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Disturbance persistence in managed grasslands: shifts in aboveground community structure and the weed seed bank

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Abstract The length of time and form in which disturbances persist in systems depends on the intensity and frequency of disturbance and on the abilities of resident species to recover from such events. In grazed grasslands, trampling by large mammalian herbivores can periodically facilitate weed establishment by exposing patches of bare ground but whether an intense soil disturbance event results in a temporary increase in weed abundance or a persistent weed problem remains unclear. In May 2002, cattle trampling following heavy rain caused severe damage to nine-month old, rotationally grazed, cool-season pastures (Midwest USA). In September 2002, we compared the aboveground composition of paddocks (i.e., fenced pasture sections) that were heavily disturbed to those that received no damage. Relative to undisturbed paddocks, forage species relative cover was 17% lower in disturbed paddocks, and weed species and bare ground relative cover was 61% and 100% higher, respectively. By September 2004, paddock types did not differ in all aboveground community components. However, the abundance and species richness of weed seeds in the soil seed bank averaged respectively 82% and 30% higher in disturbed paddocks between 2003 and 2004. These findings indicate that a spatially extensive, intense soil disturbance event may soon become undetectable in components of aboveground pasture structure but can persist as an augmented weed seed bank. Because of high weed seed bank longevity, disturbances to formerly disturbed pastures would likely result in higher weed recruitment, with more species represented, than in those which lack previous disturbance. Disturbance history may thus be a useful predictor of weed community composition following subsequent disturbance. Based on empirical data supporting this proposition, we recommend that grassland managers explicitly incorporate disturbance history into dynamic management planning and do not rely exclusively on aboveground characters to evaluate the invasion status or colonization potential of an area by undesirable plants. We emphasize that the ecological legacies of past soil disturbance events cannot only influence the contemporary patterns and processes of grasslands, but importantly, affect their compositional trajectories following subsequent perturbation.

Keywords Ecological legacies · Site history · Community trajectories · Soil seed bank · C3 pasture invasions · Weed recruitment dynamics

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Introduction

The ecological legacies of past disturbance events structure the patterns and processes of contemporary systems and affect future community trajectories (Foster et al. 1997, 1999; Sankaran and McNaughton 1999; Davis and Pelsor 2001). Depending on disturbance frequency and spatial intensity, resident species resiliency and the degree to which edaphic conditions change, disturbances may persist in systems for varying lengths of time and in different forms (Dale et al. 1998; Shea et al. 2004; Suding et al. 2004). The manifestation of disturbance legacy on community dynamics has largely been studied in forest systems, where the effects of past disturbance can persist for decades to several centuries (Bellemare et al. 2002; Chazdon 2003; Kwit and Platt 2003; Uriarte et al. 2004). In grasslands, the long-term effects of historic fire and grazing regimes on community structure are well documented (McNaughton 1983, 1985; Oesterheld and Sala 1990; Smith and Knapp 1999; Keeley et al. 2003; Wilsey and Polley 2003; Altesor et al. 2005; Peco et al. 2005), but few studies explicitly integrate the persistent effects of past soil disturbance events on contemporary dynamics. Failure to consider the potential interactions between site history and a range of possible future disturbances limits community response predictability to perturbation (Fukami 2001) and thus compromises the potential of dynamic management planning.

Pastures, which are managed grazing lands dominated by perennial grasses and forbs, are increasingly being valued as self-sustaining crops because of low energy, fertilizer and pesticide inputs, low rates of soil erosion and nutrient leaching, and a temporal accumulation in soil carbon and nitrogen content (Fales et al. 1993; Pimentel and Kounang 1998; Bakker and ter Heerdt 2005). One of the greatest threats to the sustainability of pastures and other grazed grasslands is the establishment and growth of low palatability weed species (DiTomaso 2000; Tracy et al. 2004; Tracy and Sanderson 2004). Weed invasions can markedly lower their value as grazing lands and rank high among current management issues (Pimentel et al. 2000; Watkinson and Ormerod 2001; Sheley and Krueger-Mangold 2003).

Broadly defined, a disturbance is "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment" (Pickett and White 1985). In rotationally grazed pasture systems, cattle constitute the predominant disturbance force by periodically consuming aboveground vegetative tissue and releasing nutrients via manure and urine. During occasional periods of unusually high soil moisture, cattle trampling can also cause extensive damage to the belowground tissue of desirable forage species, resulting in a matrix of exposed bare ground patches. Given sufficient seed availability, these latter events can facilitate the colonization of grasslands by problematic, opportunistic species that depend on bare ground for successful recruitment (Burke and Grime 1996; Buckland et al. 2001).

In August 2001, we established eight 4–5 ha pastures containing mixtures of C3 forage species in western Illinois and began rotational cattle grazing the following April. In late May 2002, intense cattle trampling following heavy rain occurred in one paddock in each of the eight pastures. The objectives of this study were to assess whether: (1) forage and weed species relative cover and the amount of bare ground initially differed between disturbed and undisturbed paddocks, (2) paddock differences in aboveground community structure persisted through time, and (3) the abundance and species richness of weed seeds in the soil seed bank were higher in disturbed relative to undisturbed paddocks. Following a spatially extensive soil disturbance event, vegetative growth by the perennial forage species may eventually reduce weed establishment sites by occupying available bare ground. However, if an augmented weed seed bank results from an initial increase in weed abundance, then pasture disturbance history may be important in predicting weed recruitment patterns following additional perturbation. Moreover, management plans based only on an evaluation of current aboveground structure will be of limited success if the manifestation of disturbance history in grasslands depends on subsequent environmental and biotic conditions, including those implemented by management.

Methods

Study site

This study took place at the University of Illinois' Orr Beef Research Center in Baylis, Illinois (39.8 N, 90.9 W, Midwest USA), where rolling deep-loess soils (primarily Hapludalfs, Ochraqualfs and Albaqualfs) characterize the property. In August 2001, eight 4–5 ha pastures dominated by tall fescue (*Lolium arundinaceum* (Schreb.) S.J. Darbyshire), Kentucky bluegrass (*Poa pratensis* L.) and red clover (*Trifolium pratense* L.) were treated with glyphosate isopropylamine salt herbicide (1.12 kg a.i. ha^{-1}) and the resulting sod was plowed and harrowed to prepare a seedbed. Seed mixtures consisting of three, five and eight perennial grass and forb species (Table 1) were then sown for a separate biodiversity experiment and allowed to establish for the next 9 months. Forage species establishment was initially deemed successful and rotational grazing of the six, 1 ha paddocks (i.e., fenced pasture sections) in each pasture began in April 2002. In late May 2002, cattle trampling following heavy rain caused large-scale damage to forage species in one paddock in each of the eight rotationally grazed pastures (Fig. 1). Since this time, relatively light grazing, average rainfall and removal of cattle under high soil moisture conditions have contributed to forage species recovery and ensured that another large-scale soil disturbance event did not occur.

Fig. 1 Following heavy rain, cattle trampling damage to 9-month old pastures in May 2002 (picture taken in July 2002; Photo credit: I.J. Renne)

Assessment of aboveground community structure

One month after the cattle trampling event, we recorded bare ground coverage along two randomly placed 50 m transects in one disturbed and one undisturbed paddock in each of the eight pastures. We also measured the aboveground structure of one disturbed and two undisturbed paddocks in each pasture (n = 8 and 16 paddocks, respectively). In each paddock, the amount of bare ground, and percent cover and identity of each forage and weed species were recorded in 6–10, 2 × 0.5 m randomly placed plots. We define weed species as those not originally sown in the forage species mixtures. The relative cover of

Table 1 Composition and seeding rate of three, five and eight forage species mixtures

Species	Common name	Family	Seeding rate (kg ha^{-1})		
			3 Species	5 Species	8 Species
Lolium arundinaceum (Schreb.) S.J. Darbyshire	Tall fescue	Poaceae	13	6	3
Dactylis glomerata L.	Orchard grass	Poaceae	6	2	2
Trifolium repens L.	White clover	Fabaceae	3	1	1
Bromus inermis Leysser	Smooth brome	Poaceae		9	6
Trifolium pratense L.	Red clover	Fabaceae		4	3
Lolium perenne L.	Perennial rye	Poaceae			3
Medicago sativa L.	Alfalfa	Fabaceae			3
Chicorium intybus L.	Chicory	Asteraceae			1
Total seed amount			22	22	22

Tracy and Renne (2005) provide additional seeding and site information the three components of aboveground pasture structure (i.e., bare ground, weed and forage species) summed to 100% for each plot and these measurements were made in September 2002–2004.

Assessment of the weed seed bank

Fifteen soil cores were removed from one disturbed and one undisturbed paddock in each of the eight pastures in March 2003 and 2004 (n = 240 cores per year). Within each paddock, three 32 cm^2 circular cores were taken to a depth of 5 cm at five randomly selected locations. Cores from each location were then placed in a plastic bag and refrigerated at 3°C. After one week of refrigeration, soil from each bag was placed on top of 4 cm of potting soil mixture (1:1:1—soil:peat:perlite) in 30 × 30 × 6 cm germination flats and was distributed to a depth of 0.5 cm. Flats were regularly watered in a greenhouse and the number and species identity of emerged seedlings were periodically recorded and removed for 10 weeks. Average photon flux density was 1,100 μmol s^{-1} m^{-2} at noon and temperature ranged from 32/20 °C under ambient light conditions (14 h light/10 h dark).

Data analysis

The experimental design was a one-way randomized complete-block, with two levels of paddock type (i.e., disturbed and undisturbed; fixed effect) and eight replications. Dependent variables that were measured multiple times on the same experimental unit were analyzed using a repeated measures ANOVA procedure, where we modeled the variance-covariance matrix of the residuals. For this approach, the REPEATED statement in the MIXED procedure of SAS (SAS 2003) was used. The Akaikes Information Criterion and the Schwarzs Bayesian Criterion were used to select the variance-covariance matrix model and degrees of freedom were adjusted using the Kenward-Roger correction (Littell et al. 2002). Data on aboveground relative cover as well as those relating to soil seed bank abundance and species richness were pooled within forage and weed species groups. Between-treatment heteroscedacity of soil seed bank data was eliminated using log-transformations. Paddock differences in the soil seed bank density of the 24 most common weed species were evaluated using t tests with unequal variance (Appendix 1).

Results

Immediately following the May 2002 cattle trampling event, the estimated amount of bare ground was 116% higher in disturbed relative to undisturbed paddocks (P < 0.0001; line transect data). In September 2002, the relative cover of weed species and bare ground was respectively 61% and 100% higher, and that of forage species was 17% lower in disturbed compared to undisturbed paddocks (Fig. 2a–c, P < 0.007 for all comparisons). Through time, differences in all measured components of aboveground pasture structure diminished such that by September 2004, paddocks with differing disturbance histories were indistinguishable based on all aboveground characters (Fig. 2a–c, P > 0.470 for all comparisons).

The respective median abundance and species richness of the weed seed bank was 54% and 20% higher in disturbed relative to undisturbed paddocks in 2003, and 81% and 50% higher in 2004 (estimates based on untransformed data; also see Fig. 3). Boxplot and skewness statistics indicated that weed seed abundance and richness distributions in disturbed paddocks were heavily right-skewed in 2003 but became more uniformly distributed by 2004 (data not shown). In addition, weed seed abundance and species richness were 54% and 32% higher in 2004 compared to 2003 (P ≤ 0.012 for each comparison of log-transformed data). The estimated germinable weed seed bank in disturbed and undisturbed paddocks over the 2 years respectively averaged 4,980 ± 1,070 and 1,830 ± 1070 seeds m^{-2} (1 SE). These consisted primarily of non wind-dispersed species (Appendix 1). Seeds of forage species accounted for 13% of the soil seed bank and did not differ between paddock types (P > 0.860, linear contrast).

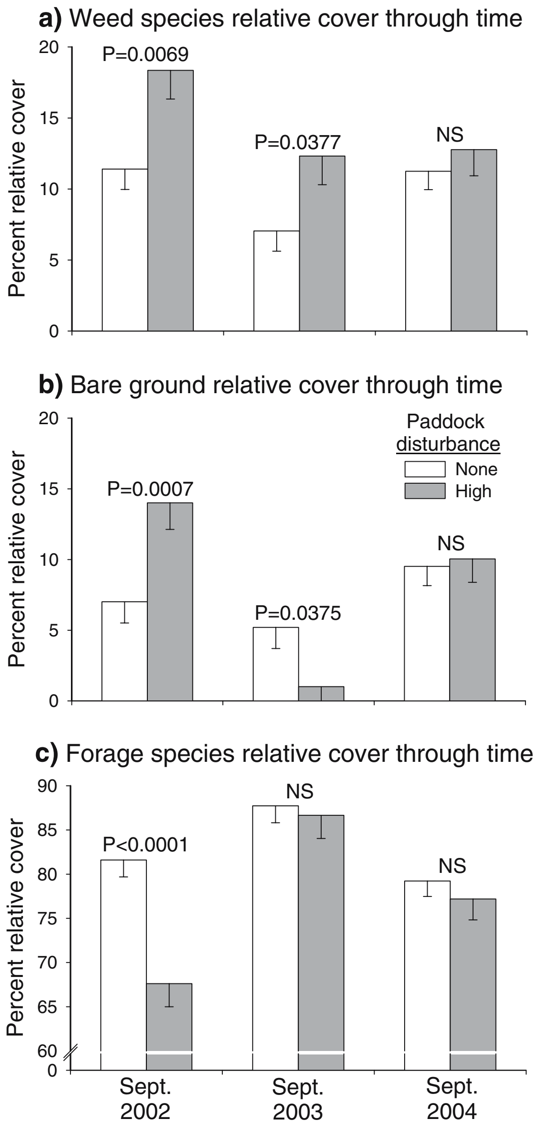

Fig. 2 The relative cover of (a) weed species, (b) bare ground and (c) forage species in disturbed and undisturbed paddocks in September 2002–2004. Means – 1 SE are given. *P*-values indicate level of statistical significance between disturbed and undisturbed paddocks; NS = $P > 0.05$

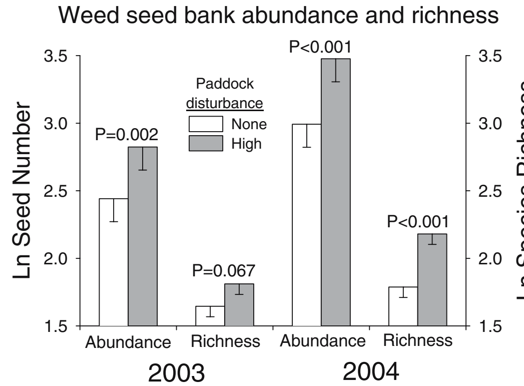

Fig. 3 Abundance and species richness of germinable weed seeds in the soil seed bank of disturbed and undisturbed paddocks. Means –1SE are given. *P*-values indicate level of statistical significance between disturbed and undisturbed paddocks

Discussion

Post-disturbance shifts in aboveground community structure and the weed seed bank

Differences in all aboveground components of the pasture community diminished following the spatially extensive soil disturbance event such that after 1.5 years, previously disturbed and undisturbed paddocks were indistinguishable based on aboveground characters. This resiliency was driven primarily through the vegetative encroachment of bare ground by forage species, as this group was poorly represented as seedlings (pers. obs.) and in the soil seed bank (also see Tracy and Sanderson 2000). However, the 2 years of greater coverage by weed species in disturbed paddocks (Fig. 2a) resulted in a weed seed bank that remains locally augmented in both seed number and species richness (Fig. 3). In addition, as weed seed bank abundance and richness increased in disturbed paddocks, their spatial distribution became more uniform through time. Given the potential for high seed bank longevity among many weed species (Davis et al. 2005), disturbances to formerly disturbed pastures would likely result in greater weed recruitment, with more species represented, than in those without previous disturbance. Pasture disturbance history may thus be useful in predicting the composition and abundance of the weed community following subsequent perturbation. These findings highlight the importance of disturbance history as a potential driver of grassland community dynamics and suggest the aboveground structure of contemporary systems might be a poor indicator of their invasion status or colonization potential by undesirable plants.

Management implications

Results presented here indicate the potential for weed recruitment in pastures increases if prior disturbance events result in an augmented weed seed bank. However, the realization of this problem depends heavily on the degree to which weed populations are limited by the availability of seeds and establishment safe sites (Harper 1977; Eriksson and Ehrlén 1992; Kalamees and Zobel 2002). Whereas recruitment limitation in grasslands has been attributed exclusively to low seed numbers (Tilman 1997; Turnbull et al. 2000; Seabloom et al. 2003), it is frequently a combination of limited seed and microsite availabilities that constrains recruitment (Zobel et al. 2000; Foster 2001; Austrheim and Eriksson 2003; Foster et al. 2004; Eskelinen and Virtanen 2005; Zeiter et al. 2006). Management that affects the spatial and temporal occurrence of suitable establishment sites, particularly in areas of high seed abundance, thus has high potential of affecting subsequent recruitment patterns.

In our system, the decline in weed species relative cover despite weed seed bank augmentation indicates microsite limitation is driving recruitment. Otherwise, temporal trends in weed cover should have remained the same or increased with increases in weed seed number and species richness. Average precipitation, low grazing intensity and no significant soil disturbance events over 2.5 years likely contributed to this decline (Tracy and Renne 2005). We add that in September 2003, the relative cover of forage species did not differ between paddock types but otherwise available bare ground was occupied by more weeds in disturbed paddocks (Fig. 2). Weed seed availability thus remains important to the weed recruitment dynamics of this system.

In addition to recruitment limitations, the growth, survival and reproductive success of established seedlings depends on how species-specific attributes interact with the spatial and temporal availabilities of above-and belowground resources (Higgins and Richardson 1998; Davis et al. 2000; Woitke and Dietz 2002; Tilman 2004). Renne et al. (2006) found that simulated cattle trampling in pastures facilitated the growth of established weed seedlings and recruitment of those emerging from seed, but that these effects diminished or reversed, depending on the local resident composition and the availability of water and soil nutrients. Moreover, they suggested that grazing intensity, neighborhood composition, soil resource availability and disturbance patch size are inextricably linked to grassland invasibility by mediating above- and belowground resource availability. The manifestation of disturbance history on weed demographics thus depends not only on the prevailing environmental conditions (Cleland et al. 2004), but importantly on subsequent biotic processes (e.g., priority effects, competitive outcomes, local propagule pool), including those implemented by management (e.g., grazing intensity, nutrient inputs and soil disturbance).

The fundamental question that remains is whether future disturbance regimes will differentially affect weed recruitment patterns in areas with different disturbance histories. We tested this by simulating levels of cattle trampling intensity in previously disturbed and undisturbed paddocks. We found that weed recruitment did not differ between paddock types when subjected to low soil disturbance intensity, but that moderate and high intensity disturbance caused a greater number and diversity of established weeds in previously disturbed paddocks (Renne and Tracy unpubl. data). The effect of disturbance history on weed recruitment patterns therefore depends heavily on the quality of subsequent perturbation.

There are several ways that managers can reduce the potential realization of persistent weed problems. First, newly renovated or restored grasslands are particularly vulnerable to trampling damage by large mammals because their poorly developed root systems compromise their ability to quickly recover from tissue damage. As such, managers should avoid excessive damage to these young systems to limit initial weed recruitment opportunities. Second, sowing and maintaining a functionally diverse, evenly distributed assemblage of grassland species can stabilize productivity at relatively high levels and reduce the incidence of undesirable plants (Naeem et al. 2000; Wilsey and Polley 2002; Tracy and Sanderson 2004; Tracy et al. 2004; Fargione and Tilman 2005; Tilman et al. 2006).

Communities containing species which differ in resource use phenology may be particularly effective in reducing temporal resource availability and hence, invasion opportunities (Tilman 2004; Hooper et al. 2005). Consideration should also be given to sowing species with a high capacity for colonizing bare ground via vegetative growth so that the number of potential establishment sites is reduced (e.g., white clover *Trifolium repens* L. in cool-season pastures; Tracy and Renne 2005). We note that this latter approach may not be best in restoration projects designed to maximize the long-term potential of grassland diversity, as microsite availability can drive local diversity patterns (Foster et al. 2004).

Lastly, these findings highlight the importance of managing disturbance in areas where past events contributed to high weed abundance, even if the events are not currently detectable in aboveground community structure. Our results indicate that previous disturbance which results in weed seed bank augmentation increases pasture vulnerability to weed recruitment, but subsequent soil disturbance may need to be of sufficient intensity to elicit a recruitment response. Other factors that can interact with soil disturbance intensity to affect the quality and availability of recruitment microsites include grazing intensity, soil resource availability and resident species composition (Foster 2001; Woitke and Dietz 2002; Austrheim and Eriksson 2003; Huston 2004; Milbau et al. 2005; Renne et al. 2006). If events promoting an initial increase in weed abundance occur in renovated or restored grasslands, managers should subsequently avoid high intensity grazing and soil disturbance to minimize weed recruitment opportunities.

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Appendix

Table 2 Unsown weed species with average soil seed bank densities > 20 seeds m^{-2}

Species[a]	Common name	Seeds m^{-2}		*P*-value[c]	Primary dispersal by wind
		Disturbed paddock[b]	Undisturbed paddock[b]		
Mollugo verticillata L.	Carpetweed	1540 ± 545	178 ± 545	*	No
Poa annua L.	Annual bluegrass	513 ± 128	332 ± 128	NS	No
Taraxacum officinale G.H. Weber ex Wiggers	Common dandelion	273 ± 147	319 ± 147	NS	Yes
Capsella bursa-pastoris (L.) Medik.	Shepherd's purse	280 ± 121	176 ± 121	NS	No
Oxalis stricta L.	Yellow oxalis	224 ± 29.8	193 ± 29.8	NS	No
Amaranthus retroflexus L.	Redroot amaranth	329 ± 94.0	15.6 ± 94.0	**	No
Veronica peregrina L.	Purslane speedwell	246 ± 92.3	92.5 ± 92.3	NS	No
Cyperus esculentus L.	Yellow nutsedge	281 ± 86.8	27.3 ± 86.8	****	No
Setaria faberi Herrm.	Giant foxtail	173 ± 98.4	2.60 ± 98.4	NS	No
Plantago major L.	Common plantain	105 ± 44.3	44.3 ± 44.3	NS	No
Chenopodium album L.	Lambsquarters	95.1 ± 35.0	26.0 ± 35.0	NS	No
Polygonum pensylvanicum L.	Pa. smartweed	65.1 ± 38.2	56.0 ± 38.2	NS	No
Digitaria sanguinalis (L.) Scop.	Large crabgrass	97.7 ± 20.1	14.3 ± 20.1	***	No
Verbena hastata L.	Blue vervain	39.1 ± 22.0	71.6 ± 22.0	NS	No
Setaria glauca (L.) Beauv.	Yellow foxtail	83.3 ± 22.5	18.2 ± 22.5	***	No
Euphorbia nutans Lag.	Nodding spurge	52.1 ± 14.4	23.4 ± 14.4	*	No
Conyza canadensis (L.) Cronq.	Canadian horseweed	26.0 ± 9.14	28.7 ± 9.14	NS	Yes
Verbena stricta Vent.	Hoary verbena	30.0 ± 8.61	24.7 ± 8.61	NS	No
Ambrosia artemisiifolia L.	Common ragweed	35.2 ± 19.6	18.2 ± 19.6	NS	No
Amaranthus rudis Sauer	Common waterhemp	48.2 ± 31.9	2.60 ± 31.9	NS	No

Table 2 continued

Species[a]	Common name	Seeds m^{-2}		*P*-value[c]	Primary dispersal by wind
		Disturbed paddock[b]	Undisturbed paddock[b]		
Amaranthus spinosus L.	Spiny amaranth	46.9 ± 29.9	0.0 ± 29.9	NS	No
Digitaria ischaemum (Schreb.) Schreb. ex Muhl.	Smooth crabgrass	44.3 ± 14.1	2.60 ± 14.1	**	No
Echinochloa crus-galli (L.) Beauv.	Barnyardgrass	37.8 ± 13.4	7.81 ± 13.4	*	No
Rumex crispus L.	Curly dock	32.6 ± 10.3	10.4 ± 10.3	**	No

[a] Taxonomy follows Uva et al. (1997).

[b] Note that back-transformed soil seed bank data do not equal those found in Fig. 2, because $\mathrm{Ln}(\bar{x}) \neq \sum \mathrm{Ln}(x_i)/n$

[c] Results of *t* tests with unequal variance using log-transformed data for each species. NS = $P \geq 0.10$; * = $0.10 > P \geq 0.05$; ** = $0.05 > P \geq 0.01$; *** = $0.01 > P \geq 0.001$; **** = $0.001 > P \geq 0.0001$

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