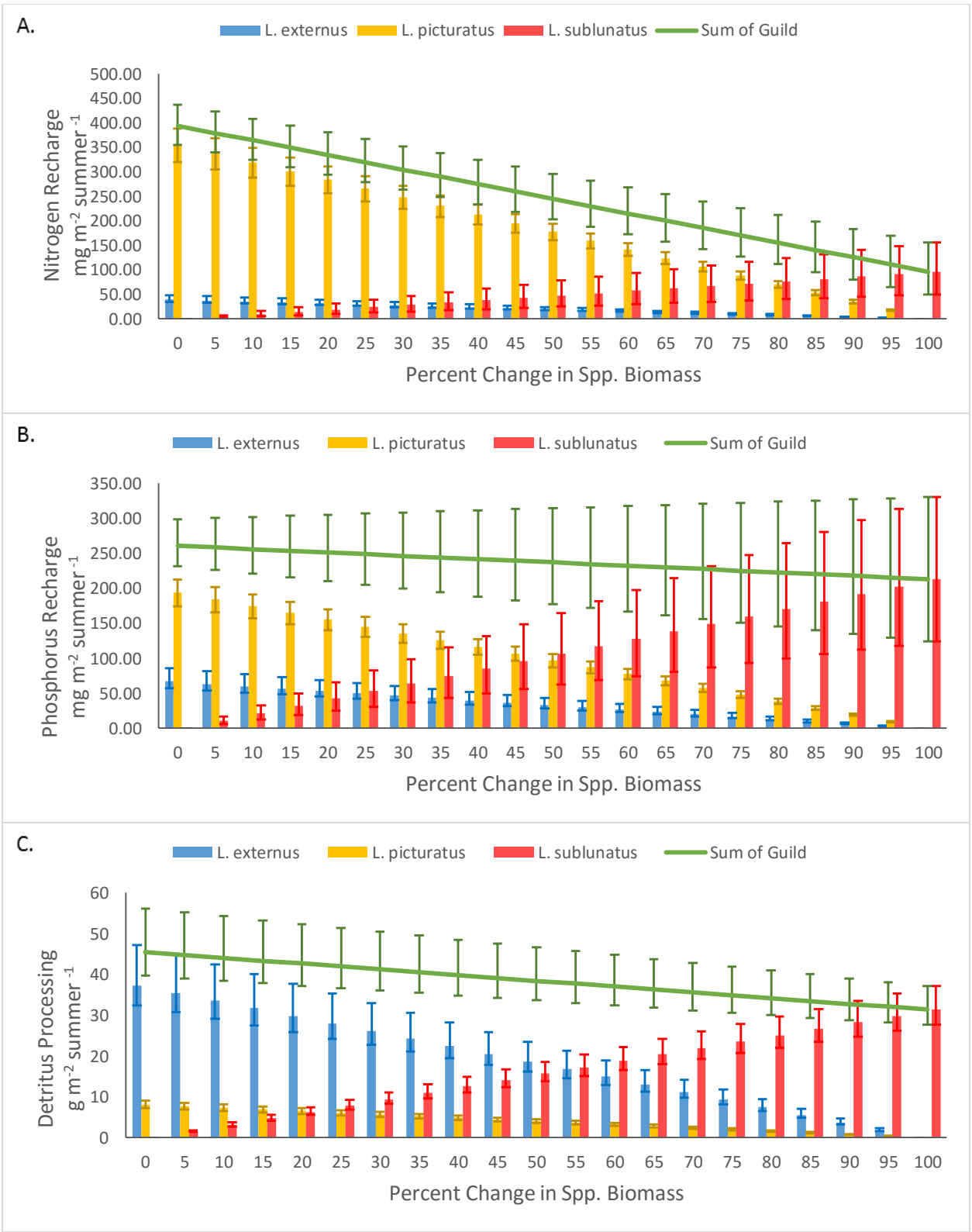
Appendix A Fig. 3: Upslope invasion in a subalpine semi-permanent pond: *A. nigriculus* invaded by *L. picturatus.* Competition-extinction outcome. Panel A shows nitrogen regeneration, panel B shows phosphorus regeneration, and panel C shows detritus processing.



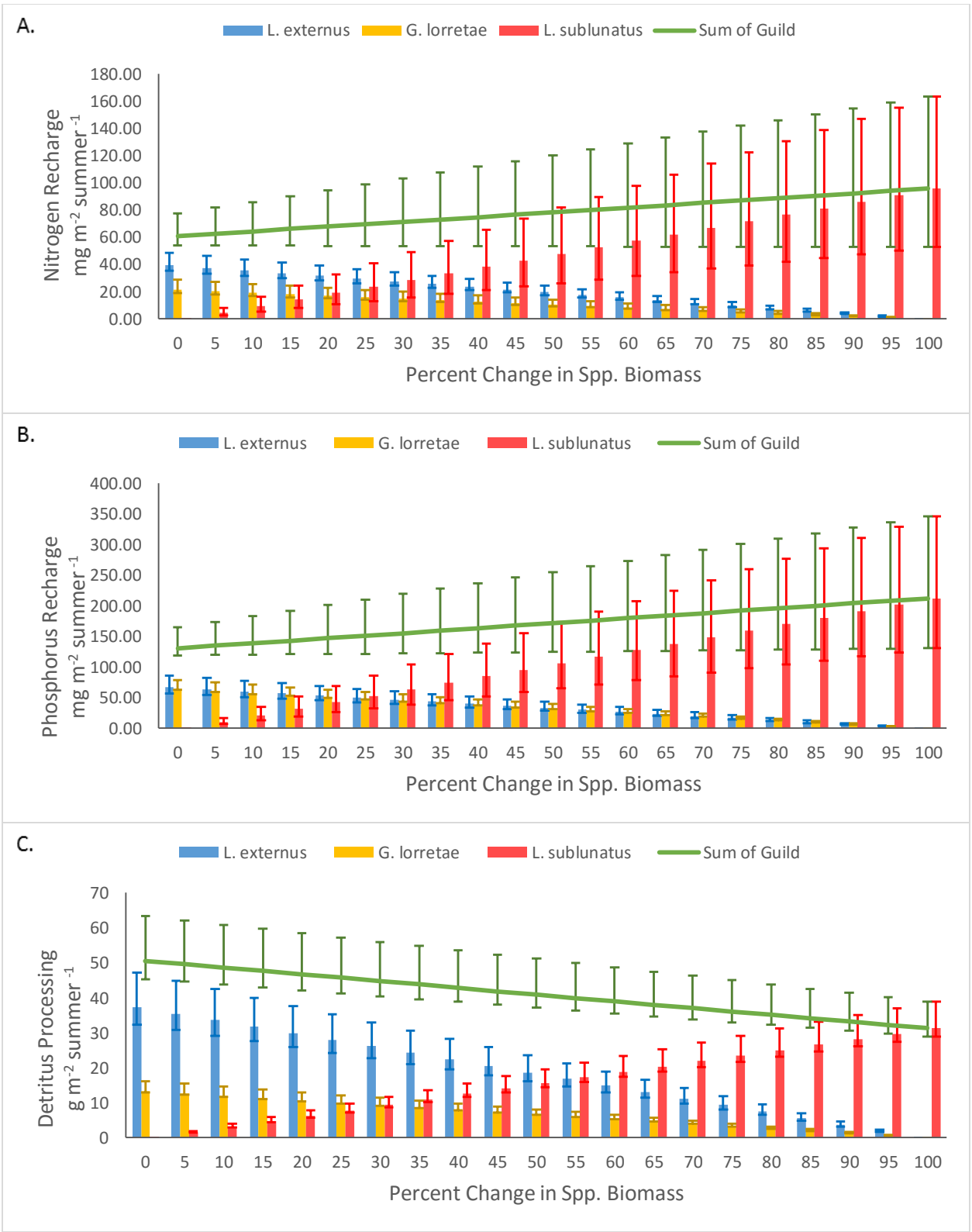
Appendix A Fig. 4: Upslope invasion in a subalpine semi-permanent pond: *A. nigriculus* invaded by *L. secludens.* Competition-extinction outcome. Panel A shows nitrogen regeneration, panel B shows phosphorus regeneration, and panel C shows detritus processing.



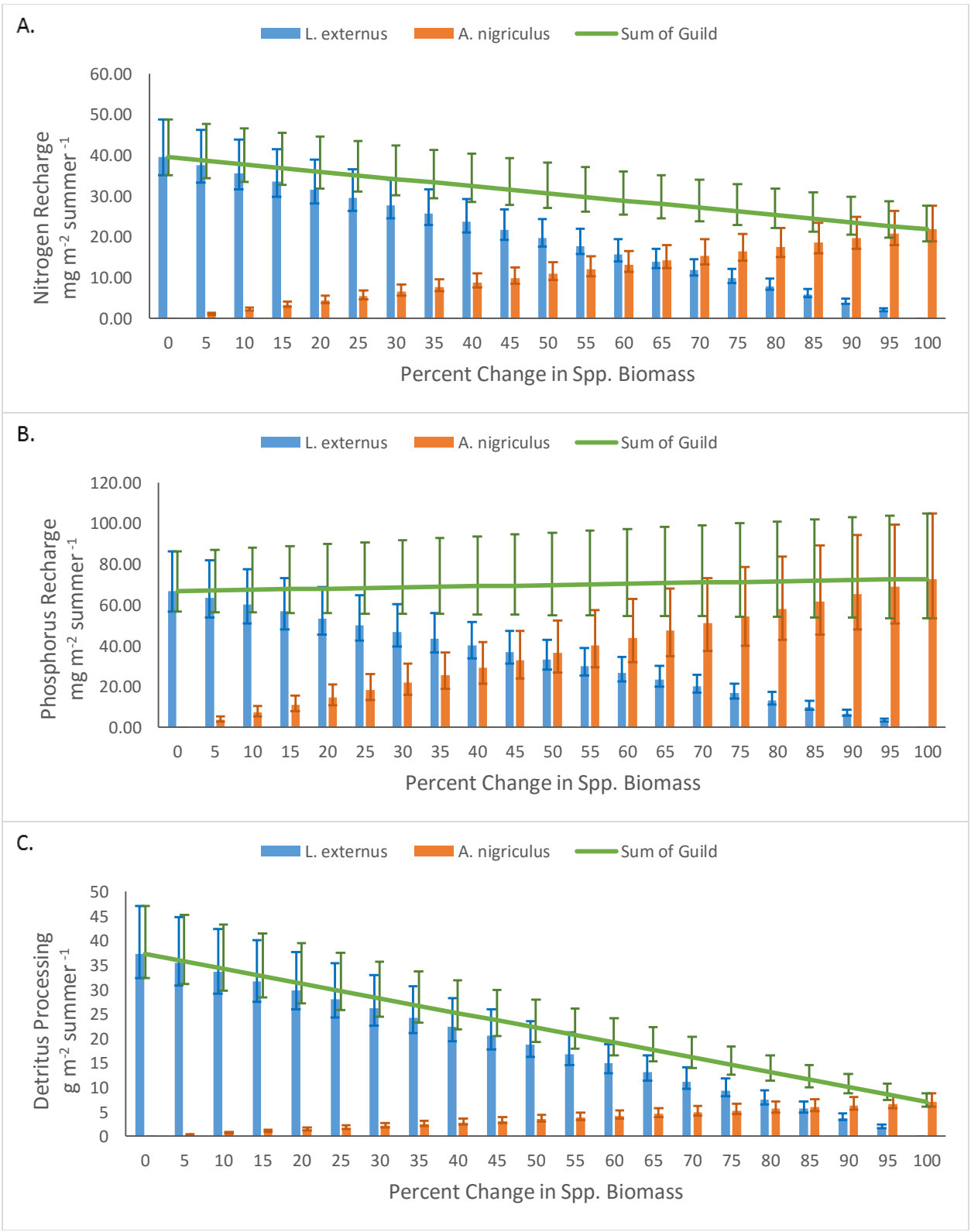
Appendix A Fig. 5: Upslope invasion in a subalpine temporary pond: *A. nigriculus* invaded by *L. tarsalis.* Competition-extinction outcome. Panel A shows nitrogen regeneration, panel B shows phosphorus regeneration, and panel C shows detritus processing.



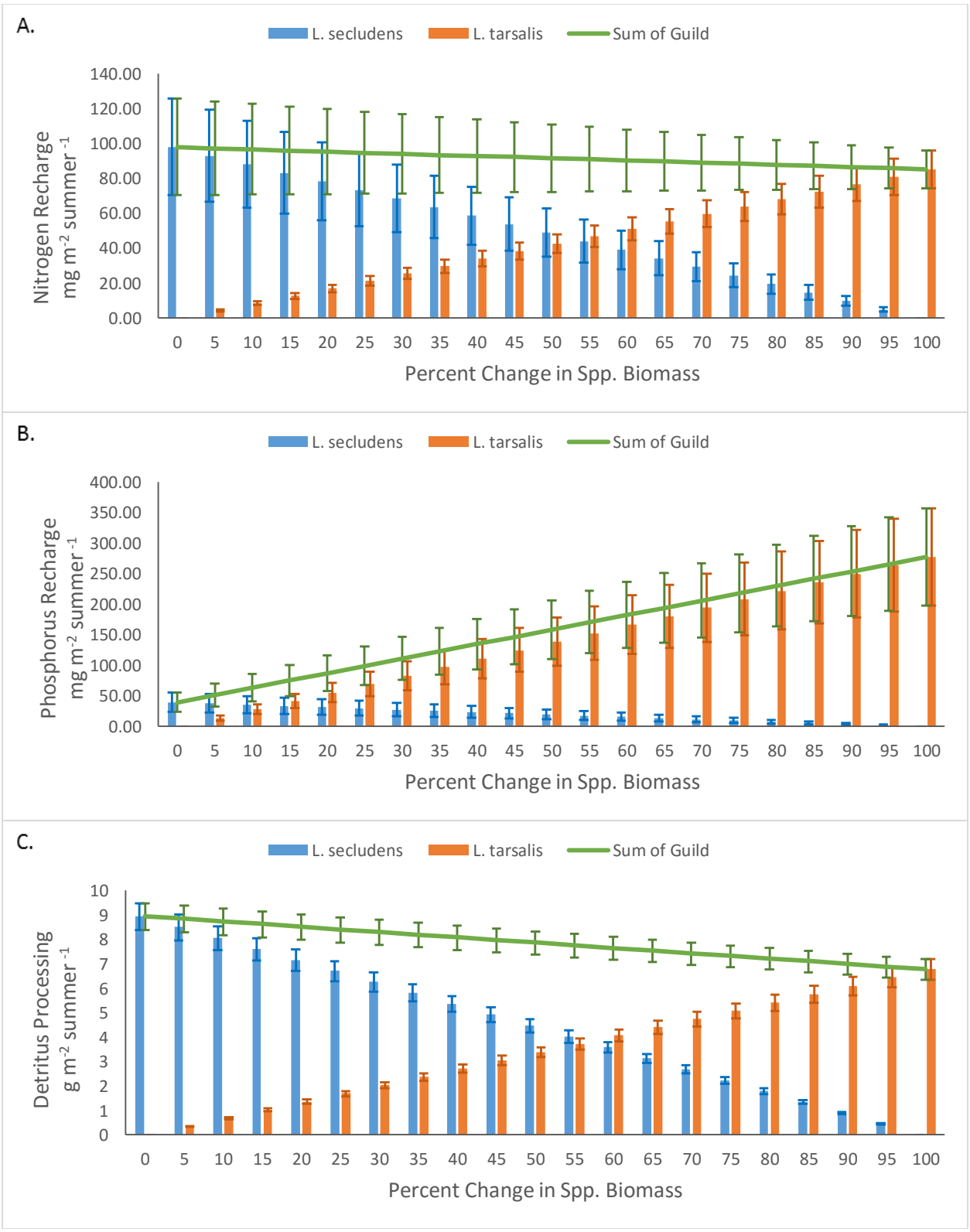
Appendix A Fig. 6: Upslope invasion in a montane permanent pond: *L. externus* and *L. picturatus* are invaded by *L. sublunatus.* Competition-Extinction outcome. Panel A shows nitrogen regeneration, panel B shows phosphorus regeneration, and panel C shows detritus processing.



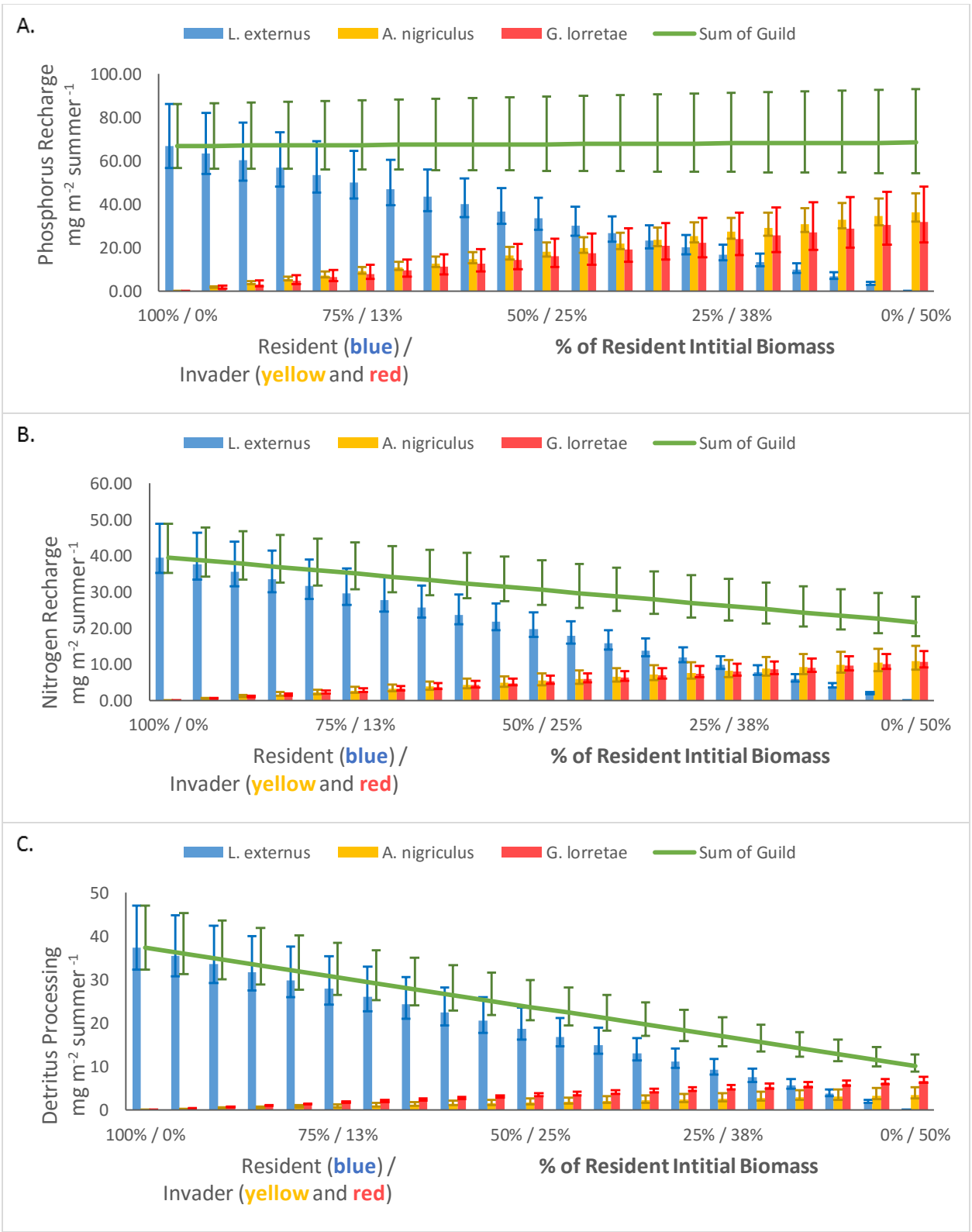
Appendix A Fig. 7: Upslope invasion in a montane permanent pond: *L. externus* and *G. lorretae* are invaded by *L. sublunatus.* Competition-extinction outcome. Panel A shows nitrogen regeneration, panel B shows phosphorus regeneration, and panel C shows detritus processing.



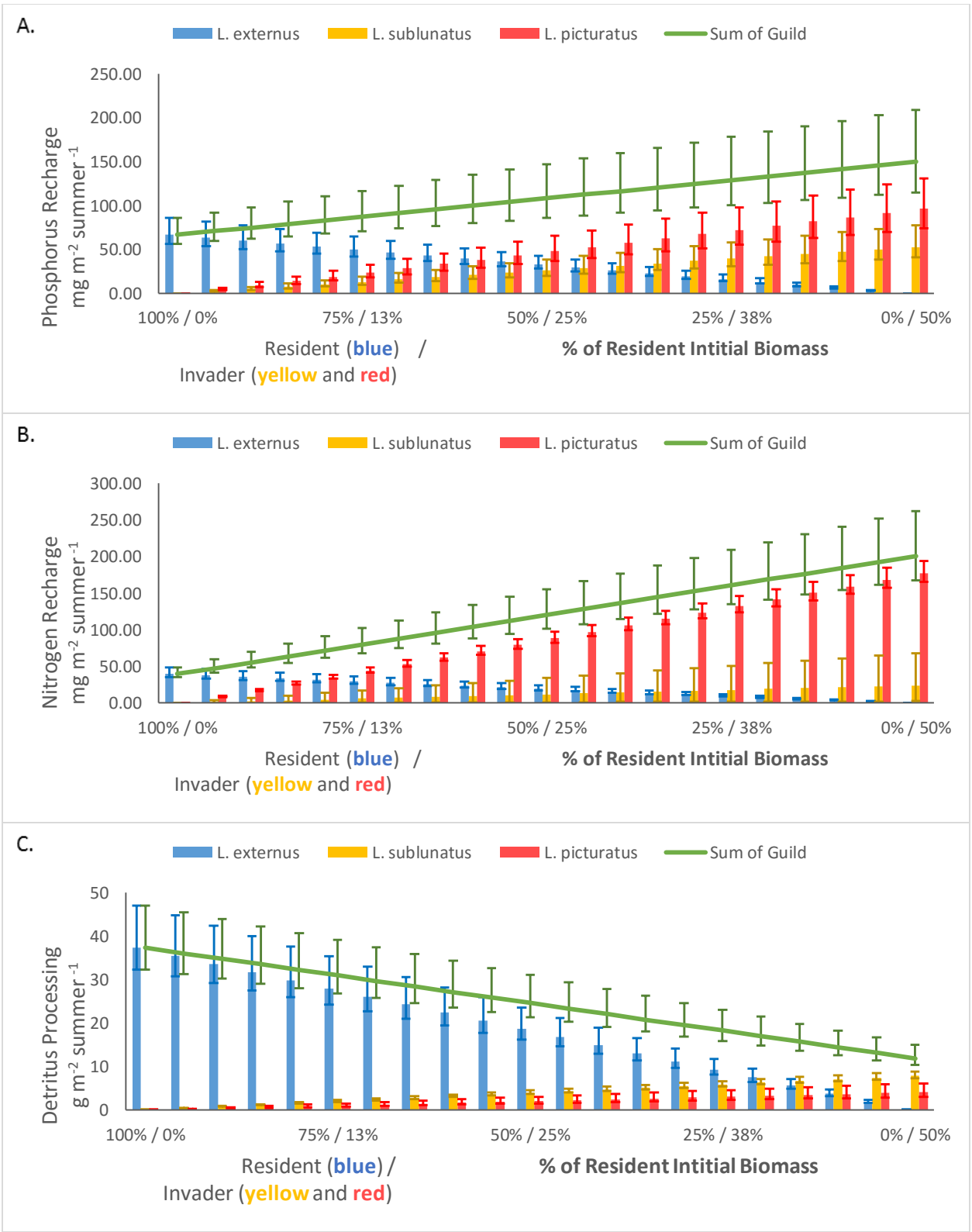
Appendix A Fig. 8: Upslope invasion in a montane permanent pond: *L. externus* is invaded by *A. nigriculus.* Competition-extinction outcome. Panel A shows nitrogen regeneration, panel B shows phosphorus regeneration, and panel C shows detritus processing.



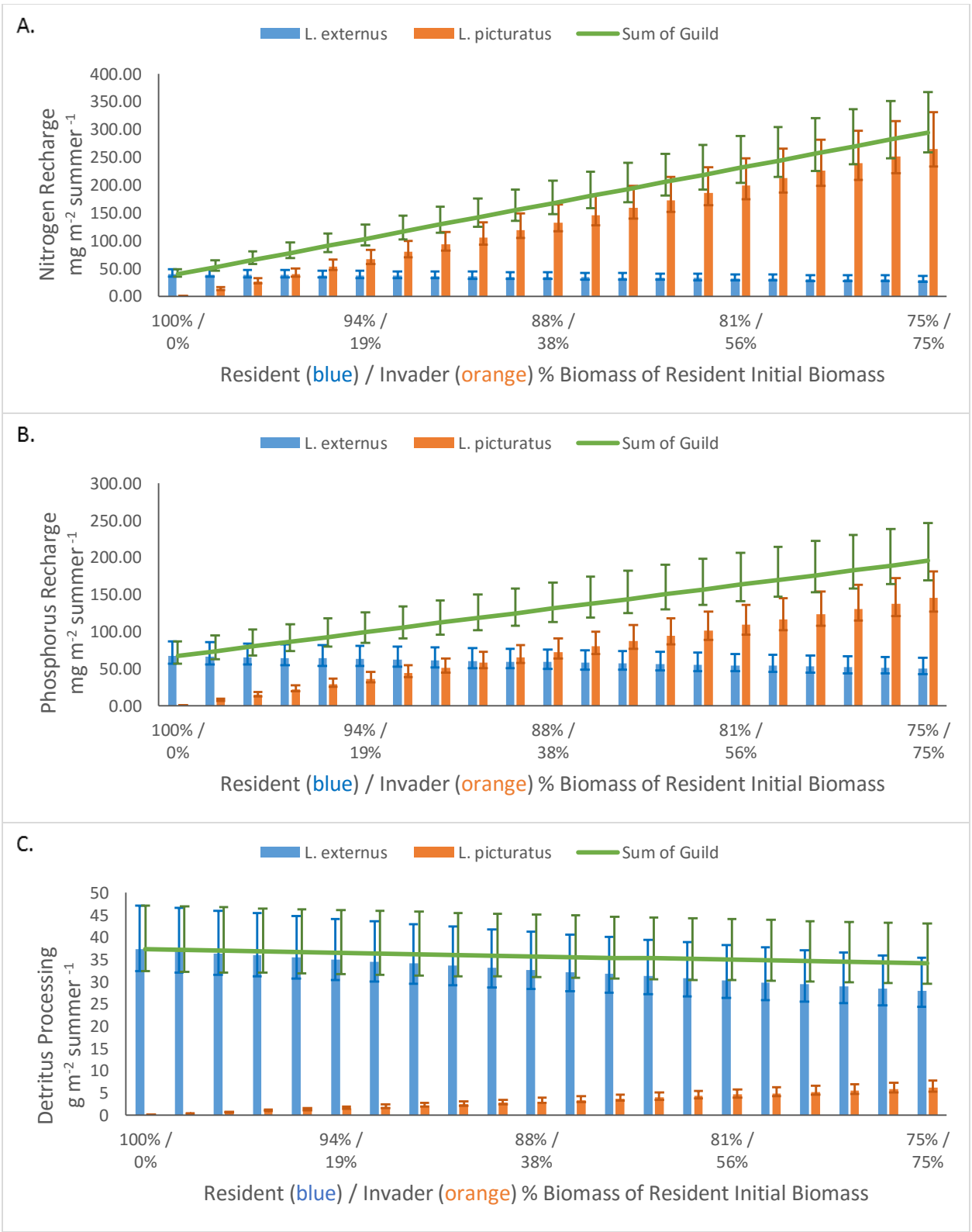
Appendix A Fig. 9: Upslope invasion in a montane permanent pond: *L. secludens* is invaded by *L. tarsalis.* Competition-extinction outcome. Panel A shows nitrogen regeneration, panel B shows phosphorus regeneration, and panel C shows detritus processing.



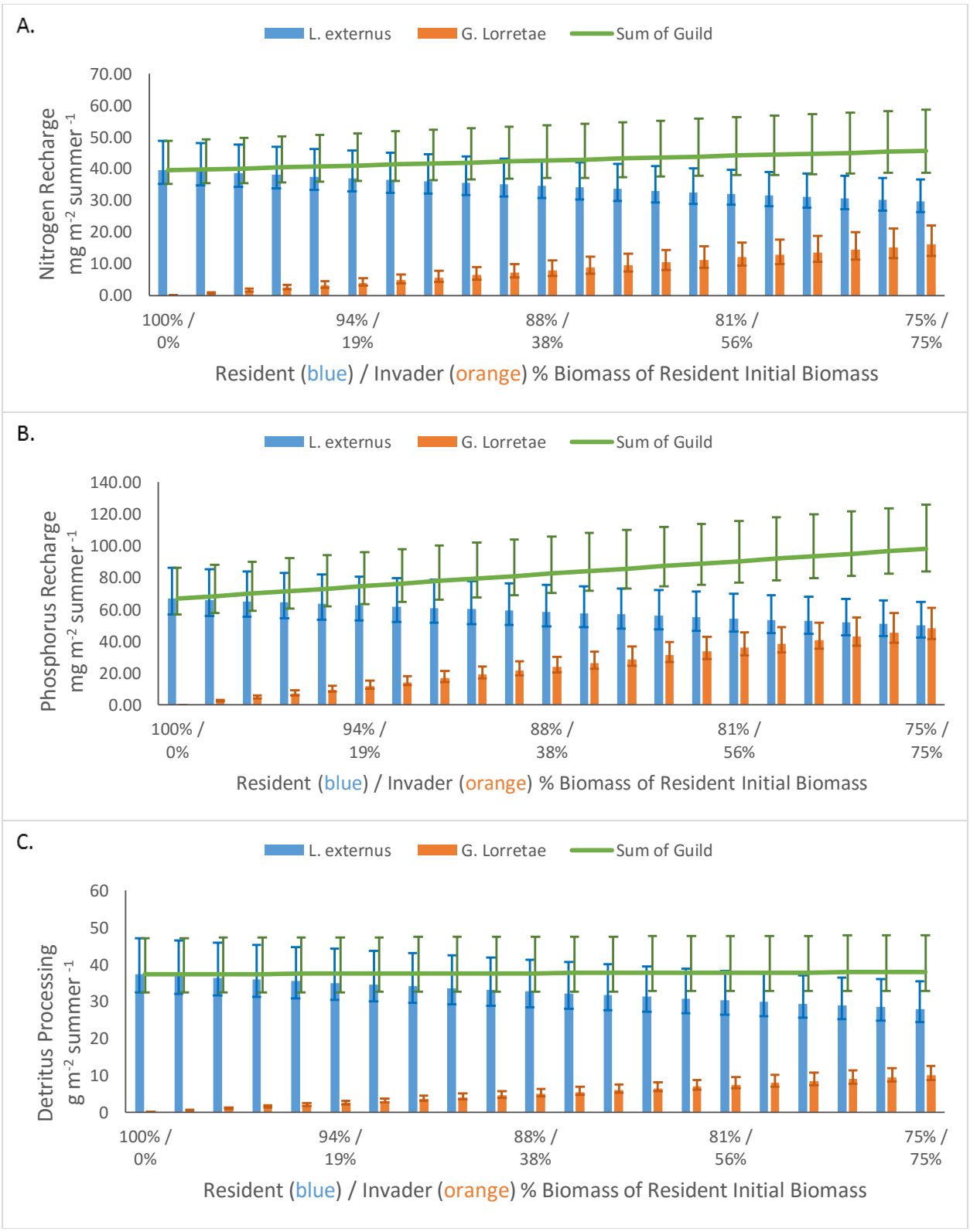
Appendix A Fig. 10: Upslope invasion in a montane permanent pond: *L. externus* is invaded by *A. nigriculus* and *G. lorretae.* Competition-extinction outcome. Panel A shows nitrogen regeneration, panel B shows phosphorus regeneration, and panel C shows detritus processing.



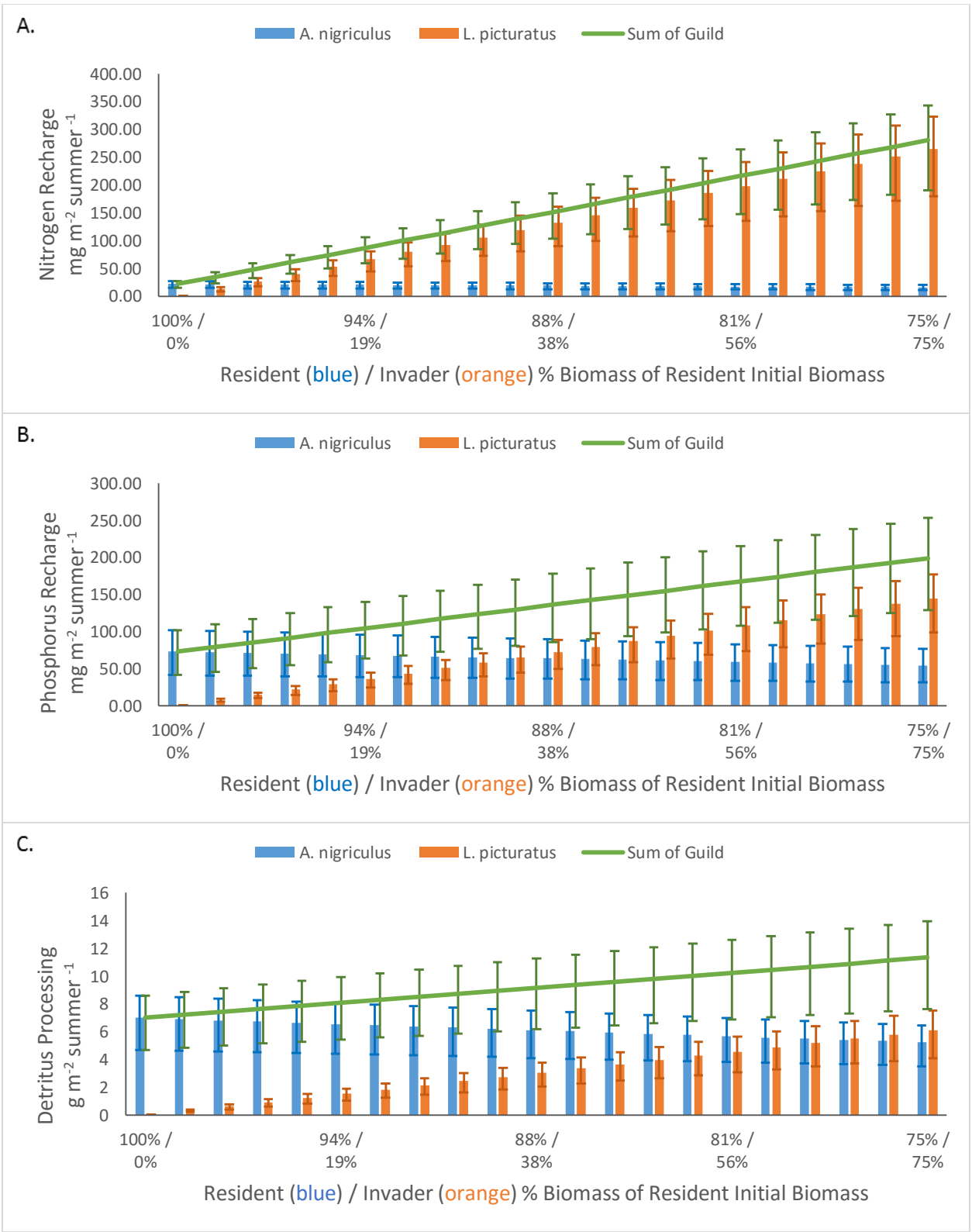
Appendix A Fig. 11: Upslope invasion in a montane permanent pond: *L. externus* is invaded by *L. picturatus* and *L. sublunatus.* Competition-extinction outcome. Panel A shows nitrogen regeneration, panel B shows phosphorus regeneration, and panel C shows detritus processing.



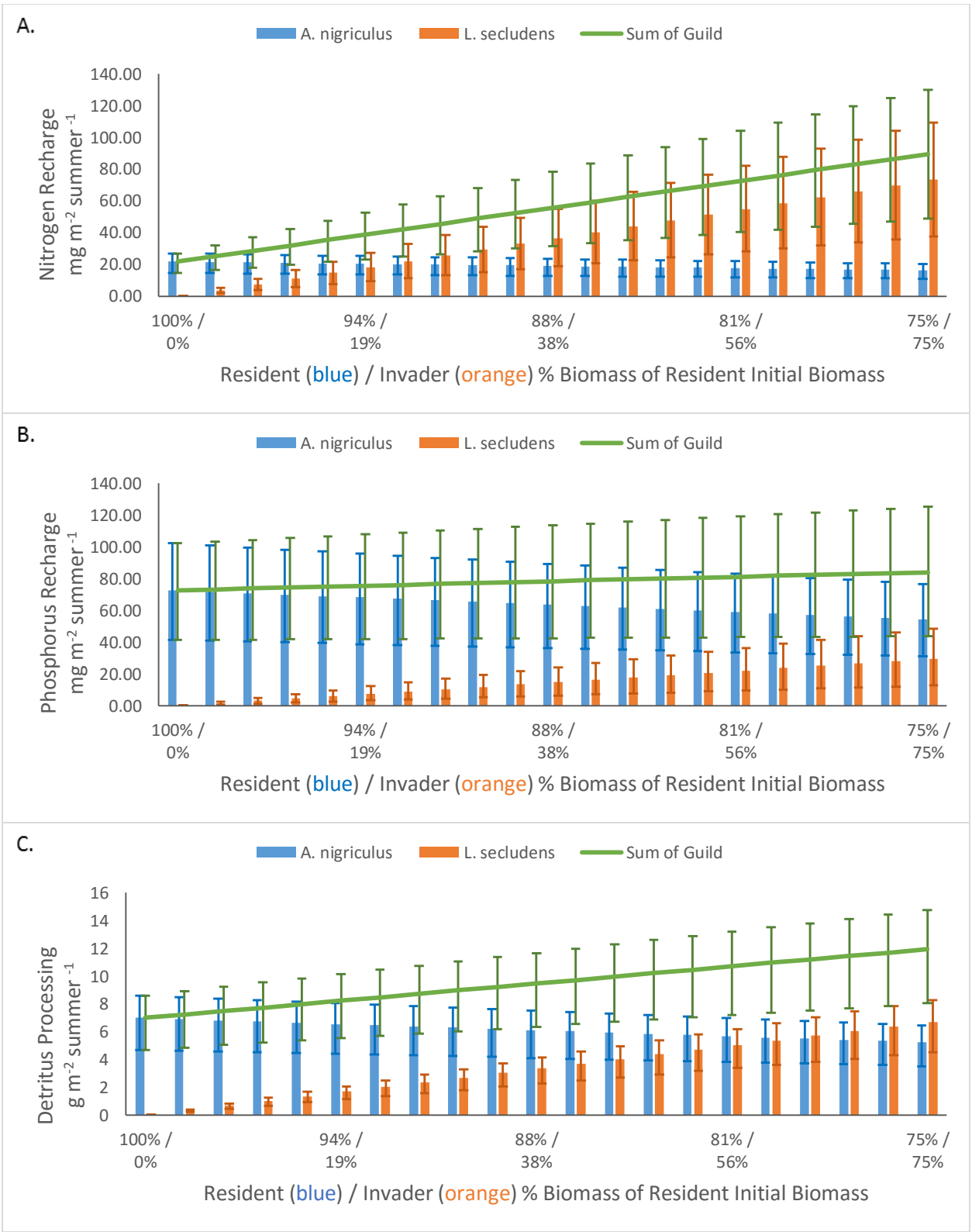
Appendix B Fig. 1: Upslope invasion in a subalpine permanent pond, or permanence invasion in a Montane Semi-Permanent Pond: *L. externus* replaced by *L. picturatus*. Partial Replacement outcome. Panel A shows nitrogen regeneration, panel B shows phosphorus regeneration, and panel C shows detritus processing.



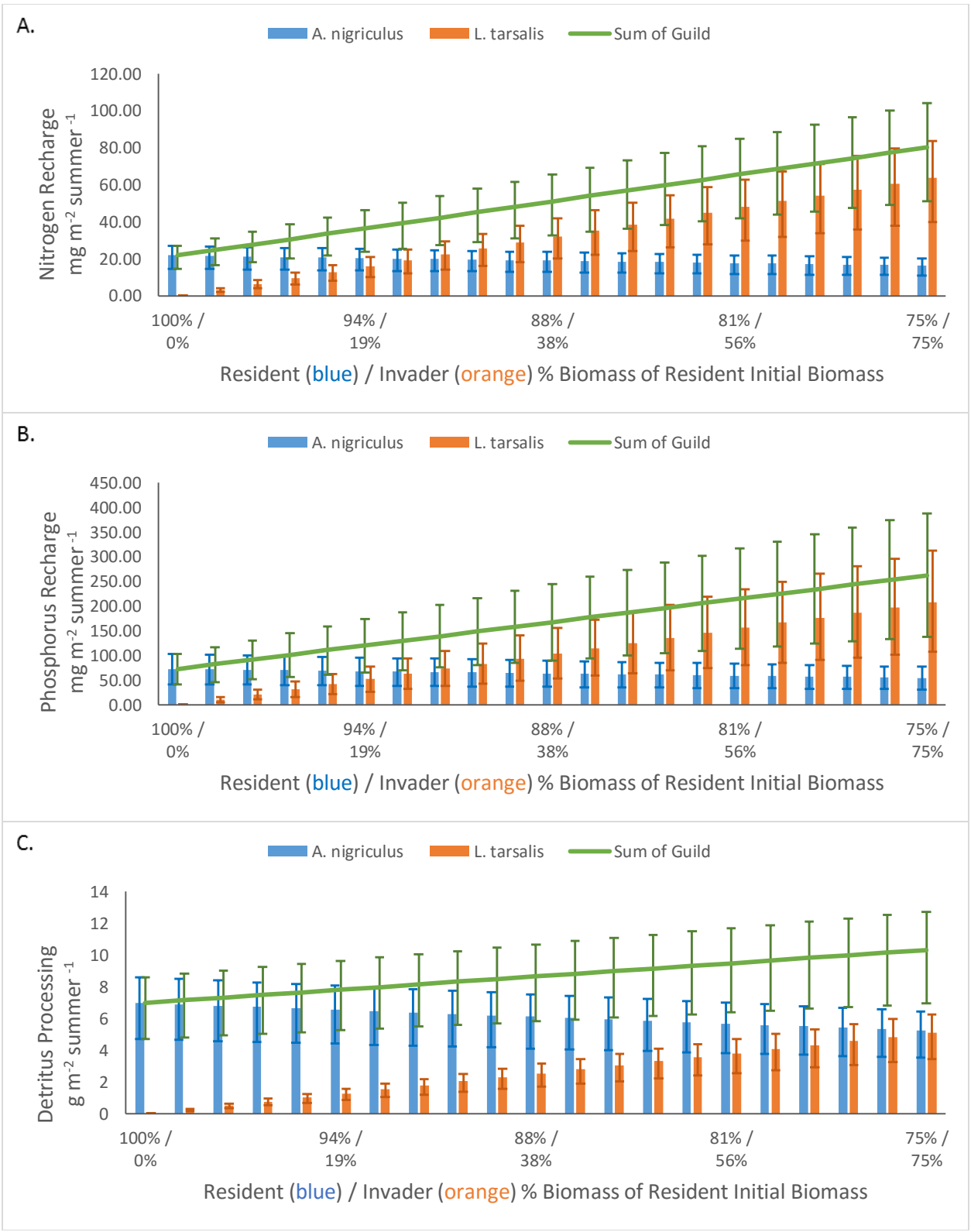
Appendix B Fig. 2: Upslope invasion in a subalpine permanent pond: *L. externus* invaded by *G. lorettae.* Partial replacement outcome. Panel A shows nitrogen regeneration, panel B shows phosphorus regeneration, and panel C shows detritus processing.



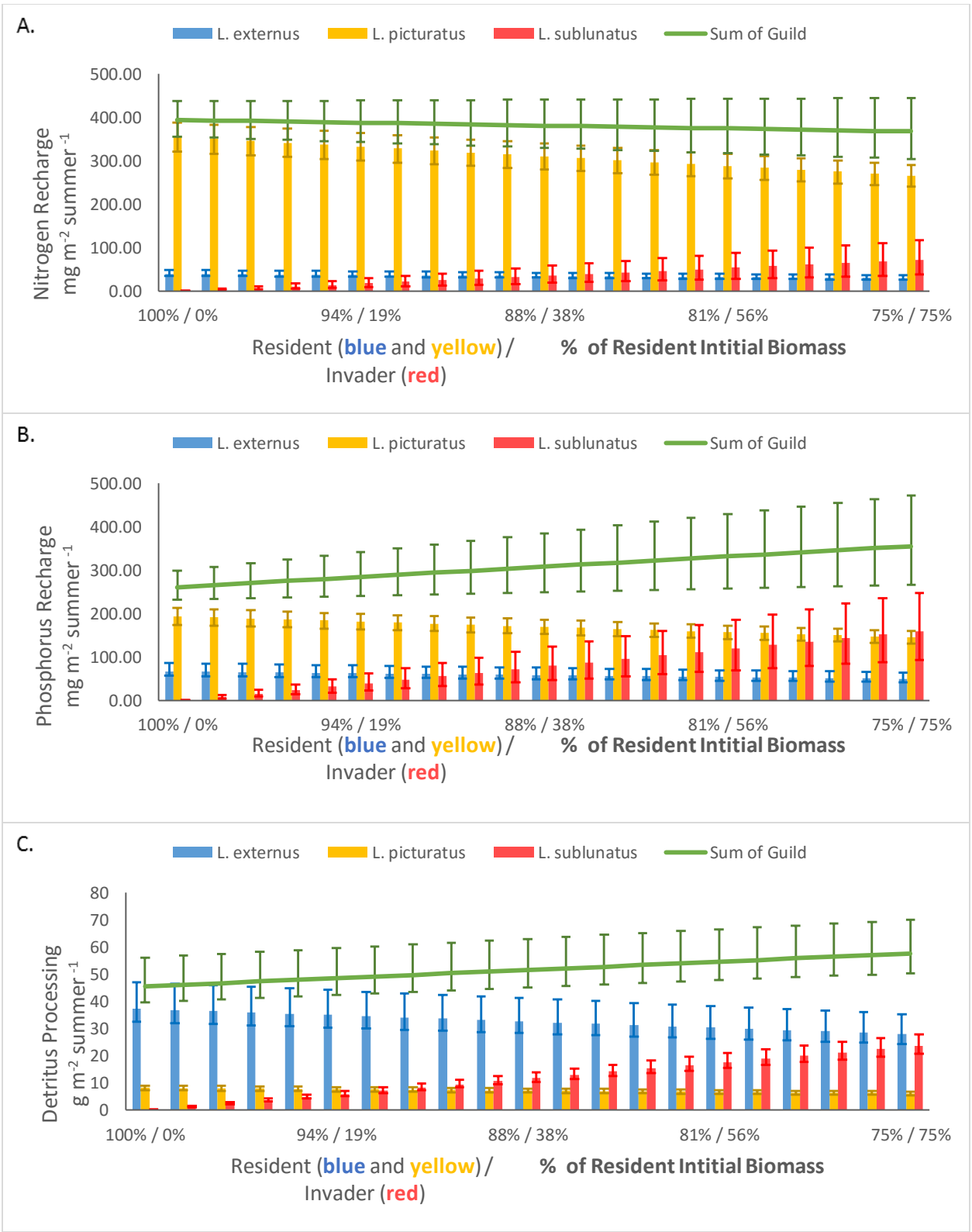
Appendix B Fig. 3: Upslope invasion in a subalpine semi-permanent pond: *A. nigriculus* invaded by *L. picturatus.* Partial replacement outcome. Panel A shows nitrogen regeneration, panel B shows phosphorus regeneration, and panel C shows detritus processing.



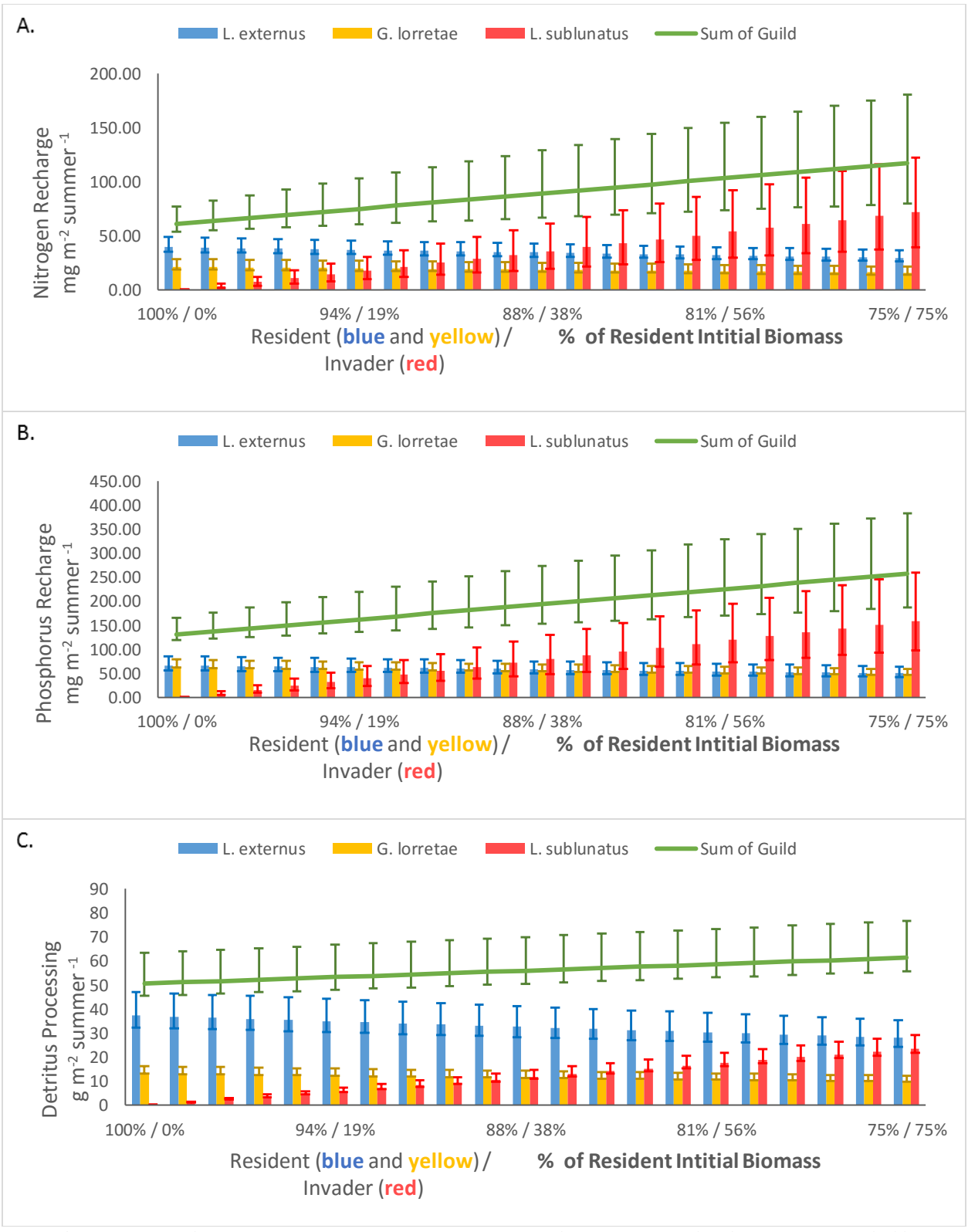
Appendix B Fig. 4: Upslope invasion in a subalpine semi-permanent pond: *A. nigriculus* invaded by *L. secludens.* Partial replacement outcome. Panel A shows nitrogen regeneration, panel B shows phosphorus regeneration, and panel C shows detritus processing.



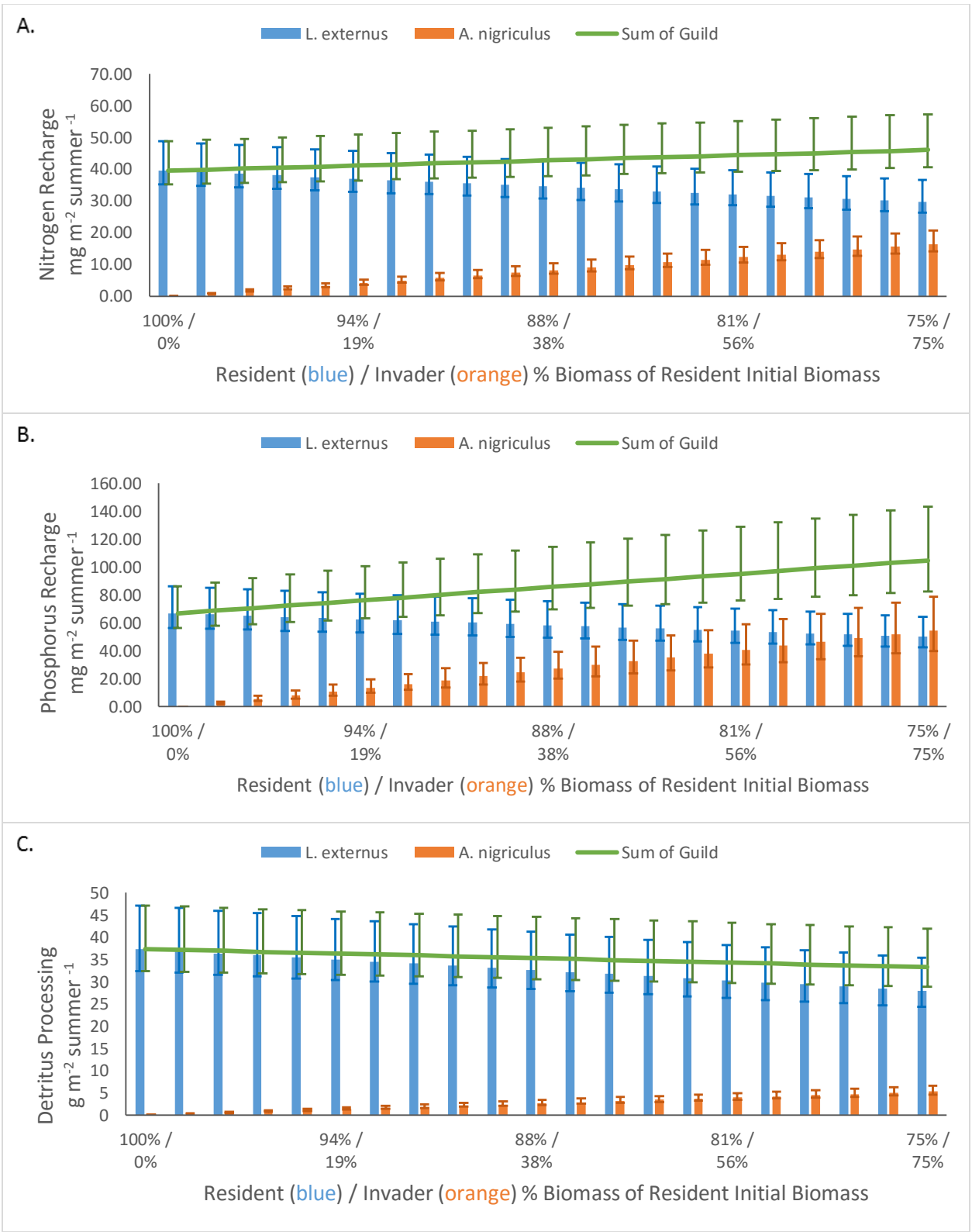
Appendix B Fig. 5: Upslope invasion in a subalpine temporary pond: *A. nigriculus* invaded by *L. tarsalis.* Partial replacement outcome. Panel A shows nitrogen regeneration, panel B shows phosphorus regeneration, and panel C shows detritus processing.



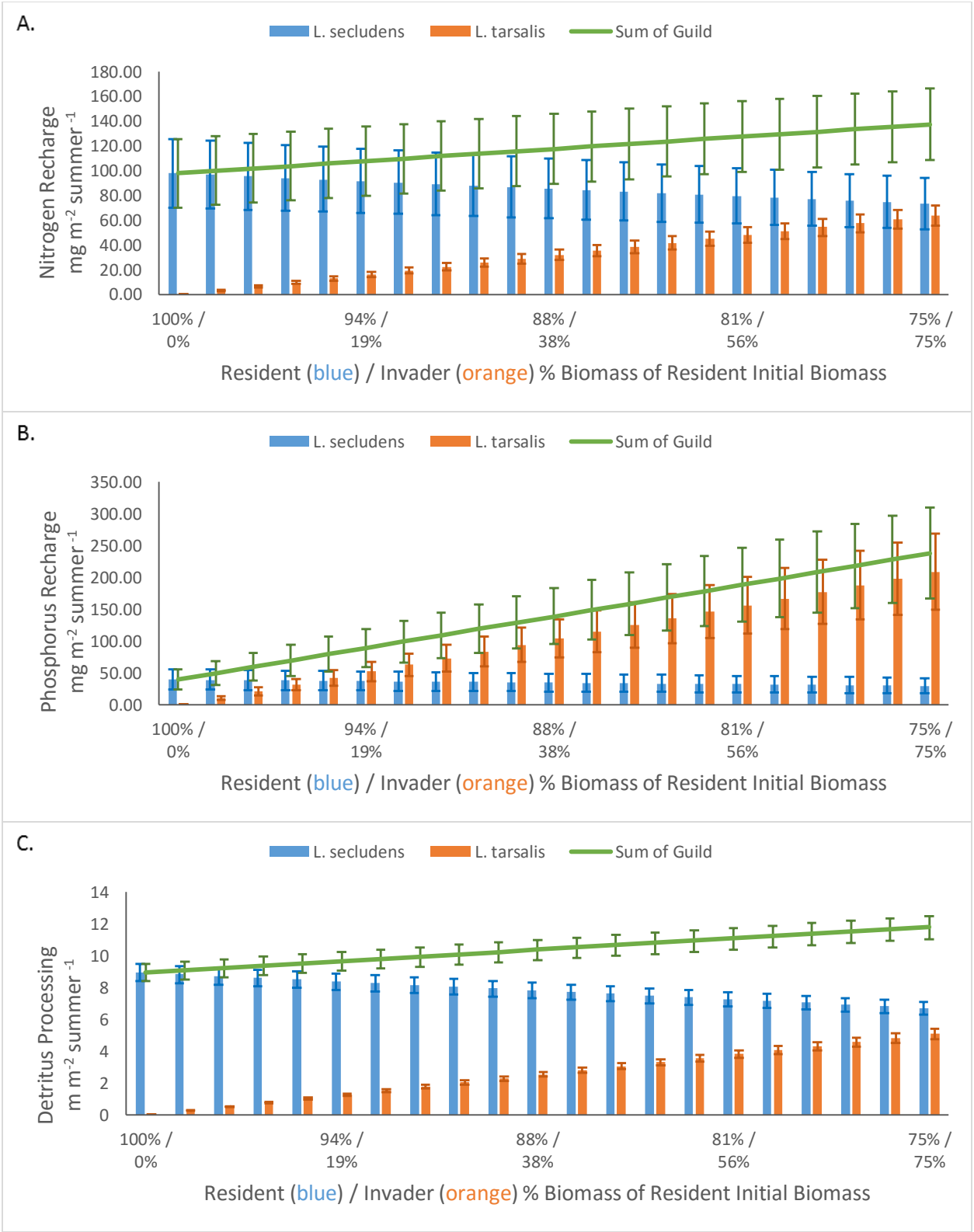
Appendix B Fig. 6: Upslope invasion in a montane permanent pond: *L. externus* and *L. picturatus* are invaded by *L. sublunatus.* Partial replacement outcome. Panel A shows nitrogen regeneration, panel B shows phosphorus regeneration, and panel C shows detritus processing.



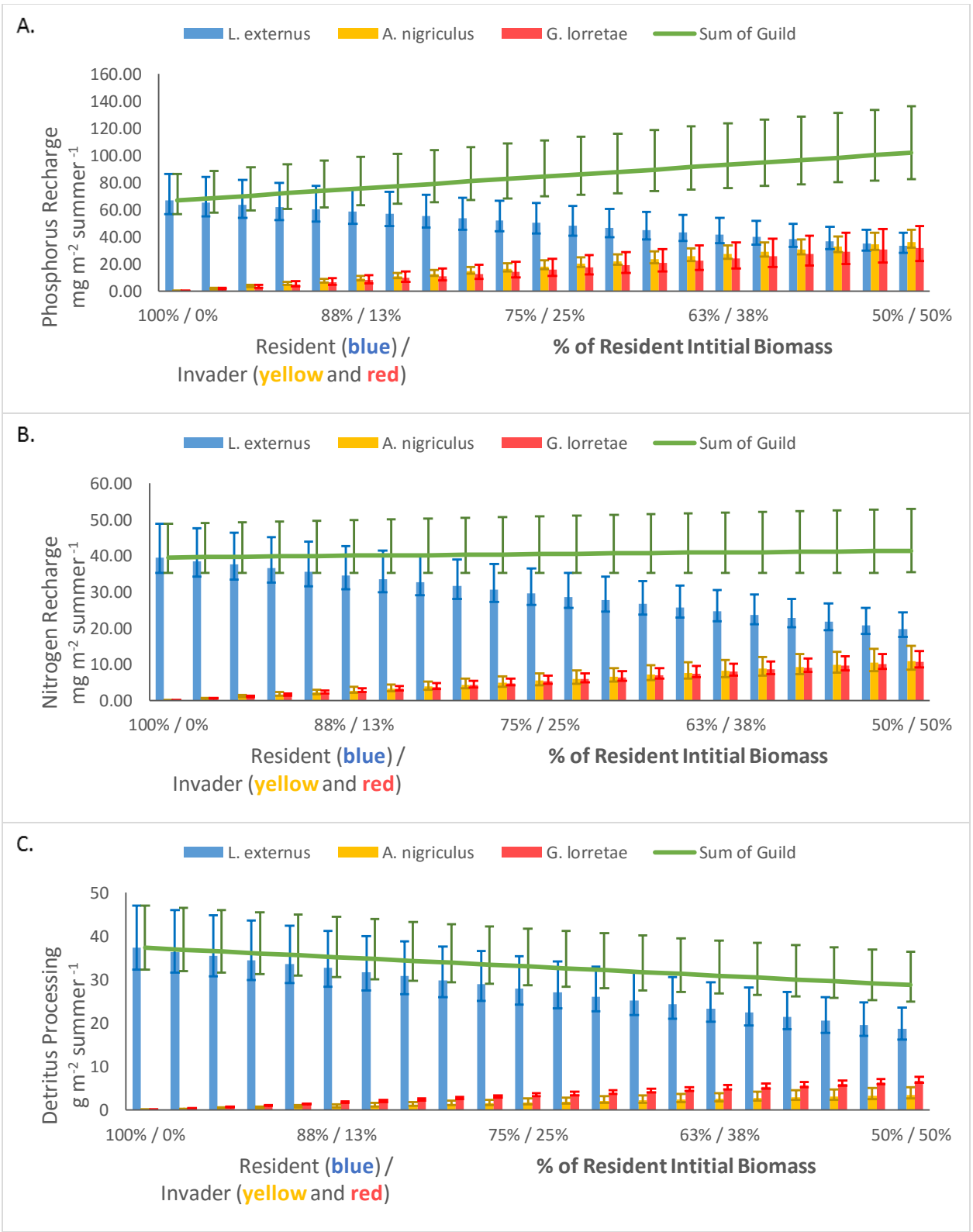
Appendix B Fig. 7: Upslope invasion in a montane permanent pond: *L. externus* and *G. lorretae* are invaded by *L. sublunatus.* Partial replacement outcome. Panel A shows nitrogen regeneration, panel B shows phosphorus regeneration, and panel C shows detritus processing.



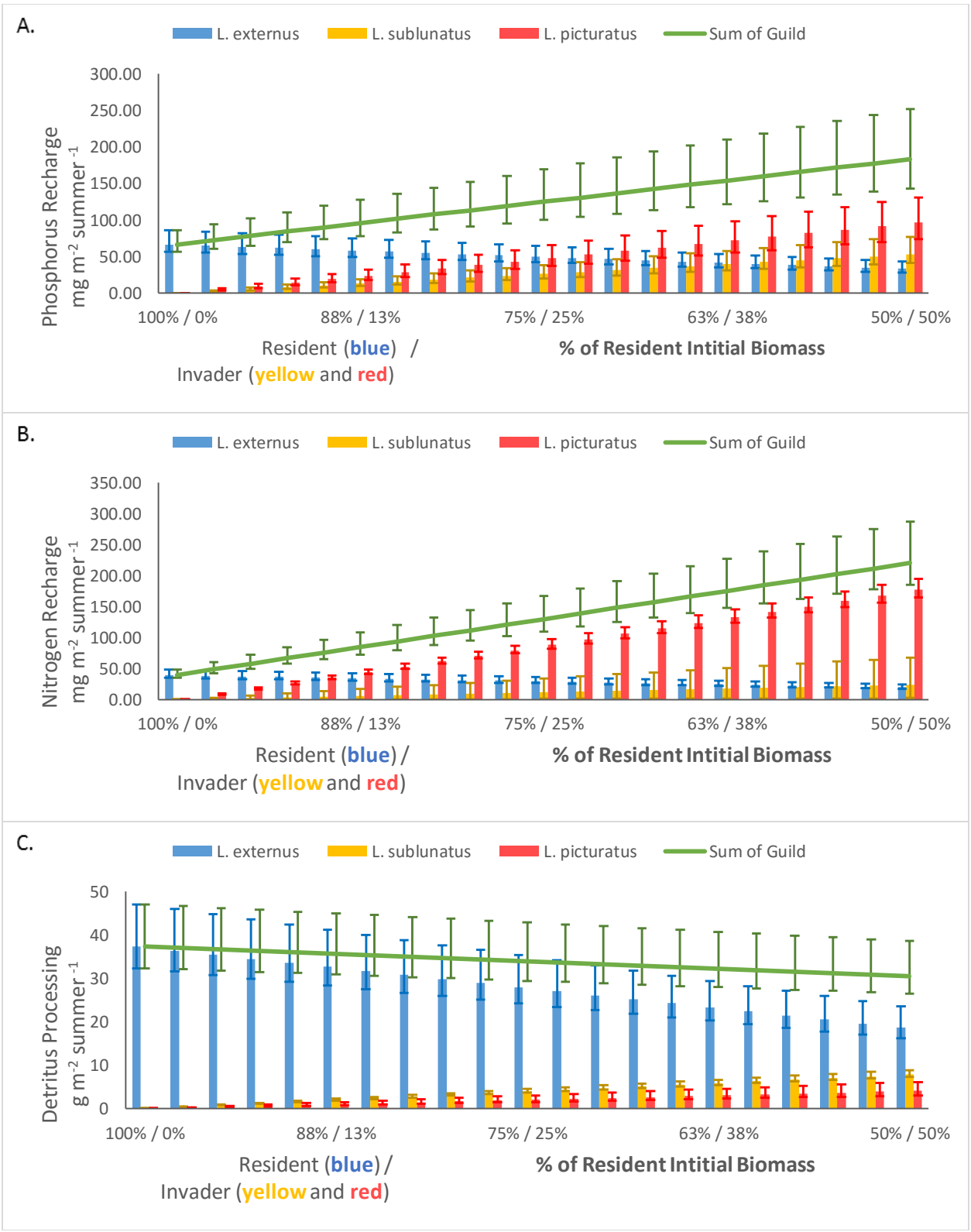
Appendix B Fig. 8: Upslope invasion in a montane permanent pond: *L. externus* is invaded by *A. nigriculus.* Partial replacement outcome. Panel A shows nitrogen regeneration, panel B shows phosphorus regeneration, and panel C shows detritus processing.



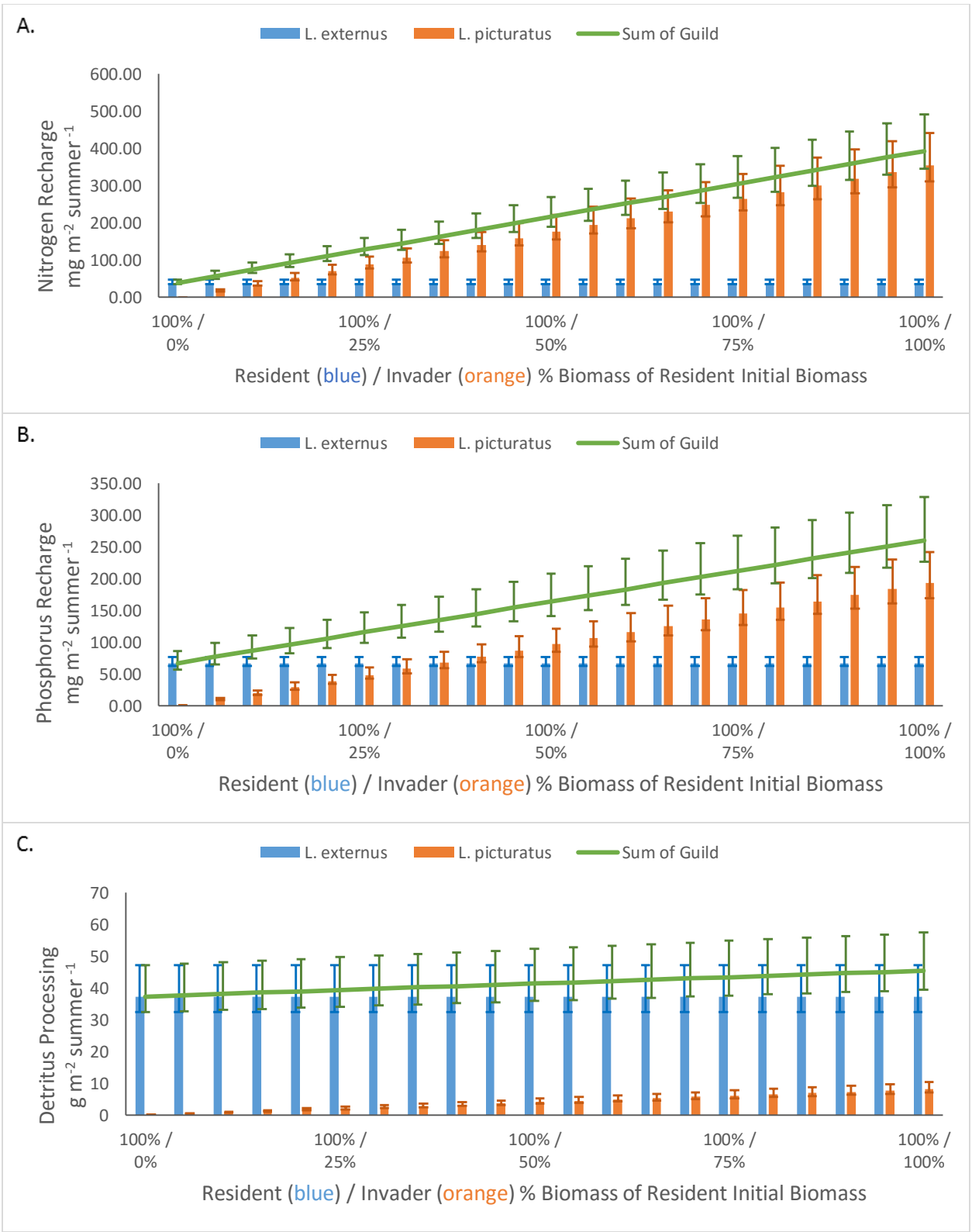
Appendix B Fig. 9: Upslope invasion in a montane permanent pond: *L. secludens* is invaded by *L. tarsalis.* Partial-replacement outcome. Panel A shows nitrogen regeneration, panel B shows phosphorus regeneration, and panel C shows detritus processing.



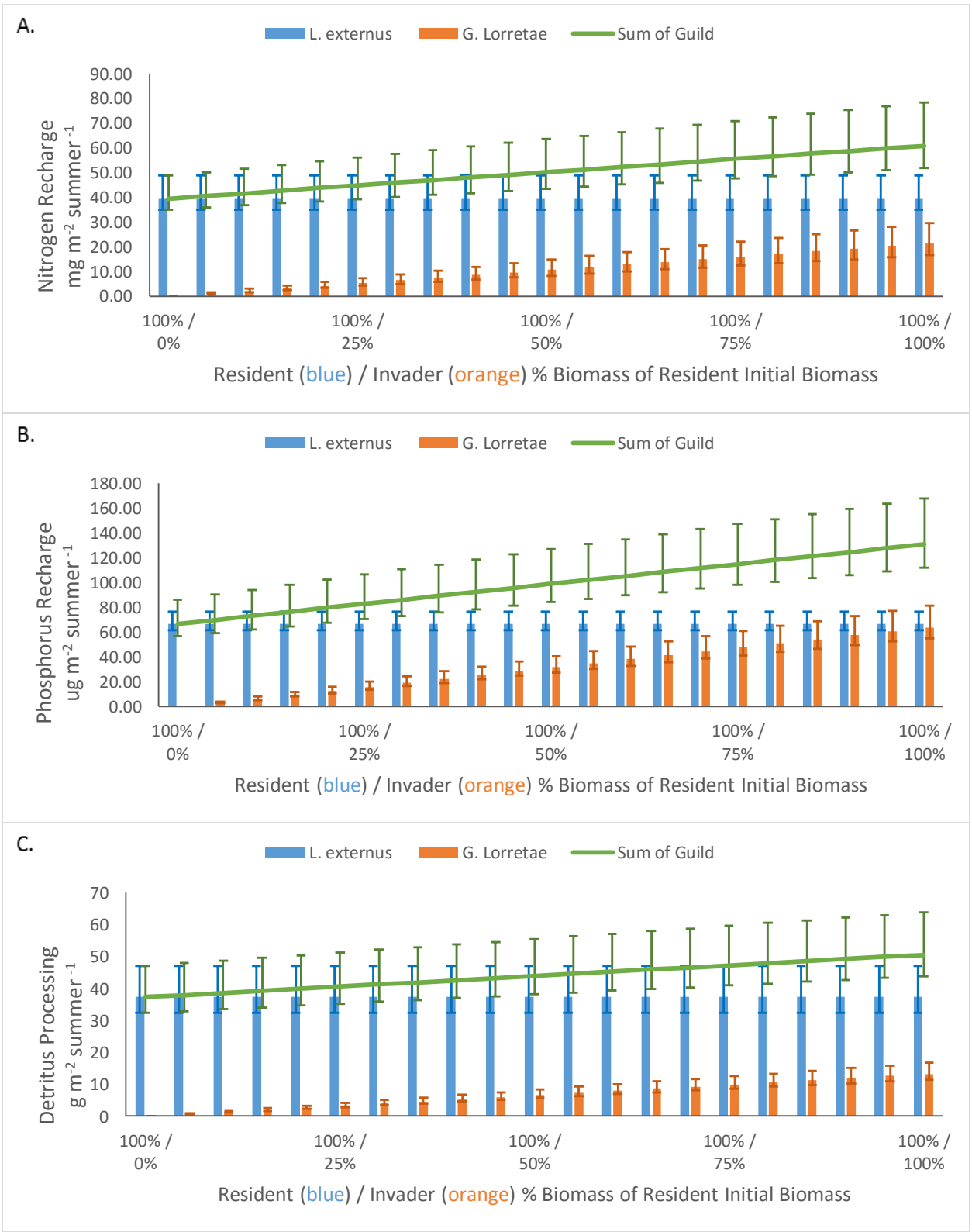
Appendix B Fig. 10: Upslope invasion in a montane permanent pond: *L. externus* is invaded by *A. nigriculus* and *G. lorretae.* Partial replacement outcome. Panel A shows nitrogen regeneration, panel B shows phosphorus regeneration, and panel C shows detritus processing.



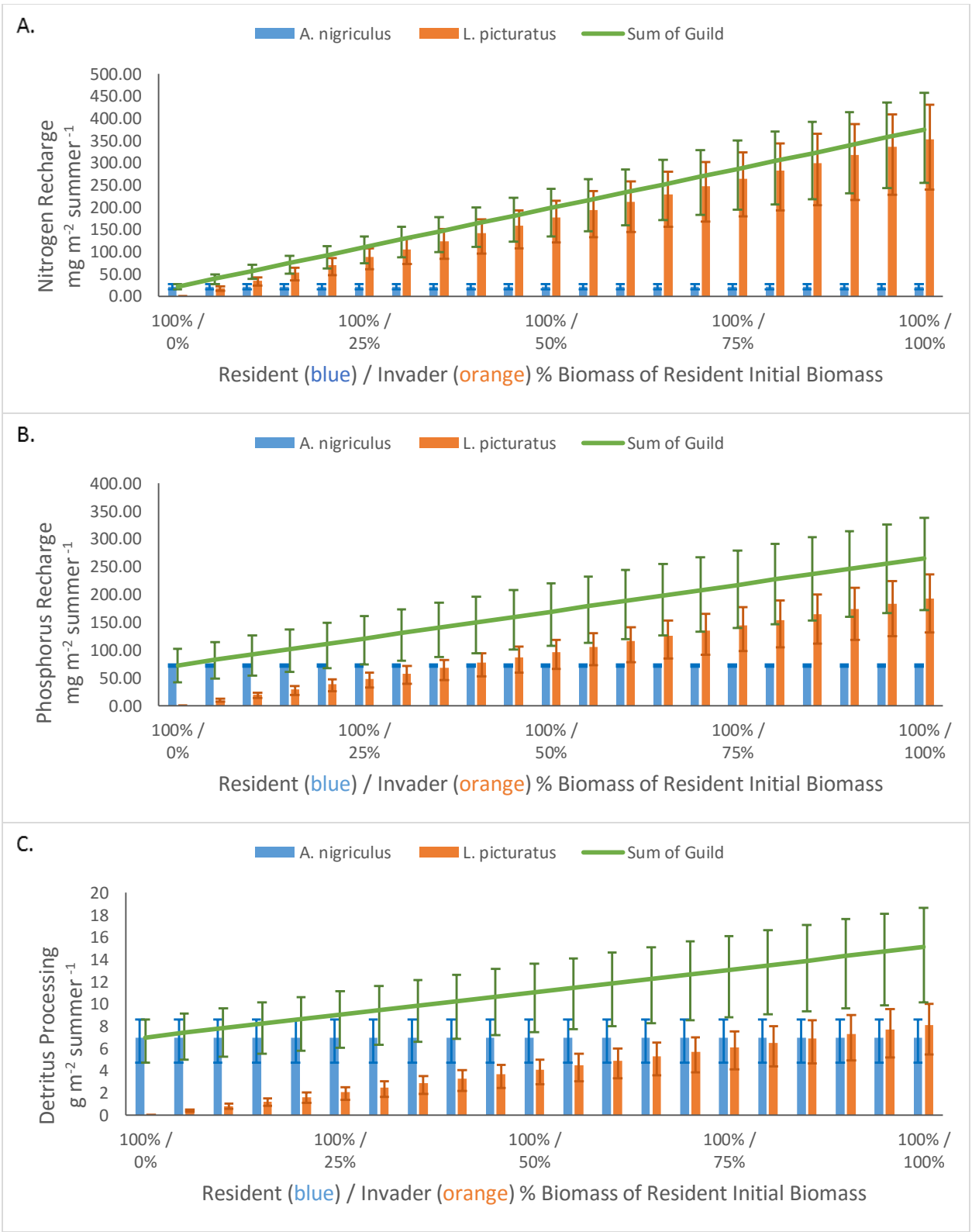
Appendix B Fig. 11: Upslope invasion in a montane permanent pond: *L. externus* is invaded by *L. picturatus* and *L. sublunatus.* Partial replacement outcome. Panel A shows nitrogen regeneration, panel B shows phosphorus regeneration, and panel C shows detritus processing.



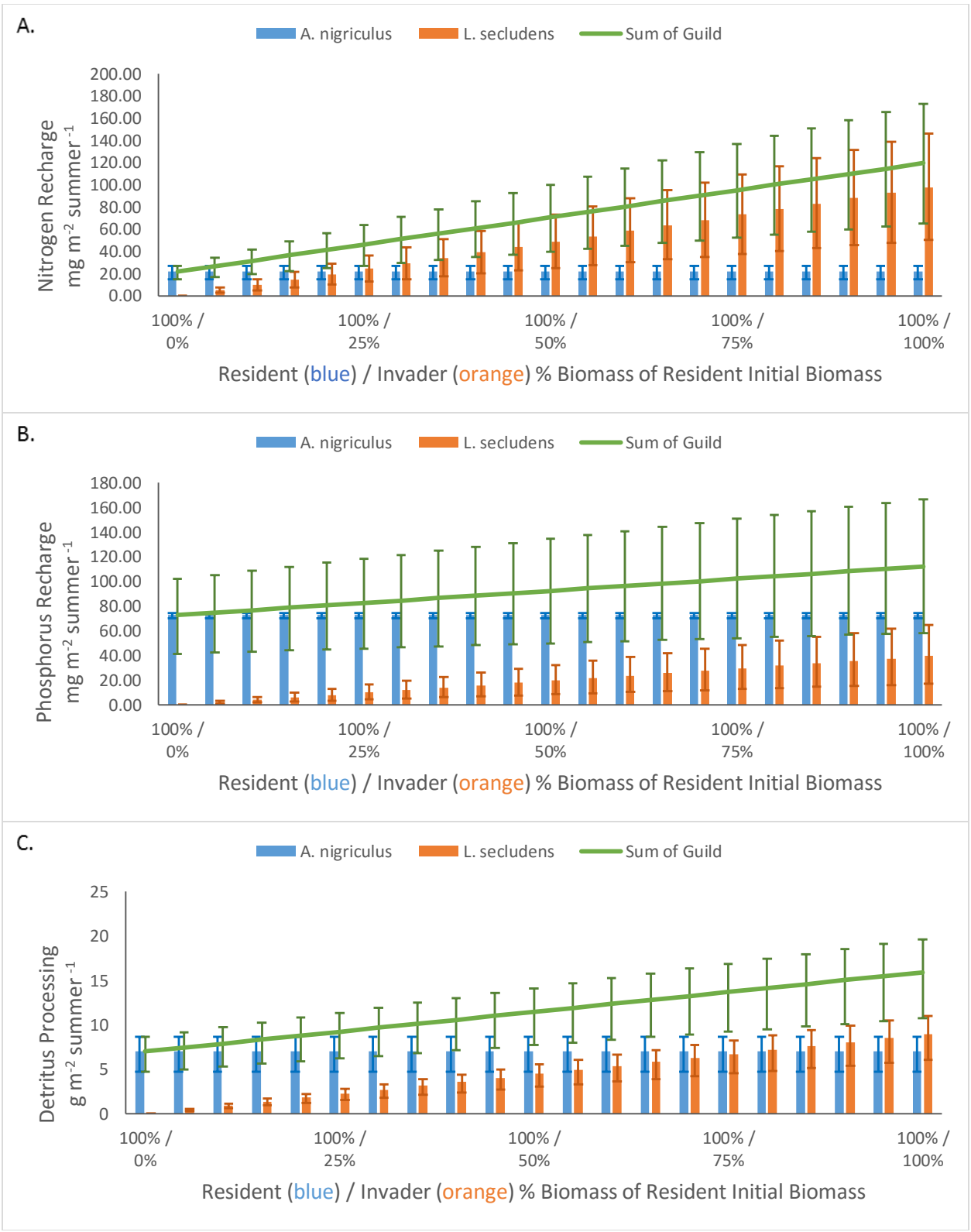
Appendix C Fig. 1: Upslope invasion in a subalpine permanent pond, or permanence invasion in a Montane Semi-Permanent Pond: *L. externus* replaced by *L. picturatus*. Niche-splitting outcome. Panel A shows nitrogen regeneration, panel B shows phosphorus regeneration, and panel C shows detritus processing.



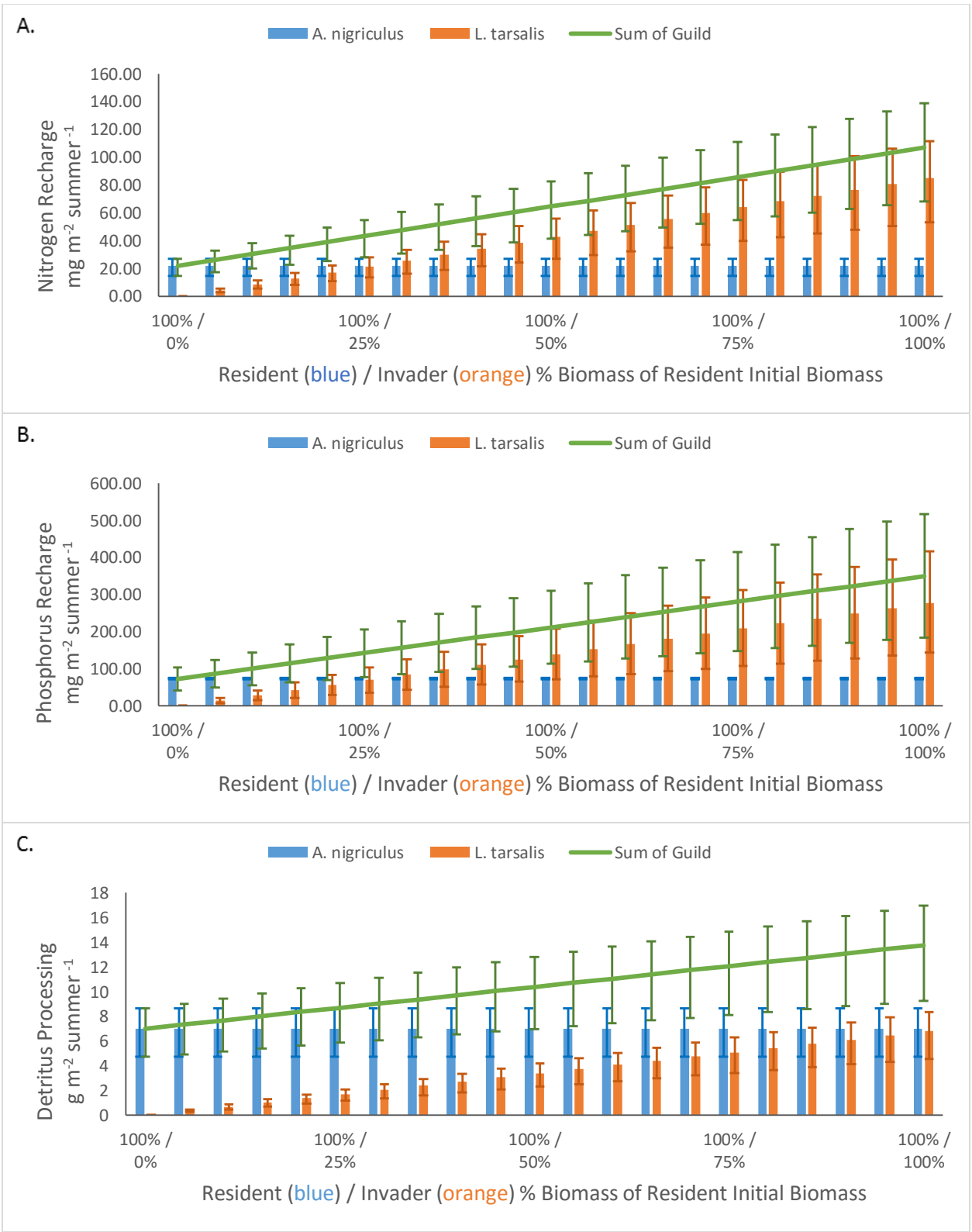
Appendix C Fig. 2: Upslope invasion in a subalpine permanent pond: *L. externus* invaded by *G. lorettae*. Niche-splitting outcome. Panel A shows nitrogen regeneration, panel B shows phosphorus regeneration, and panel C shows detritus processing.



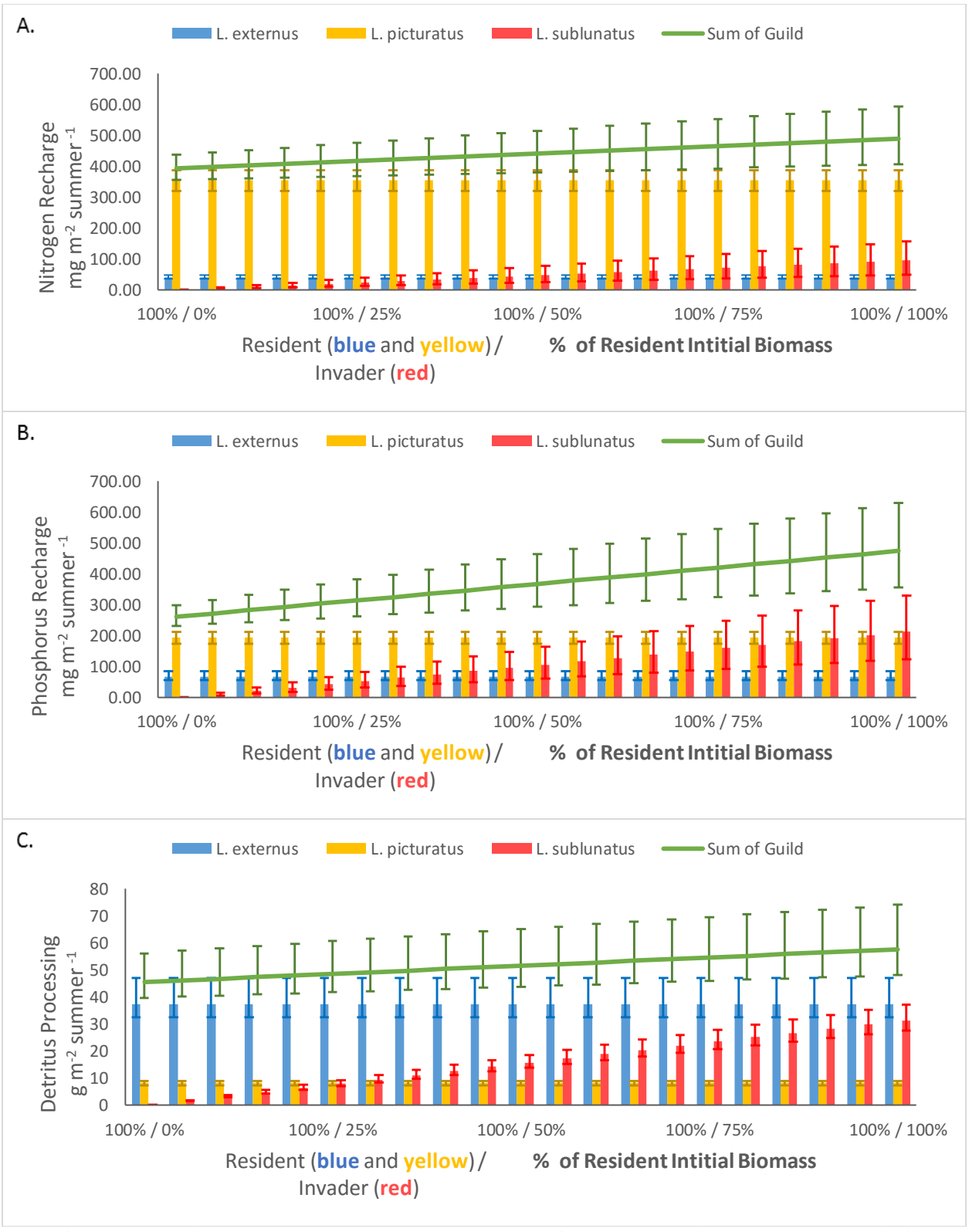
Appendix C Fig. 3: Upslope invasion in a subalpine semi-permanent pond: *A. nigriculus* invaded by *L. picturatus.* Niche-splitting outcome. Panel A shows nitrogen regeneration, panel B shows phosphorus regeneration, and panel C shows detritus processing.



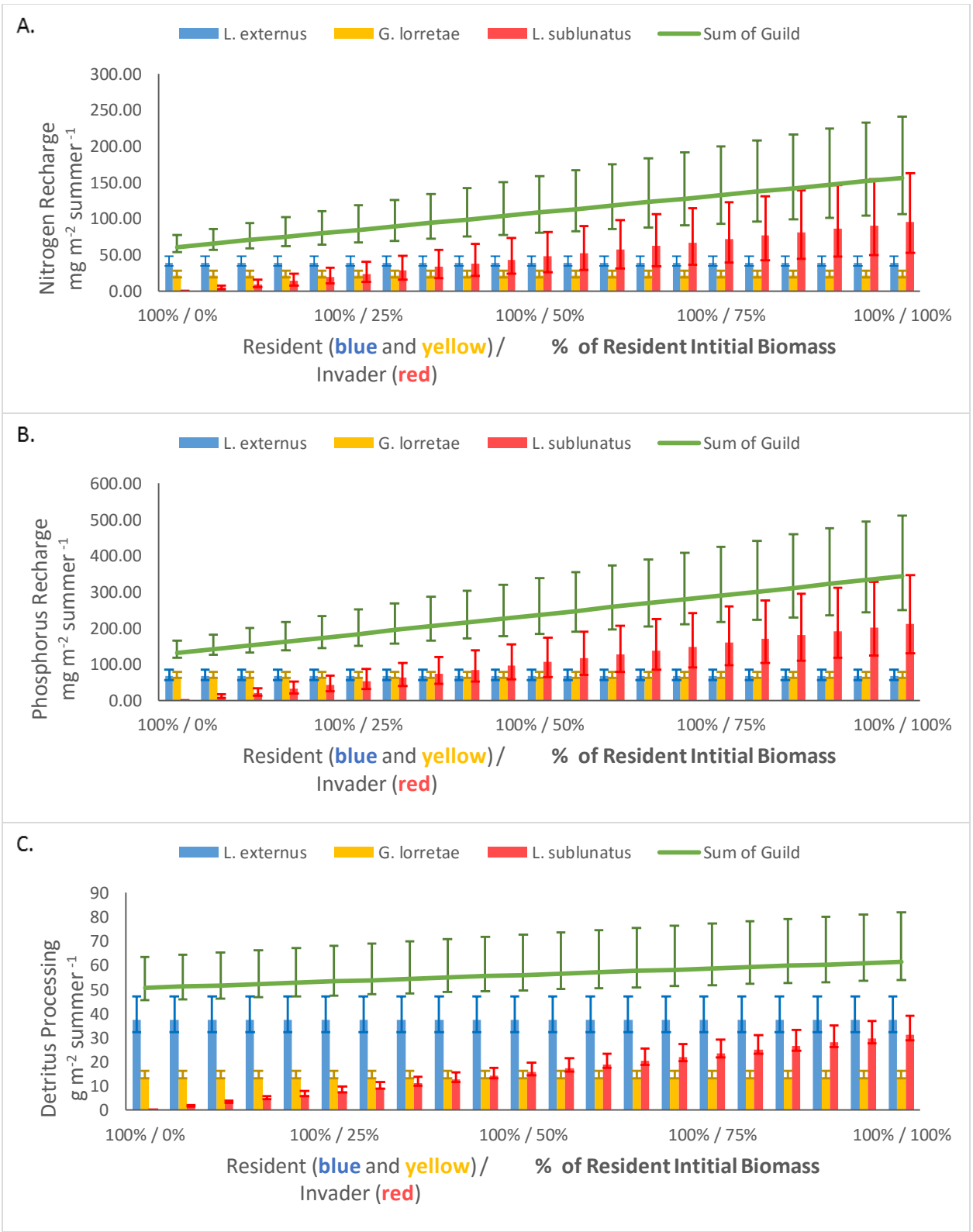
Appendix C Fig. 4: Upslope invasion in a subalpine semi-permanent pond: *A. nigriculus* invaded by *L. secludens.* Niche-splitting outcome. Panel A shows nitrogen regeneration, panel B shows phosphorus regeneration, and panel C shows detritus processing.



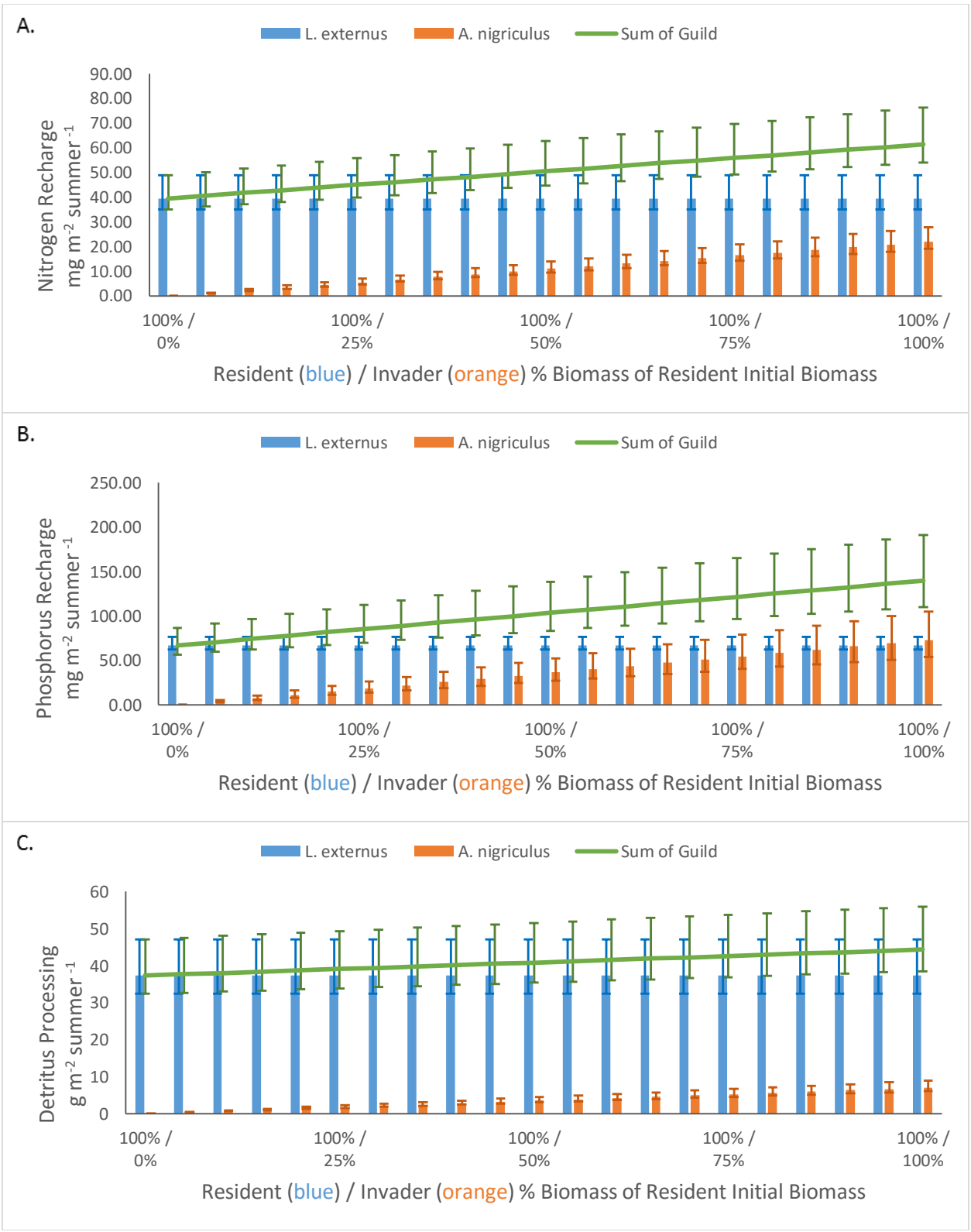
Appendix C Fig. 5: Upslope invasion in a subalpine temporary pond: *A. nigriculus* invaded by *L. tarsalis.* Niche-splitting outcome. Panel A shows nitrogen regeneration, panel B shows phosphorus regeneration, and panel C shows detritus processing.



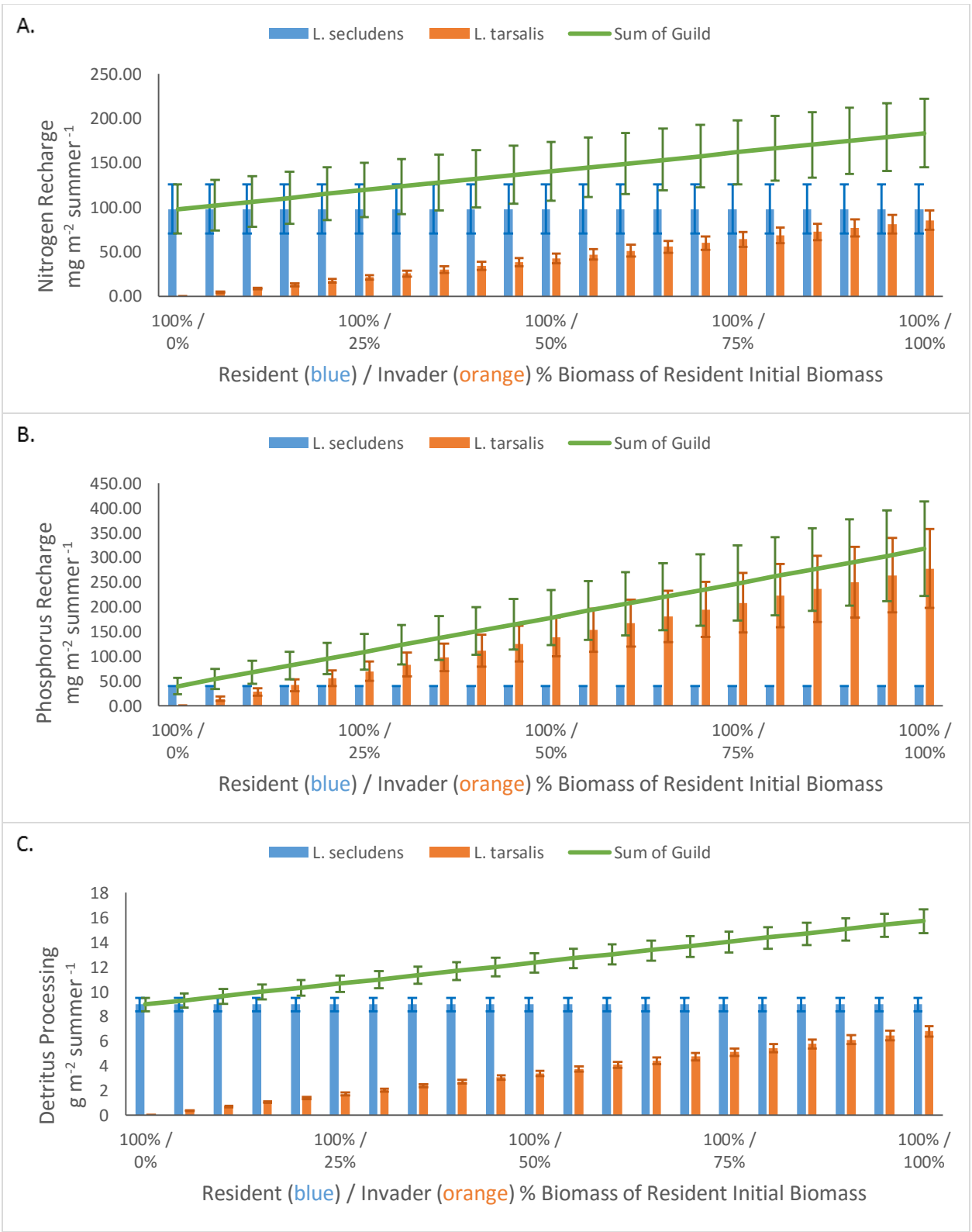
Appendix C Fig. 6: Upslope invasion in a montane permanent pond: *L. externus* and *L. picturatus* are invaded by *L. sublunatus.* Niche-splitting outcome. Panel A shows nitrogen regeneration, panel B shows phosphorus regeneration, and panel C shows detritus processing.



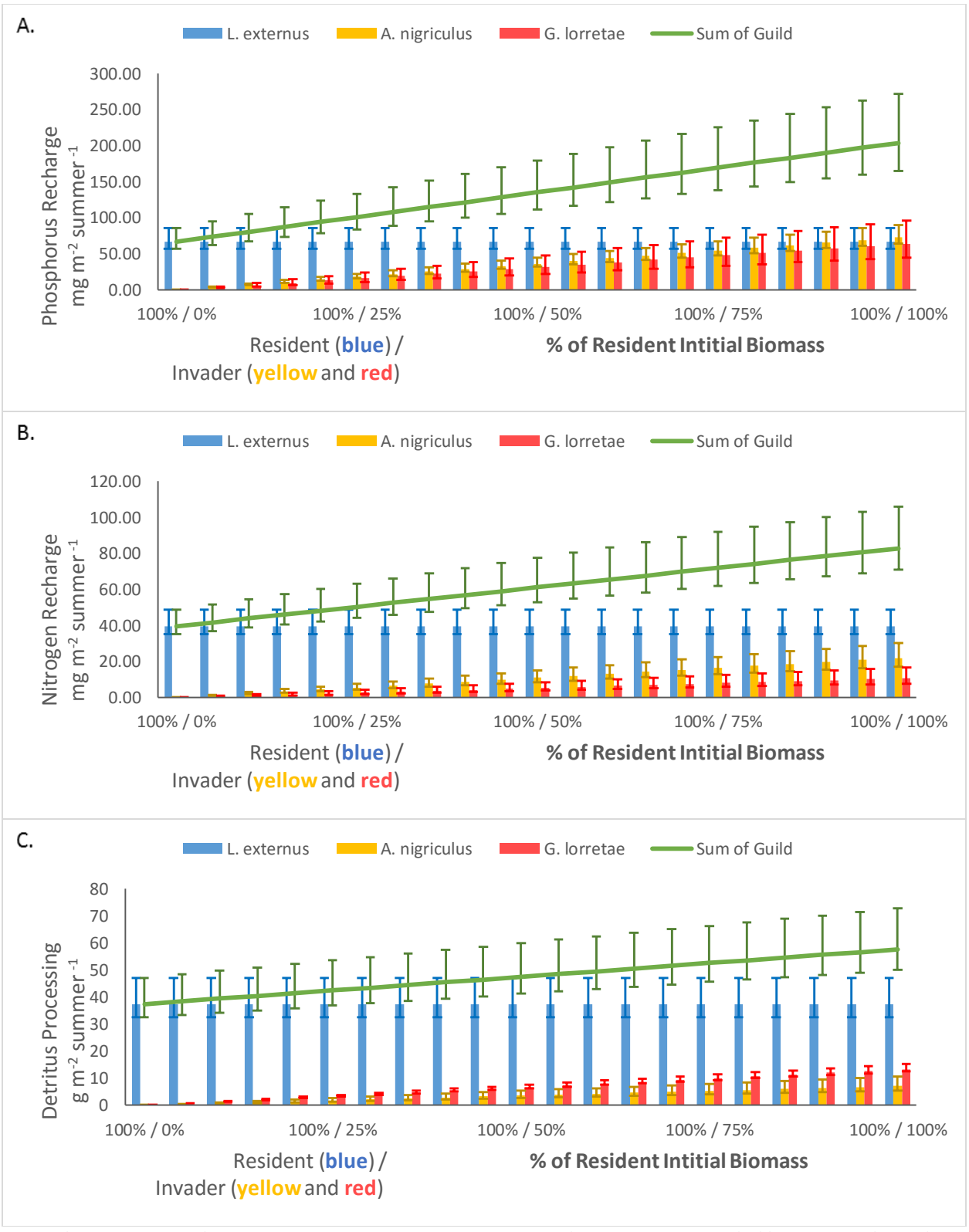
Appendix C Fig. 7: Upslope invasion in a montane permanent pond: *L. externus* and *G. lorretae* are invaded by *L. sublunatus.* Niche-splitting outcome. Panel A shows nitrogen regeneration, panel B shows phosphorus regeneration, and panel C shows detritus processing.



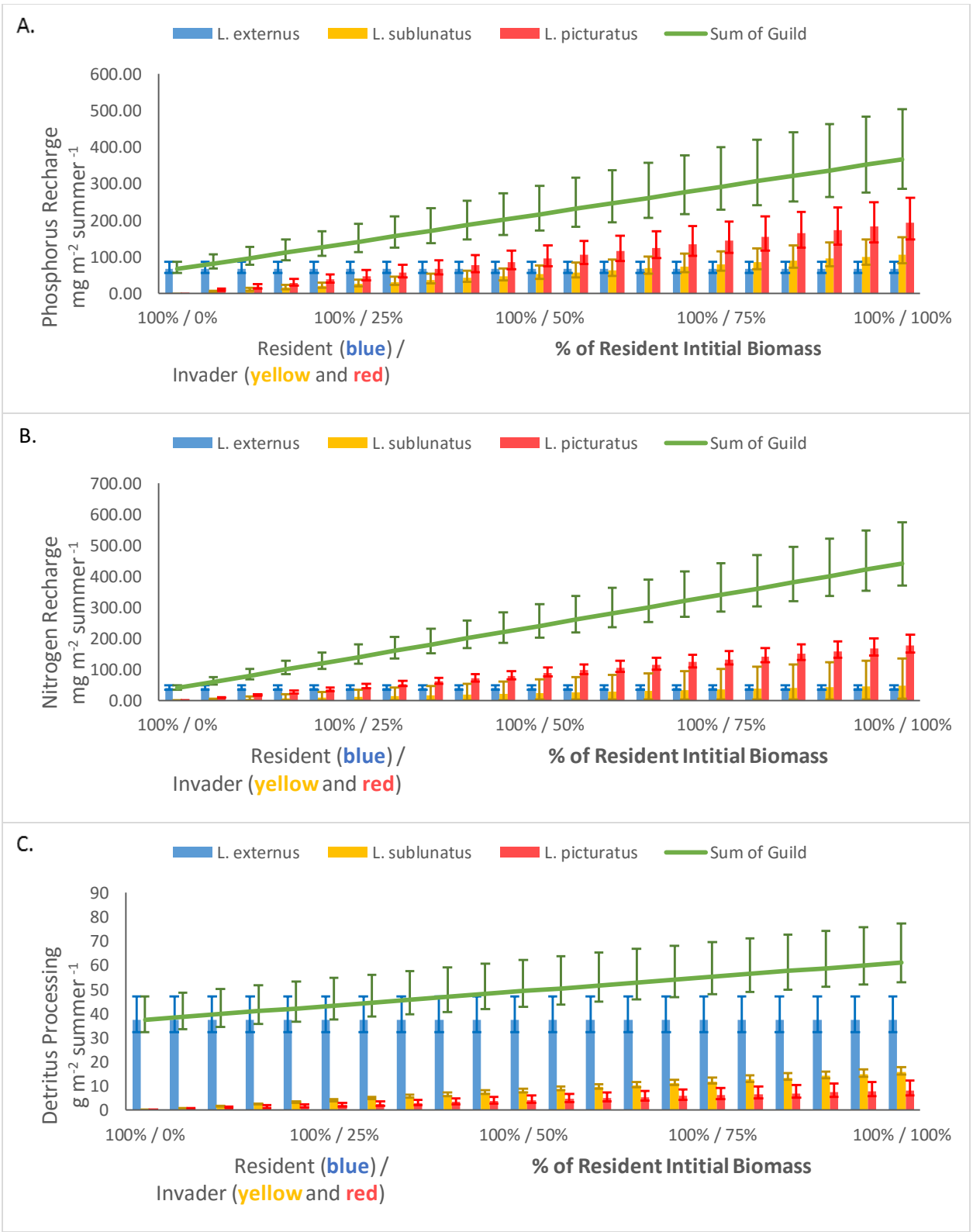
Appendix C Fig. 8: Upslope invasion in a montane permanent pond: *L. externus* is invaded by *A. nigriculus.* Niche-splitting outcome. Panel A shows nitrogen regeneration, panel B shows phosphorus regeneration, and panel C shows detritus processing.



Appendix C Fig. 9: Upslope invasion in a montane permanent pond: *L. secludens* is invaded by *L. tarsalis.* Niche-splitting outcome. Panel A shows nitrogen regeneration, panel B shows phosphorus regeneration, and panel C shows detritus processing.



Appendix C Fig. 10: Upslope invasion in a montane permanent pond: *L. externus* is invaded by *A. nigriculus* and *G. lorretae.* Niche-splitting outcome. Panel A shows nitrogen regeneration, panel B shows phosphorus regeneration, and panel C shows detritus processing.



Appendix C Fig. 11: Upslope invasion in a montane permanent pond: *L. externus* is invaded by *L. picturatus* and *L. sublunatus.* Niche-splitting outcome. Panel A shows nitrogen regeneration, panel B shows phosphorus regeneration, and panel C shows detritus processing.