Shifting N and P concentrations and stoichiometry during autumn litterfall: Implications for ecosystem monitoring

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ABSTRACT

Leaf litterfall nutrient concentrations and their ratios are a common indicator of site nutrient status and a critical component of many ecosystem calculations. Concentrations of nitrogen (N) and phosphorus (P) in leaf litter are related to foliar concentrations, but they are reduced by nutrient resorption during senescence. Although nutrient resorption occurs gradually during the autumn in winter-deciduous species, no study to date has assessed how the timing of litter collection affects estimates of nutrient concentration. To quantify the importance of this effect we analyzed the nutrient concentrations of leaf litter collected weekly in two northern hardwood sites at the Hubbard Brook Experimental Forest for three dominant tree species: *Acer saccharum*, *Betula alleghaniensis*, and *Fagus grandifolia*. Both N and P concentrations declined significantly during the litterfall season in all species ($p < 0.001$). Because P concentrations declined proportionately more than N concentrations, leaf litter N:P ratios increased throughout the season ($p < 0.001$), likely reflecting the ordered breakdown of the different cellular constituents containing these nutrients. Our results suggest that sampling senesced leaf tissue at a single point in time leads to biased estimates of nutrient concentrations, stoichiometry, and litterfall and resorption fluxes. This bias is likely greater for P than for N.

1. Introduction

Leaf litter constitutes one of the largest annual nutrient fluxes to soils in terrestrial ecosystems and forms the base of brown food webs. Reliable estimates of nutrient concentrations in senesced leaf tissue are needed to calculate litterfall nutrient flux and foliar nutrient resorption (Killingbeck, 1996) and are critical to understanding litter decomposition in systems around the globe (Cornwell et al., 2008). Leaf litter nutrient concentrations and their ratios are an indicator of producer nutrient limitation (Richardson et al., 2008; Reed et al., 2012; See et al., 2015) and directly affect higher trophic levels in both terrestrial (Wardle, 2002) and aquatic (Demi et al., 2018) systems.

Despite the ubiquitous use of litter chemistry in ecological studies, obtaining representative samples of leaf litter for chemical analysis is challenging. All leaves do not abscise simultaneously, and litterfall phenology differs among species (e.g. Kramer, 1995; Vitasse et al., 2009). In temperate deciduous forests, most trees lose their leaves over time frames that span several weeks. By the time the last leaves abscise, the earliest leaves to fall may have been on the ground or in collectors long enough to be subject to considerable decomposition and leaching.

To avoid this issue, researchers often sample freshly fallen leaves at a single point in the season. This approach assumes that concentrations of freshly fallen leaves remain constant throughout the autumn season. If this is not a valid assumption (Gosz et al., 1972; Killingbeck et al., 1990), then using concentrations from a single time point to represent the entire season will lead to biased estimates.

Nutrient concentrations in senescing leaves might be expected to vary over time due to nutrient resorption, leaching, and canopy position. The process of nutrient resorption begins at the onset of senescence, and continues until the abscission layer has fully formed (Killingbeck et al., 1990). The environmental cues for leaf senescence in winter-deciduous species include temperature, soil moisture, and photoperiod (Lambers et al., 2008). Shifting temperature and moisture regimes are thus expected to influence the phenology of senescence under climate change, depending on the relative importance of these factors at a particular location (Estiarte and Peñuelas, 2015; Gill et al., 2015). Regardless of the environmental cause, leaves falling before senescence is complete should have higher concentrations of mobile elements such as nitrogen and phosphorus due to the interruption of the resorption process. Nutrients are also leached from senescing leaves in

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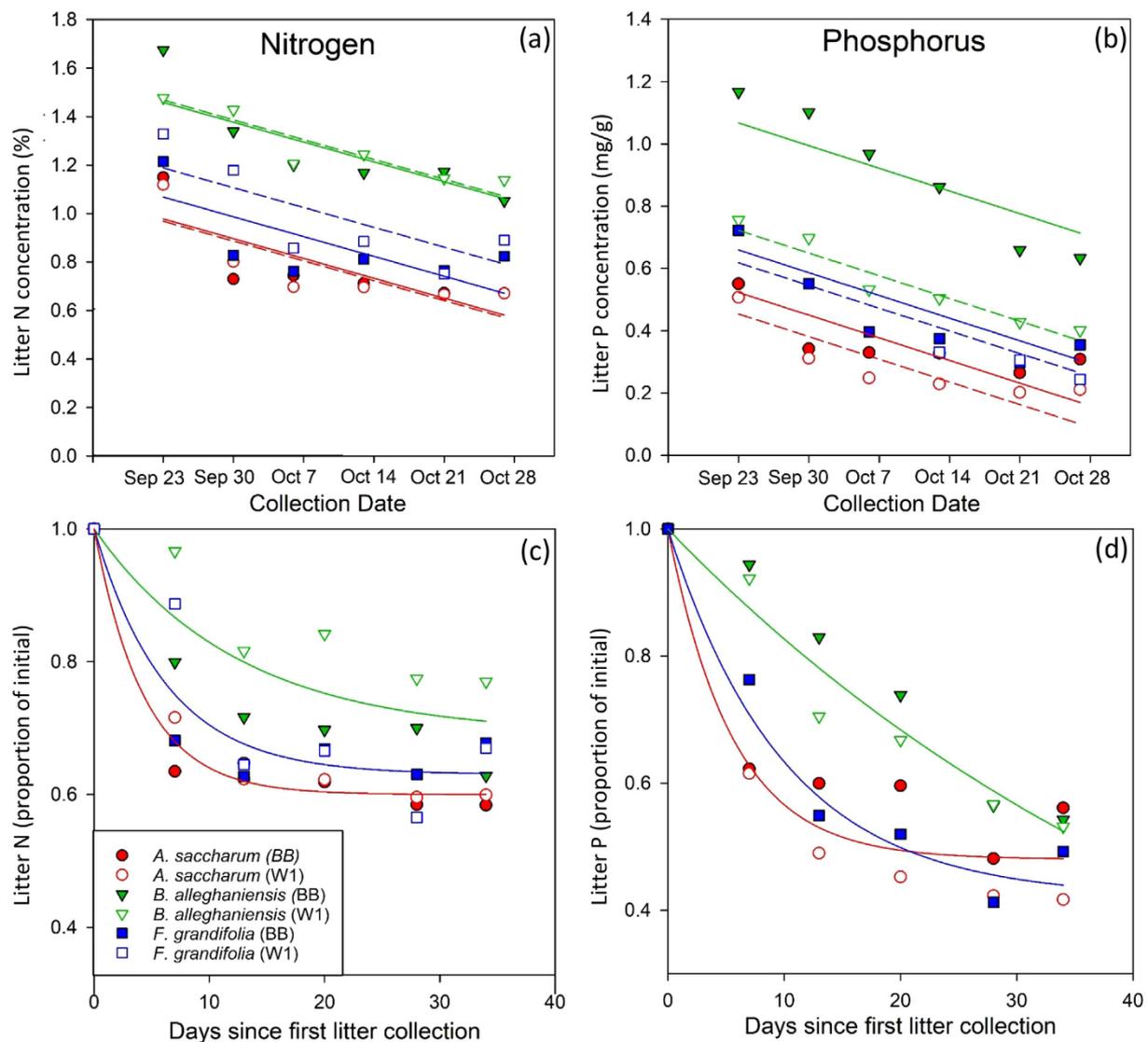E-mail address: crsee@umn.edu (C.R. See).

Fig. 1. Seasonal declines in N (a) and P (b) in recently senesced leaves of three tree species at two sites in the Hubbard Brook Experimental Forest, USA. Lines depict results of multiple linear regression, with Bear Brook (BB) shown with solid lines and Watershed 1 (W1) with dashed lines. Both elements declined significantly throughout the autumn litterfall season ($p < 0.001$ in both cases). When considered as a proportion of the concentration of the first leaves collected, the seasonal decline in both N (c) and P (d) was best described using exponential decay functions (Table 1).

the canopy during precipitation events, as evidenced by autumn throughfall measurements (Brant and Chen, 2015); however, in northern hardwood forests this flux of N and P is relatively minor in comparison with resorption (Ryan and Bormann, 1982). Finally, because foliar nutrient concentrations vary with canopy position (Yang et al., 2016), temporal differences in litterfall chemistry might be expected when leaf abscission does not occur randomly throughout the canopy. While there are many reasons to expect nutrient concentrations to change during the litterfall season, no study to date has explicitly addressed this source of variability or considered the implications for forest ecosystem monitoring.

We compared changes in litter nutrient concentrations throughout the litterfall season for three dominant tree species in two northern hardwood forest sites in the northeastern United States. Our objectives were to describe the pattern and magnitude of nutrient concentration changes over the litterfall season, determine whether such changes vary among species, and evaluate their importance to estimates of nutrient fluxes in litterfall and foliar resorption.

2. Methods

This study took place in the Hubbard Brook Experimental Forest (3° 57′ 1.8036″ N, 71° 43′ 24″ W), New Hampshire, USA. Mean annual precipitation is 1400 mm, and mean monthly temperatures range from –9 to 18 °C. The species we studied are the three dominant species of northern hardwoods in this site: *Acer saccharum* (sugar maple), *Betula alleghaniensis* (yellow birch), and *Fagus grandifolia* (American beech).

Live foliage and fresh leaf litter were collected in two sites: Bear Brook (elevation 525 m) and Watershed 1 (elevation 488 m). Both sites are typical northern hardwood forests located on south-facing slopes on well-drained Spodosols. Watershed 1 was treated with wollastonite in 1999 in an experiment designed to replace calcium lost during the 20th century as a result of anthropogenic activity (Battles et al., 2014).

Litter traps were cleared of summer litter in late August 2004, and freshly senesced leaf litter was collected weekly from a total of twelve litter traps per site from September 23 until October 27 (6 collection dates). These sampling dates cover the period of leaf fall at this site, except that a small proportion of dead *Fagus* leaves remain on the trees through midwinter. All litter from each site for each collection date was

composited by species, dried, and ground to pass through a 40 mesh screen.

Carbon and N concentrations were determined using a CN elemental analyzer (EA1112 elemental analyzer; Thermo Electron Corporation). Phosphorus concentrations were determined by ashing ~ 0.25 g of sample at 470 °C followed by digestion in 10 ml of 6 mol/L HNO₃. Phosphorus concentrations of solutions were determined using inductively coupled plasma optical emission spectrometry (ICP-OES, Optima 3300DV, Perkin Elmer Corporation). Analyses of standard reference leaf material (NIST 1515) digested with these samples averaged 99% (range = 97–101%) of certified concentrations for P. Results for additional elemental concentrations (Ca, Mg, K, Mn, Sr) can be found in supplementary material (Appendix A).

We used the date of collection (as a continuous variable), site (as a class variable), and species (as a class variable) in multiple linear regressions to predict changes in N and P concentrations and N:P ratios. In addition to main effects, we initially included date-by-species and date-by-site interactions. These interaction terms were omitted from our final models if they were not significant at $\alpha = 0.05$.

To better describe change over time, we calculated nutrient concentrations for each collection date as a proportion of the concentration at the first collection date, separately for each species but averaging over the two sites, and fit various functions to describe the decline over time. We fit a linear decay model of the form $C_t = C_i^*(1 + x^*t)$, where C_t is the proportion of initial nutrient concentrations C_i remaining at time t, t is the number of days since the initial collection, and x is the linear rate of decline. We also fit a simple exponential decay model of the form $C_t = C_i^* e^{-kt}$, where k is the exponential rate of decline. Finally, we fit an asymptotic exponential model of the form $C_t = C_i^*(A + (1 - A)e^{-kt})$, where A is the asymptote (i.e. the fraction remaining after concentrations stop declining), and k is the exponential rate for the declining fraction $(1 - A)$. We compared the three decay models for each species using Akaike's Information Criterion (AIC). All analyses were conducted using the R base package (R core team, 2016).

3. Results

Leaf litter concentrations of both N and P declined significantly throughout the season (Fig. 1). The rates of decline were similar between the two sites; the site-by-date interactions were not significant ($p = 0.91$ for N and $p = 0.18$ for P). The rate of decline of N concentration throughout the litterfall season was $0.12 \, \text{mg g}^{-1} \, \text{day}^{-1}$ while litterfall P declined by $0.011 \, \text{mg g}^{-1} \, \text{day}^{-1}$ ($p < 0.001$ for both elements for the main effect of date). Bear Brook had higher litter P concentrations than Watershed 1 ($p < 0.001$), while the two sites did not differ systematically in litter N concentrations ($p = 0.35$). Yellow birch had consistently higher concentrations of both N ($p < 0.001$) and P ($p < 0.001$), but the rate of decline was similar among species; species-by-date interactions were not significant ($p = 0.90$ for N; $p = 0.08$ for P; Fig. 1).

Nutrient resorption proficiency is defined by concentrations of a nutrient in senesced leaves. The observed differences in litterfall concentrations of N and P across collection dates resulted in substantial differences in estimates of resorption proficiency. On average, N concentrations declined by 34% between the first and last collections, and P concentrations declined by 49%, In other words, resorption proficiency was much higher in leaves that remained attached until later in the season. Estimates of nutrient resorption efficiency, defined by the difference between green leaves and senesced leaves, were similarly affected by the variation in leaf litter concentrations over time (Appendix C).

When considered as a fraction of initial concentration, the change in N and P through time was best described (based on AIC) by the asymptotic exponential decay equation (Fig. 1, Table 1). The only exception was for P concentrations of *B. alleghaniensis*, which were better described by simple exponential decay (Table 1). Based on the

asymptotic model, N concentrations declined faster (higher k values) and had higher asymptotes (higher A values) than P concentrations in all species (Table 1).

The early decline in litterfall N followed by a more gradual and proportionally larger decline in P resulted in an increase in N:P ratios throughout the autumn ($p < 0.001$, Fig. 2). Litterfall N:P ratios also varied by site and species ($p < 0.001$ for both main effects). While the slope for N:P ratios did not differ significantly among species (species-by-date interaction $p = 0.25$), it was significantly higher at Watershed 1 than at Bear Brook (site-by-date interaction $p = 0.03$, Fig. 2).

4. Discussion

Our results show that N and P concentrations of recently senesced leaves are sensitive to the timing of collection at the sites we studied. We were surprised by the consistent increase in litterfall N:P as the litterfall period progressed (Fig. 2). Changing leaf N:P ratios over the litterfall season may complicate the use of litter N:P ratio as an indicator of relative nutrient limitation (*e.g.* Richardson et al., 2008; See et al., 2015; Ji et al., 2018), if phenology is not taken into account during sampling.

Our results imply that weather events leading to premature abscission of autumn leaves (e.g. heavy winds, severe drought, water stress, frosts; Lambers et al., 2008) will result in a larger litterfall P flux relative to N in these forests (i.e. a lower N:P ratio of litterfall flux). Such events would increase P limitation during the following growing season because of lower internal P stores, thereby promoting more intense competition for soil P. Warmer autumn temperatures are leading to a later onset of senescence in northern latitudes (Gill et al., 2015). If delayed senescence causes more frequent premature abscission events due to late-autumn frosts (Norby et al., 2003), the net result would be a higher N:P of annual litterfall flux. Alternatively, warmer autumns could lead to a prolonged period of senescence and more complete resorption (Estiarte and Peñuelas, 2015), resulting in a lower annual N:P of litterfall.

If our results reflect a broader pattern, they may also shed light on the wide range in P resorption efficiencies reported across studies (Aerts and Chapin, 1999). That is, P resorption may appear more variable in part because of its sensitivity to the timing of sampling. This would be especially true of studies sampling litter on the same date along a climatological gradient, as temperature and moisture affect the onset of senescence (Estiarte and Peñuelas, 2015). Indeed, across an elevation gradient of 13 of sites in the White Mountains, variation in green leaf N concentrations were similar to those of P (CV = 12% for both), but variation in litter concentrations were greater in P (CV = 20%) than in N (CV = 15%; data from See et al. (2015) and Yang et al. (2017). We suggest that this may result in part from differences in the phenology of senescence, as all stands were sampled at the same time, despite differences in elevation and thus climate.

Differences in the timing of N and P resorption (Fig. 2) are probably caused by the sequence of physiological changes during leaf senescence, as Rubisco and other chloroplast proteins which collectively account for most of the resorbed N pool (Chapin and Kedrowski, 1983; Makino et al., 1984) are degraded early in the process (Inada et al., 1998). In contrast, nuclear and mitochondrial DNA are late to be catabolized (Mae, 2004); nucleic acids and phospholipids account for 66–85% of resorbed P (Chapin and Kedrowski, 1983). The P in phospholipid cell membranes is also not resorbed until later, as cell structures (chloroplasts, mitochondria, peroxisomes, and vacuoles) remain intact until the late stages of senescence (Krupinska and Humbeck, 2004). Thus, shifting nutrient ratios throughout the season likely reflect the ordered loss of cellular components associated with these nutrients. Although our study includes only three northern hardwood species, it may reflect broader-scale patterns, because the order of organelle catabolism during leaf senescence (beginning with chloroplast breakdown and ending with organelle membranes) has been observed in many distinct

Table 1

Comparison of three models describing the decline in litterfall nutrient concentrations between the first and last collection. Linear model: $C_t = C_i^\circ(1 + x^\circ t)$, where C_t is the proportion of initial nutrient concentrations C_i, remaining at time t (in days), and x is the linear rate of decline in days. Exponential model: $C_t = C_i^\circ e^{-kt}$, where k is the exponential rate of decline in days. Asymptotic exponential model: $C_t = C_i^\circ(A + (1 - A)e^{-kt})$, where A is the asymptote and k is the exponential rate for the declining fraction $(1 - A)$ in days. Statistical significance: $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

| Species and Nutrient	Linear		Simple Exponential		Asymptotic Exponential	
	Coefficient	AIC	Coefficient	AIC	Coeff. & asymptote	AIC
Nitrogen *A. saccharum*	x = −0.016***	−11.7	k = 0.022***	−16.2	k = 0.23*** A = 0.60***	−53
Nitrogen *F. grandifolia*	x = −0.014***	−13.2	k = 0.018***	−16.5	k = 0.16* A = 0.63***	−29.7
Nitrogen *B. alleghaniensis*	x = −0.01***	−23.1	k = 0.012***	−24.6	k = 0.08′ A = 0.69***	−26.7
Phosphorus *A. Saccharum*	x = −0.02***	−6.6	k = 0.032***	−13	k = 0.18** A = 0.48***	−30.8
Phosphorus *F. grandifolia*	x = −0.02***	−4.7	k = 0.031***	−9.5	k = 0.10* A = 0.42***	−16.3
Phosphorus *B. alleghaniensis*	x = −0.015***	−24.5	k = 0.019***	−39.1	k = 0.01 A = −0.53	−37.5
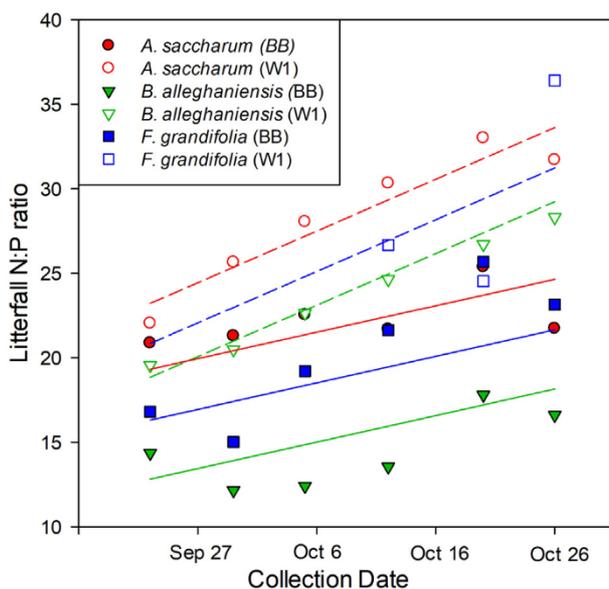
Fig. 2. Litterfall N:P ratios increased throughout the litterfall season in all three study species. The increase was greater at Watershed 1 (dashed lines) than at Bear Brook (solid lines). Lines depict results of multiple linear regression with species-specific intercepts and site-specific slopes.

plant lineages (Smart, 1994; Noodén, 2004). Further studies are needed to confirm these results and quantify the magnitude of the effects of collection timing in other types of ecosystems.

Other explanations for the seasonal decline in litter nutrient concentrations include canopy leaching and effects of canopy position on the progression of leaf senescence, but we suspect that these processes had minor impacts on our results. While nutrient loss from the canopy during rain events undoubtedly occurred, throughfall measurements of N and P at Hubbard Brook showed that leaching during senescence accounts for only ~ 3% of the N and P content in fresh leaves (Ryan and Bormann, 1982), which is a small fraction of the range observed in resorption efficiencies throughout the season (Appendix C). There may be systematic differences in the timing of leaf fall based on canopy position (Koike, 2003), which would lead to differences in litterfall chemistry over time, based on differences between sun and shade leaves (Hollinger, 1989). However, a recent analysis at Hubbard Brook of the species we studied found little variation in foliar N and P concentrations as a function of canopy position (coefficient of variation for N = 2% and for P = 3%; Yang et al., 2016).

Our findings highlight the importance of obtaining a representative sample of litterfall throughout the season when calculating nutrient fluxes. The common approach of sampling for litter chemistry over a short time interval and then multiplying by a mass for the entire season may result in considerable bias. It is unlikely that researchers would choose to collect the very first leaves of the season for chemistry, but even after excluding the first collection the average decline in concentrations across all species and sites was 15 ± 4% for N concentrations and 35 ± 5% for P concentrations. We conducted a sensitivity analysis of N and P flux in sugar maple litter and found that using early-season nutrient concentrations (mean of first two collections) overestimated N flux by 27% and P flux by 58% (Appendix B). Using the two late-season collections was much more accurate, underestimating these fluxes by only 4% and 8%. Collecting litter for chemistry halfway through the litterfall season, and again at the end of the year (i.e. using our 3rd and 6th collections) led to the smallest error, underestimating both N and P fluxes by less than 3%. For perspective, a 5% error in litterfall N flux at Hubbard Brook would be comparable to estimates of annual wet N deposition (Bormann et al., 1977; Yanai et al., 2013). A 10% error in litterfall P flux would amount to ~ 0.4 kg ha^{-1}, or 30% of the estimated annual P accumulation in biomass for the entire ecosystem (Yanai, 1992).

Our results also point to the importance of obtaining a representative leaf litter sample for calculating nutrient resorption. Resorption efficiency is calculated as the difference between green and senesced litter concentrations expressed as a percentage of fresh litter concentrations (Aerts, 1996). Thus, uncertainty in litterfall concentrations will be reflected in uncertainty in estimates of resorption efficiency. In contrast, resorption estimates are probably not as sensitive to the timing of green leaf collection; in the species we studied, N and P concentrations in foliage have been shown to remain nearly constant from the time that leaves are fully expanded until senescence begins (Duchesne et al., 2001). We analyzed the effects of litter collection timing on estimates of resorption efficiency in our study. The difference in resorption efficiency between the highest and lowest litterfall concentrations of the season averaged 19 ± 3% (mean and standard deviation, in units of resorption efficiency) for estimates of N resorption, and 23 ± 3% for P resorption (Appendix C). These ranges are of similar magnitude to the variation in N and P resorption efficiency observed across sites of varying soil fertility (e.g. Boerner, 1984; Côté et al., 2002; See et al., 2015) and therefore deserve attention.

5. Recommendations

For studies in which a homogeneous leaf litter sample is important

(e.g. for leaf decomposition studies), we recommend using leaves that have fallen over a period of days (not weeks). For purposes of calculating litterfall nutrient flux and nutrient resorption efficiency, researchers should collect samples for nutrient concentrations multiple times spanning the litterfall season, distributed across the period of greatest litterfall mass. Decisions about allocating effort to better characterize litterfall chemistry should be made in the context of other sources of variation in litterfall nutrient flux, such as spatial and interannual variability in chemistry and variability in litterfall mass (Yang et al., 2017).

Author contributions

RDY proposed this study and TJF designed and directed the field collections. A decade later, CRS analyzed the samples. CRS led the analysis of the data and the writing of the paper while RDY insisted on exactness in reporting and TJF pushed for closure.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2019.04.017.

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