Land management practices interactively affect wetland beetle ecological and phylogenetic community structure

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Abstract. Management practices can disturb ecological communities in grazing lands, which represent one-quarter of land surface. But three knowledge gaps exist regarding disturbances: disturbances potentially interact but are most often studied singly; experiments with multiple ecosystems as treatment units are rare; and relatively new metrics of phylogenetic community structure have not been widely applied. We addressed all three of these needs with a factorial experiment; 40 seasonal wetlands embedded in a Florida ranch were treated with pasture intensification, cattle exclosure, and prescribed fire. Treatment responses were evaluated through four years for aquatic beetle (Coleoptera: Adephaga) assemblages using classic ecological metrics (species richness, diversity) and phylogenetic community structure (PCS) metrics. Adephagan assemblages consisted of 23 genera representing three families in a well-resolved phylogeny. Prescribed fire significantly reduced diversity one year post-fire, followed by a delayed pasture × fire interaction. Cattle exclosure significantly reduced one PCS metric after one year and a delayed pasture × fence × fire interaction was detected with another PCS metric. Overall, effects of long-term pasture intensification were modified by cattle exclosure and prescribed fire. Also, PCS metrics revealed effects otherwise undetected by classic ecological metrics. Management strategies (e.g., "flash grazing," prescribed fires) in seasonal wetlands may successfully balance economic gains from high forage quality with ecological benefits of high wetland diversity in otherwise simplified grazing lands. Effects are likely taxon specific; multiple taxa should be similarly evaluated.

Key words: cattle grazing; disturbance; diversity; NRI; NTI; pasture intensification; phylogenetic community structure; prescribed fire; richness; seasonal wetland.

Introduction

Disturbance is essential to community ecology as a mechanism causing changes in space and time, and as a process to understand in conservation and restoration ecology (Sousa 1984, Pickett and White 1985, Temperton et al. 2004). Based on decades of experiments and quantification of disturbed communities, including studies within ecosystems and whole-ecosystem treatments, we know that disturbance can reduce biological diversity within affected communities (e.g., Cairns et al. 1976, Winner et al. 1980, Sousa 1984, Pickett and White 1985, Webster et al. 1992, Temperton et al. 2004, Chase 2007).

A general and useful definition of disturbance for community ecology derives from hierarchy theory, where disturbance is a change to community membership caused by a factor external to the community (Pickett et al. 1989). Also, studies of disturbance need to be explicit in spatial and temporal scales used, and those scales should match the studied system (Connell et al.

1997, Peterson et al. 1998). Here we address disturbance effects in multiple natural communities over the course of four years. We compare several measures of change in community membership. Communities likely exist in a larger metacommunity, but this was a community-scale study; we did not study dispersal among communities or experimentally treat replicate metacommunities.

Multiple disturbances affect natural communities, but most studies focus on one such factor, so that comparatively less is known about effects of multiple, interacting disturbances (Seifan et al. 2012). For example, fertilizers, herbivory, and prescribed fire are commonly applied to manage grazing lands, which are "the single most extensive form of land use on the planet" and represent 25% of global land surface, ignoring Antarctica (Asner et al. 2004). While the effects of each factor on natural communities in rangelands have been studied separately or in pairs (e.g., Rogler and Lorenz 1957, Perevolotsky and Seligman 1998, Collins and Smith 2006), potential interactions between all three have not been studied prior to this experiment.

If disturbance is a change to community membership, effects should be revealed in diversity. Diversity of an assembled community has been studied in progressively more refined terms; a spectrum of metrics now exists

that vary in age and evidence (Magurran 1988, Jost 2006). We address alpha diversity here; beta diversity and similarity indices answer different questions. Recent metrics include phylogenetic community structure (PCS), which assess distribution of an assemblage in a clade (reviewed by Webb et al. 2002). An assemblage clustered within a clade indicates habitat filtering of similar adaptive responses to habitat conditions, whereas an assemblage that is overdispersed (more than random) indicates repulsion among species by biotic interactions (Webb et al. 2002, Vamosi et al. 2009). Phylogenetic community structure may complement ecological metrics to better reveal community responses to disturbance (Helmus et al. 2007, Dinnage 2009, Ding et al. 2012, Banks et al. 2013). One goal of this work was to compare PCS and classic ecological measures of alpha diversity, including their responses to disturbances.

We report here on a planned, controlled experiment that evaluated interactive disturbance effects on multiple natural communities through multiple years. The factorial experiment used isolated, seasonal wetlands in a Florida cattle ranch as experimental units. The wetlands are small enough (~1 ha) to enable whole-ecosystem manipulations of three interacting treatments with well-documented individual effects: cattle exclosure, prescribed fire, and addition of nutrients and changes in hydrology due to pasture intensification (Myers and Ewel 1990, de Szalay and Resh 1997, Clark and Wilson 2001, Main and Barry 2002, Hornung and Rice 2003, Steinman et al. 2003, Gathumbi et al. 2005, Marty 2005, Boughton et al. 2010). We studied aquatic beetle assemblages (Coleoptera: suborder Adephaga); the aquatic beetles assemble anew each year in this system because wetlands are dry for several months and the beetles require aquatic habitat. The actively flying and diverse aquatic beetle assemblages in the wetlands offered the chance to study repeated community assembly from one regional source pool through multiple years. Aquatic beetles are typically a substantial component of aquatic invertebrate fauna, used widely to indicate water quality. Thus we expected adephagan beetles to represent a suitable study system: they readily reassemble to reflect current conditions, and are potentially diverse and sensitive to the multiple disturbances applied through several years.

We hypothesized that cattle exclosure (i.e., release from grazing effects) and prescribed fire (i.e., shift in vegetation structure) would mitigate pasture intensification effects on aquatic beetle assemblages. Both cattle exclosure and prescribed fire were expected to affect aquatic beetle assemblages indirectly by effects on vegetation (Gioria et al. 2010), or perhaps by direct effects, or both. For cattle exclosure and prescribed fire, we expected beetle assemblages to become more phylogenetically dispersed because habitat filtering should relax as a result of release from cattle grazing (trampling, wastes, vegetation mulching) in wetlands and successional shifts in vegetation structure. However,

we expected the effects of fencing and fire to depend on the pasture type, reflecting an interactive effect of pasture intensification. Prescribed fires are applied intermittently in rangelands; fire was applied once during the four-year study interval of this experiment to constitute a pulse treatment (Bender et al. 1984). In contrast, the permanent installation of fencing to exclude cattle constituted a persistent, press effect (Bender et al. 1984), again consistent with ranching practices. We assumed that: (a) the sum of all species collected in all experimental wetlands represents the regional species pool; (b) adephagan genera display ecological trait conservatism (Cavender-Bares et al. 2009, Lessard et al. 2009, Vamosi et al. 2009); (c) the phylogeny used represents accurate relationships, and; (d) adephagan aquatic beetle assemblages in the study system are not dispersal limited and behavioral habitat selection is generally important (Ribera and Vogler 2000, Binckley and Resetarits 2005, Yee et al. 2009).

METHODS

Study system and experimental design

The experiment was conducted at the MacArthur Agro-Ecology Research Center (MAERC), a 4170-ha working cattle ranch in south-central Florida that has >600 wetlands, and is managed by Archbold Biological Station (Appendix A). Seasonal wetlands are embedded in intensively managed or seminatural pastures. Intensively managed pastures were fertilized annually (1960s–1986) with N, P, and K, and continue to be fertilized annually with N. For effects on aquatic beetle diversity, we considered effects of nutrient supply most important, though intensively managed pastures were also extensively ditched, disced, and replanted with nonnative Bahia grass, *Paspalum notatum*, and grazed in the summer. Wetland vegetation in these pastures is dominated by soft rush (*Juncus effusus*). In contrast, seminatural pastures have never been fertilized, have fewer ditches, are grazed in the winter, and embedded wetlands are dominated by an assortment of native vegetation, including sedges, maidencane (*Panicum hemitomon*), and other emergent macrophytes. Please see Boughton et al. (2010) and Boughton et al. (2011) for additional details.

Wetlands of similar sizes (0.5–1.5 ha) were assigned to one of all possible treatment combinations (pasture intensification × cattle exclosure × fire) in a full-factorial, randomized block design, where blocks were analyzed as random factors because they accounted for spatial variation and sample timing. The experimental design provided five replicates of each of eight treatment combinations, arrayed in five spatial blocks across the ranch. Samples were collected from 40 wetlands at MAERC in September 2006, September 2008, and July 2009 (see Plate 1); sample timing related to flooding of the seasonal wetlands, and a severe drought in 2007 prevented sampling for aquatic beetles. A set of 2006 samples for one wetland was lost; analyses here are

based on 39 wetlands. The 2006 samples reflected only pasture intensification (seminatural vs. intensively managed). After the 2006 samples were collected, 20 wetlands were fully fenced to exclude cattle. Prescribed fire was applied to 20 wetlands in winter 2007, and samples were collected in the wet seasons of 2008 and 2009 to reflect the full combination of all three treatments.

Five geo-referenced sample locations were randomly placed in each wetland in a stratified-random design (central plus four quadrants, much like sampling the middle of and each quarter of a donut) to account for spatial heterogeneity during sample collection in the wetland basins. Sample locations were moved to new random locations within wetlands each year. Aquatic beetles were sampled with standardized, 1-m sweeps using a 0.5-mm mesh D-frame dip net, where two sweeps were collected at random directions and distances (≤ 5 m) from sample locations; 10 samples were collected per wetland. Organisms were preserved in 70% isopropanol until identification using Epler (1996) and Merritt and Cummins (1996). Data were analyzed per wetland to permit comparison of PCS metrics (based on a complete species list) to classic ecological metrics (e.g., total species richness and abundance per the 10 samples). Voucher specimens were deposited in the Stuart M. Fullerton Collection of Arthropods at the University of Central Florida (UCFC).

Phylogenetic analyses

We reconstructed a phylogeny for the aquatic adephagans collected in our study based on three loci with differing rates of nucleotide evolution: nuclear small-subunit ribosomal RNA (18S rRNA), mitochondrial 16S rRNA, and mitochondrial cytochrome c oxidase subunit I (COI). Sequence data were acquired from GenBank for 18 aquatic adephagan genera (Appendix B). Five of six sampled genera (*Andocheilus*, *Bidessonotus*, *Brachyvatus*, *Neobidessus*, and *Uvarus*) in the dytiscid tribe Bidessini did not have sequences in GenBank. This monophyletic tribe consists of very closely related genera (Miller et al. 2006, Ribera et al. 2008); we treated bidessinid genera as a polytomy by assigning the five genera the same sequences as the one genus (*Liodessus*) with GenBank sequences.

Each gene partition was aligned with MUSCLE (Edgar 2004) using default parameters and then concatenated using MacClade (Maddison and Maddison 2005). The best-fit model was determined using MrModelTest (Nylander 2008), which found GTR+I+G as the best model for each partition. Data were analyzed in a mixed-model partitioned Bayesian framework in MrBayes ver 3.1.1 (Huelsenbeck and Ronquist 2001). Bayesian analyses were conducted using four independent runs, each running 5 million generations and saving trees every 1000 generations. Convergence of the runs was measured in Tracer (Rambaut and Drummond 2007), and 25% were discarded as burn-in. MrBayes was used to summarize the data and to generate posterior probability values. Graphical manipulation of the phylogenetic tree was done in Mesquite (Maddison and Maddison 2009).

Measuring diversity

We evaluated adephagan aquatic beetle assemblages with classic ecological metrics and phylogenetic community structure (PCS) metrics. Classic ecological metrics were genera richness and expected number of genera $D = e^{H'}$, where $H' = -\Sigma(p_i)(\ln p_i)$ and $p_i =$ the proportional abundance of genus i (Jost 2006). Genus-level analyses for both ecological and phylogenetic metrics were more valid than species-level analyses because some adephagan larvae can not be morphologically identified to species, and molecular sequences are not available beyond genus. Genus-level analyses thus made both sets of measures directly comparable and defensible.

Phylogenetic metrics were phylogenetic diversity (PD), net relatedness index (NRI), and nearest taxon index (NTI). PD measures the nodes or branch lengths among sampled taxa in a site on the larger phylogeny of the taxa from all samples, and the value of PD increases with both species richness and phylogenetic distance between species (Faith 1992). NRI and NTI are standardized indices for calculating phylogenetic relatedness, and so can be used to test for differences among treatments and directly measure the phylogenetic structure of samples within a treatment (Webb et al. 2002). NRI is calculated from the mean phylogenetic distance (MPD; i.e., a measure of the phylogenetic distance (nodal or branch length) between each taxon and every other terminal taxon in the sample) and standardized by the standard deviation of the null distribution. The null distribution was produced by 1000 random iterations of the independent swap algorithm (Gotelli and Entsminger 2003), which has a low Type I error rate but is sensitive to patterns of nonrandom phylogenetic community structure using NRI/NTI (Kembel 2009). NTI is calculated similarly, except that it is a standardized measurement of mean nearest taxon distance (MNTD; i.e., mean phylogenetic distance between each sample taxa and its closest related neighbor in the sample). Positive values of NRI and NTI indicate phylogenetic clustering of a sample, whereas negative values indicate overdispersion. NRI is more sensitive than NTI to clustering at higher taxonomic levels, while NTI is relatively more sensitive to clustering at lower taxonomic levels. Phylogenetic community structure metrics were calculated using Phylocom (Webb et al. 2008) based on the phylogenetic tree generated here.

Statistical analyses

The 2006, 2008, and 2009 results were analyzed separately because aquatic beetles re-assemble annually in the seasonal wetlands and because treatments were
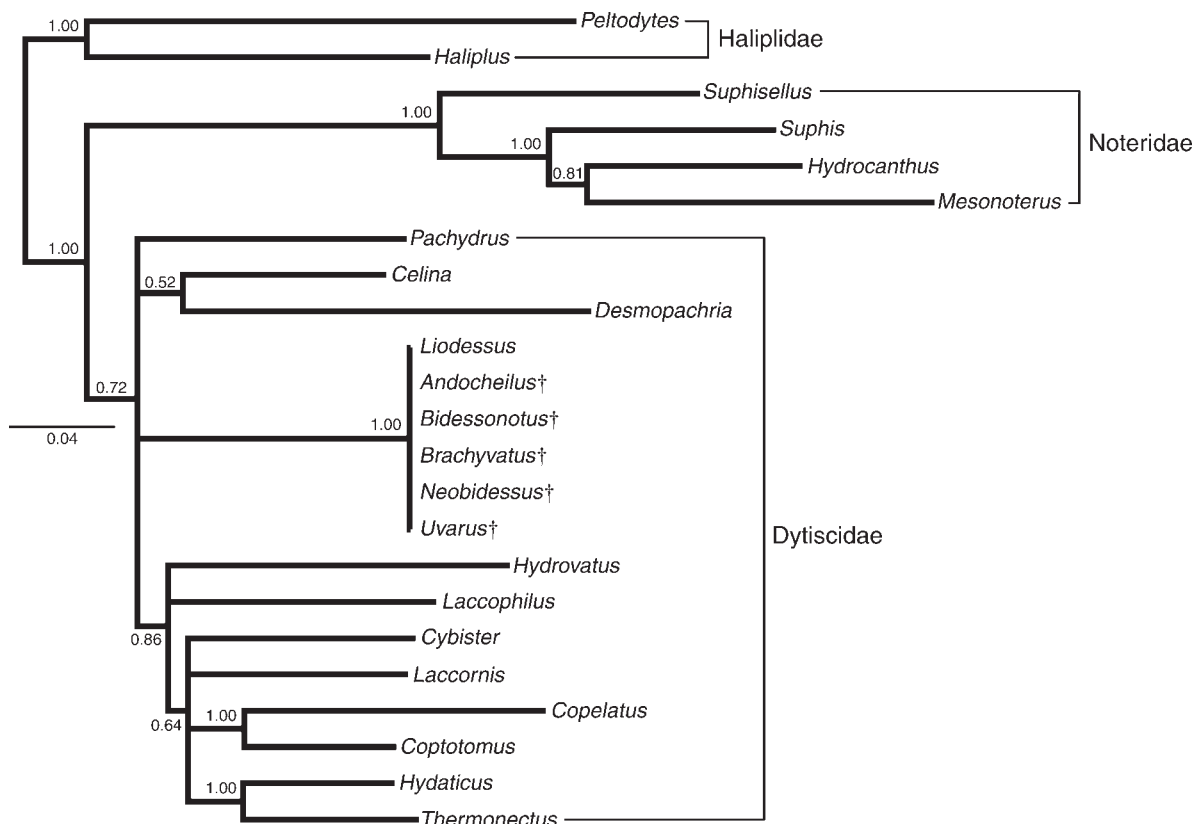
Fig. 1. Unrooted Bayesian phylogram of adephagan aquatic beetles based on 18S, 16S, and COI genes. Numbers shown above the nodes are posterior probability values. Average posterior probability = 0.86.
† Liodessus was used for all genera in the Bidessini (see Appendix B for Genbank accession numbers).

temporally sequenced. The 2006 data were analyzed for the existing pasture and block treatments. The 2008 and 2009 results (representing all three treatments) were analyzed by calculating the difference for each wetland beetle assemblage from the value obtained in 2006. This approach accounted for initial variation among wetlands recorded in 2006 (Underwood 1994).

Data were analyzed for treatment effects using a mixed-effects model with lme in the nlme package (R Development Core Team 2013), where the most complex model possible was: response = pasture × fenced × burned, random = ~1 | block. This model matched the experimental design, where treatments were added incrementally during the study period (i.e., pasture and blocks in 2006, fencing in 2007, prescribed fire in 2008). Marginal and conditional coefficients of determination (R^2) were calculated for each model using the r.squaredGLMM function in the MuMIn package, based on the lmer function in the lme4 package (Bartoń 2014, Johnson 2014). A marginal R^2 represents fixed effects, whereas a conditional R^2 represents both fixed and random (here block) effects; by difference, one can infer R^2 due to random effects alone. The lme and lmer functions yielded identical model results for fixed and random effects; lme permitted significance values for

model terms, whereas lmer permitted R^2 calculation. Following Crawley (2007), model simplification was used for each response variable to best reveal treatment and interaction effects with appropriate P values. In addition, NRI and NTI values were tested (where appropriate) for significant phylogenetic structure (i.e., different from random) using a one-sample t test.

RESULTS

Phylogenetic analyses

A total of 23 genera in three adephagan families (2 Haliplidae, 4 Noteridae, 17 Dytiscidae) were collected from the wetlands during the experiment (see Plate 1). The consensus tree from the Bayesian analysis recovered all three families of adephagan water beetles as monophyletic (Fig. 1). The relationships among families and genera were generally consistent with existing phylogenies (Ribera et al. 2002, 2008, Hunt et al. 2007). The clade was generally well resolved (mean of posterior probabilities = 86%).

2006: Pasture intensification only

Surprisingly, adephagan assemblages in wetlands did not respond significantly to pasture differences for any of the ecological or phylogenetic metrics (Table 1). As a

TABLE 1. Summary of ANOVA results for 2006, and the changes from 2006 to 2008 and 2006 to 2009.

Study year	Treatment	No. genera	D	PD	NRI	NTI
2006	pasture	0.12	0.87	0.11	0.78	0.93
	model R^2	0.04, 0.38	<0.01, 0.31	0.04, 0.37	<0.01, <0.01	<0.01, <0.01
2008	pasture	0.26	0.87	0.28	0.51	0.27
	fence	0.91	0.58	0.61	0.90	**0.03**
	fire	**0.02**	0.54	**0.02**	0.98	0.48
	model R^2	0.14, 0.24	0.02, 0.02	0.14, 0.24	0.01, 0.01	0.14, 0.14
2009	pasture	0.40	0.87	0.38	0.66	*0.08*
	fence	0.88	0.68	0.79	0.88	0.76
	fire	0.30	0.89	0.25	0.11	0.95
	pasture × fence	0.22	0.39	*0.056*	0.42	*0.09*
	pasture × fire	*0.09*	**0.01**	**0.05**	0.23	0.57
	fence × fire	0.30	0.53	0.16	0.58	0.62
	pasture × fence × fire				**0.02**	*0.06*
	model R^2	0.12, 0.42	0.18, 0.29	0.16, 0.43	0.24, 0.24	0.22, 0.22

Notes: Values listed are probabilities of effect per treatment, where significant effects ($P \leq 0.05$) are in boldface type; marginal effects ($0.05 < P < 0.10$) are italicized. Only pasture treatments were applied in 2006. Interaction terms are not listed for 2008 because effects were less than marginal and model simplification was used to better estimate individual effects in those cases (Crawley 2007). The same condition applied to the three-way interaction for number of genera, D, and PD in 2009. Model coefficients of determination (R^2) were calculated for fixed and total effects (Johnson 2014), based on factors listed per year. Listed R^2 values are fixed, then total (random + fixed). PD is phylogenetic diversity; NRI is net relatedness index; NTI is nearest taxon index.

result, the fixed pasture effect generally contributed little to R^2 values. Random blocks contributed to R^2 values among ecological metrics (and PD, which generally responded similarly to genera richness), but did not contribute to phylogenetic metrics (NRI, NTI; Table 1). Thus spatial heterogeneity represented by blocks was more important to adephagan beetle diversity than were pasture effects before fence and fire treatments were applied.

2008: Pasture intensification, cattle exclosure, and fire

Fences were installed >1 year before 2008 sampling and prescribed fires were applied in the preceding dry season. Effects of cattle exclosure and fire on genera richness, PD, and NTI were observed in 2008, but no treatment interactions occurred yet (Table 1). Pasture effects again remained unimportant for all metrics, consistent with 2006 results. Models with significant fixed effect terms in 2008 represented 24% of total variation in adephagan assemblages among the 40 wetlands (Table 1), though fixed effects represented 14%.

Prescribed fires in the 2007–2008 dry season significantly ($P = 0.02$) reduced genera richness and PD of aquatic beetles in wetlands during the 2008 wet season, compared to 2006 samples (Table 1, Fig. 2A). In contrast, unburned wetlands did not significantly change for the same metrics. Other metrics in 2008 were not significantly affected by prescribed fire.

Cattle exclosure significantly ($P = 0.03$) decreased adephagan NTI in 2008 relative to 2006 (Table 1). Assemblages in fenced wetlands typically became more phylogenetically dispersed, whereas assemblages in unfenced wetlands remained essentially the same in phylogenetic clustering (Fig. 2b). More subtle effects underlie this overall net effect. Cattle exclosure shifted random NTI values in both pasture types (2006;

intensively managed $P = 0.16$; seminatural $P = 0.35$) to become significantly overdispersed in 2008 (intensively managed $P = 0.05$; seminatural $P = 0.03$). In contrast, beetle assemblages in unfenced wetlands trended in the opposite direction; they had tended to overdispersion in 2006 (NTI; $P = 0.09$), but became random (NTI; $P = 0.40$) in 2008. The net result of the opposing trends generated the significant effect of cattle exclosure on NTI in 2008 (Fig. 2B), where the fence-based decrease caused NTI scores to change from being significantly clustered in 2006 ($P = 0.01$) to become random in 2008 ($P = 0.31$).

2009: Pasture intensification, cattle exclosure, and fire

In contrast to 2008, individual treatments did not significantly affect 2009 adephagan assemblages; instead interactions among treatments arose for some metrics. Marginal effects were observed in the 2006–2009 change for pasture on NTI ($P = 0.08$) and fire on NRI ($P = 0.11$), but no simple effect of cattle exclosure emerged (Table 1). Instead, cattle exclosure only had a marginal interaction with pasture intensification to affect the 2006–2009 change in PD and NTI. Models with significant fixed effect terms in 2009 represented up to 43% of total variation, and fixed effects represented 16–24% (Table 1).

Fire significantly ($P = 0.01$) interacted with pasture intensification to affect adephagan D and PD (Table 1, Fig. 3). Fire × pasture interaction also marginally affected the 2006–2009 change in genera richness (Table 1).

A pasture × fence × fire interaction significantly affected the 2006–2009 difference in NRI ($P = 0.02$; Fig. 4) and marginally affected NTI ($P = 0.06$; Table 1). Fenced and burned wetlands in seminatural pastures became more clustered than those in intensively managed pastures, while non-fenced and burned wetlands in seminatural pastures became more overdis-
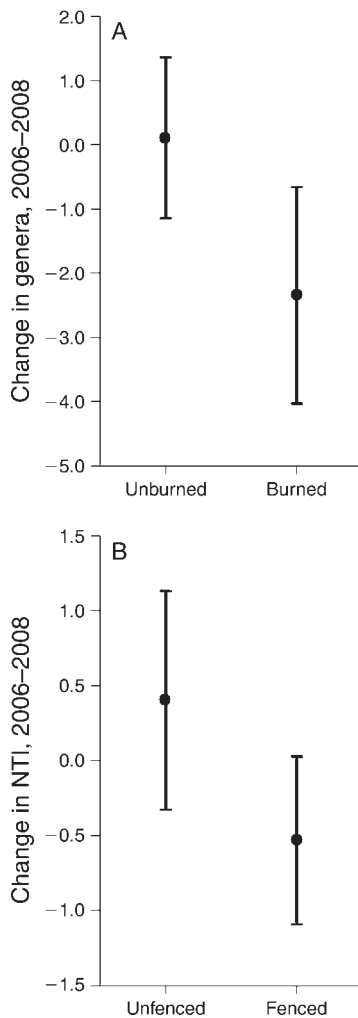
FIG. 2. (A) Mean genera richness decreased ($P = 0.027$) as a result of fire between 2006 and 2008. Phylogenetic diversity (PD) had very similar results. (B) Mean nearest taxon index (NTI) decreased ($P = 0.042$) from weakly clustered (i.e., slight positive pattern) to negative (i.e., overdispersed). Error bars in both plots represent 95% confidence intervals.

persed than those in intensively managed ones. Fenced and non-burned wetlands in both pasture types changed little, while non-fenced and non-burned wetlands in seminatural pastures became more clustered than those in intensively managed pastures. Overall, phylogenetic clustering occurred most in seminatural pastures that were fenced and burned, and in intensively managed pastures that were not fenced and burned. The new treatments (fence and fire) added to intensively managed pastures shifted aquatic beetle assemblages from random NTI in 2006 to become overdispersed in 2009 ($P = 0.02$).

DISCUSSION

Our results indicate that some land management practices may conserve regional biodiversity while serving economic needs of ranchers. Grazing land management practices imposed simple effects at first, with delayed interactive effects. Cattle exclosure and prescribed fire directly and/or indirectly affected beetle assemblages, and those effects depended on pasture conditions. However, long-term pasture intensification that obviously affected vegetation affected beetle assemblages only as a delayed effect and as an interaction with other treatments, indicating that vegetation-based evaluations of wetland quality do not translate easily to some other assemblages. Classic ecological metrics (richness, diversity) revealed some effects, but PCS metrics complemented those metrics to reveal effects that would otherwise be undetected.

We expected cattle exclosure (i.e., release from grazing effects) and prescribed fire would mitigate pasture intensification effects on aquatic beetle assemblages. This hypothesis was predicated on pasture effects, based on prior knowledge of the study system and general use of aquatic beetles as biodiversity indicators (e.g., Hornung and Rice 2003, Steinman et al. 2003, Sanchez-Fernandez et al. 2006, Boughton et al. 2010, 2011). However, pasture intensification was only significant as part of delayed interactions, which is broadly consistent with those observed in other regions that show that land use effects vary among intensities, spatial scales, and taxa (e.g., Tangen et al. 2003, Batzer et al. 2004, Rosset et al. 2014). We infer that adephagan beetle assemblages are relatively insensitive to the effects of pasture intensification within the range observed in this system, perhaps due in part to their high mobility across the study area. Moreover, this result suggests
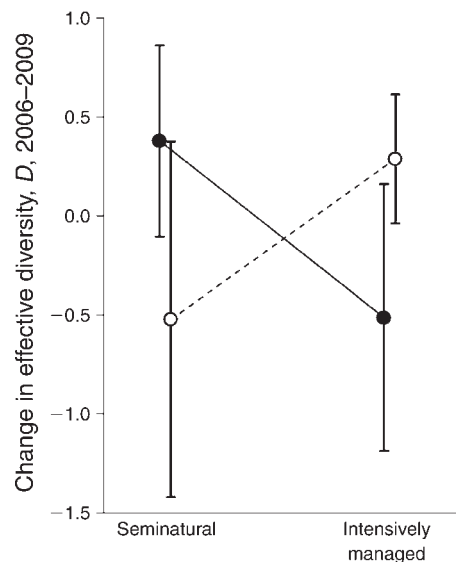

FIG. 3. Pasture and fire treatments interacted ($P = 0.01$) to cause opposite effects for the change in adephagan diversity (D; Jost 2006) between 2006 and 2009. Solid circles and solid line indicate burned wetlands; open circles and dashed line indicate unburned wetlands. Error bars represent 95% confidence intervals.

that, though vegetation may be sensitive to wetland quality (e.g., Lopez and Fennessy 2002), vegetation metrics may have limited relevance to some other taxa, even if those other taxa are often part of water quality assessments based on biological indicators. Just as multimetric approaches ensure confidence in aquatic habitat evaluations, multi-taxon approaches that include disparate taxa with different life histories and dispersal capabilities may offer a more complete assessment of biotic integrity and water quality conditions.

We expected beetle assemblages to become more diverse and phylogenetically dispersed with cattle exclosure and prescribed fire, due to a relaxation of habitat filtering. However, we expected the effects of fencing and fire to depend on the pasture type, reflecting an interactive effect of pasture intensification. Cattle exclosure (fencing) did release adephagan aquatic beetles from the habitat filter caused by cattle grazing, as evidenced by persistent expanded phylogenetic breadth due to individual and interactive effects of fencing. However, fencing effects did not carry over to classic ecological metrics (number of genera, diversity) and would have been missed without phylogenetic community structure analyses, indicating that the effect was related to interactions within assemblages having similar richness and abundance distributions.

Prescribed fire significantly but temporarily reduced the number of genera and phylogenetic diversity (PD) of adephagan assemblages, consistent with other studies of fire effects on insect assemblages (Swengel 2001, Panzer 2002). Fire may have indirectly affected beetles by altering cues for ovipositing adults (Binckley and Resetarits 2005), directly affected eggs or larvae already deposited when the dry, seasonal wetlands were burned, or both. Interestingly, the one-time fire interacted with other treatments beyond that year to enhance diversity in seminatural pastures, but decrease diversity in intensively managed pastures. This strong context dependence confirmed the value of tests for interactive effects among common ecosystem management practices. We conclude that more such interactive treatment studies should be conducted in other systems, with the goal to better understand complex, interactive effects of management practices.

The delayed, persistent, and interactive effects of ongoing treatments (pasture intensification, cattle exclosure) in the study will likely continue into the future, especially with repeated fires. Our results suggest that experimental manipulations of timing, frequency, and intensity of these management practices on wetlands should be instructive. For example, flash grazing (Heitschmidt et al. 2005) and prescribed fires applied in a shifting mosaic (Bormann and Likens 1979) may further enhance diversity of some wetland biota while providing economic value to ranchers.

Classic ecological metrics (richness, diversity) and PCS metrics (NRI, NTI) were complementary, but one category was not clearly more sensitive than the other.
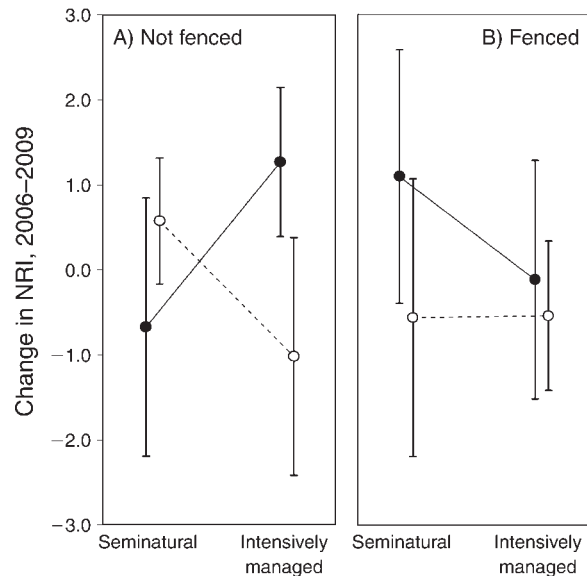

Fig. 4. Pasture, cattle exclosure (fencing), and fire treatments interacted ($P = 0.016$) to change net relatedness index (NRI) in complex ways. (A) Fire had opposite effects on adephagan assemblages in different pastures if cattle grazing was maintained. (B) Cattle exclosure (with fence) almost fully reversed this effect. In other words, the combination of cattle grazing (no fence), fire, and intensive pasture management restricted adephagan assemblages to become more phylogenetically clustered between 2006 and 2009. The lack of fire and/or release from grazing in intensively managed pastures partially relaxed the constraint on adephagan phylogenetic structure to become more dispersed. A positive NRI indicates phylogenetic clustering, and a negative NRI indicates phylogenetic overdispersion. Solid circles and solid line indicate burned wetlands; open circles and dashed line indicate unburned wetlands. Error bars represent 95% confidence intervals.

Instead, PCS metrics complemented ecological metrics by reporting effects when ecological metrics did not, revealing subtleties unacknowledged by classic metrics. In addition, NRI and NTI are standardized and thus valuable for direct comparisons between sites or studies (Webb et al. 2002). Based on our results, we recommend a combination of phylogenetic community structure and classic ecological metrics be used to compare assemblages in ecological experiments, when a phylogeny can be estimated. We note that a phylogeny is itself a hypothesis, and that the assumption of phylogenetic conservatism of ecological traits should have independent support, as for the three families of aquatic adephagans found in this study. Also, we used a genus-level phylogeny, which should be robust because many of the genera were monotypic in this system and traits are more likely phylogenetically conserved at this taxonomic level (Cavender-Bares et al. 2009, Lessard et al. 2009, Vamosi et al. 2009). This case may not apply to other assemblages.

Ecosystem services are increasingly relevant to the management of agricultural lands, including grazing lands in Florida and beyond (Naidoo et al. 2008, Bohlen
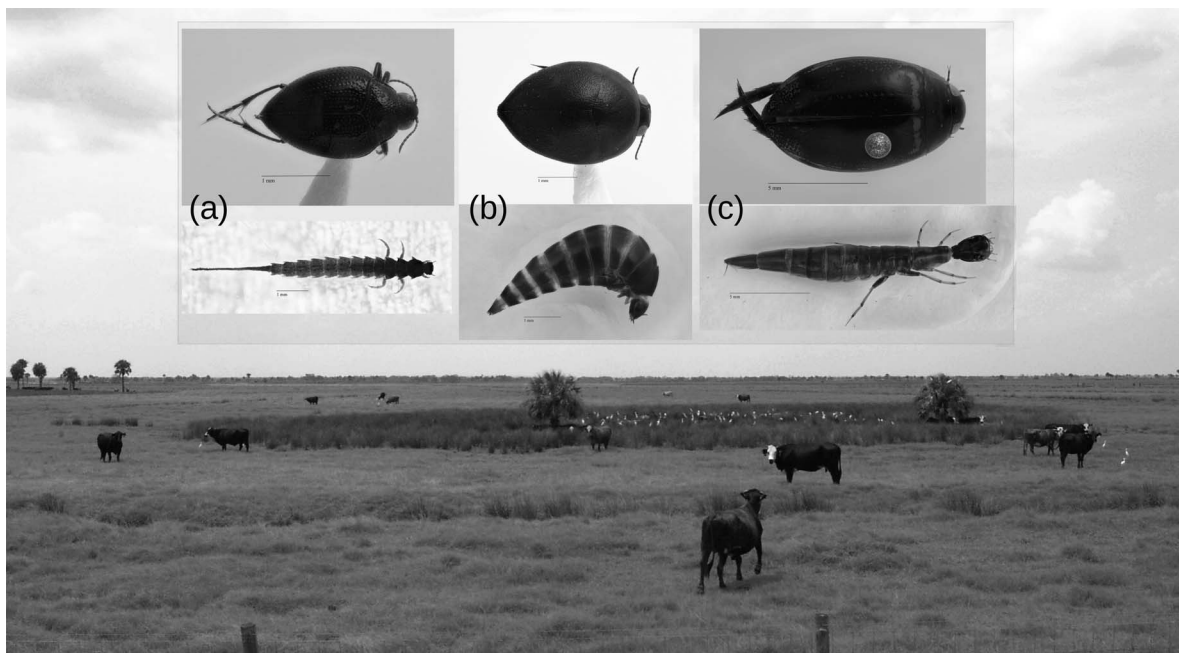
PLATE 1. Voucher specimens (adult and larva) representing each adephegan clade in the study: (a) *Haliplus* (Halipidae), (b) *Suphis* (Noteridae), and (c) *Thermonectus* (Dystiscidae). Scale bars are 1 mm for (a) and (b); 5 mm for (c). Also depicted is one of forty seasonal wetlands used as experimental units in the study that manipluated pasture management, cattle grazing, and prescribed fire. White specks in the wetland are cattle egrets perched on cows. Photo credits: S. L. Kelly and D. G. Jenkins.

et al. 2009, De Steven and Lowrance 2011, Swain et al. 2013). Amid highly simplified pastures, embedded wetlands provide local biodiversity hotspots and opportunities to manage hydrology. As such, wetlands represent high value for ecosystem services that increasingly drive management practices (Larigauderie and Mooney 2010, Perrings et al. 2011, Swain et al. 2013). Pasture intensification, rotational cattle grazing, and prescribed fire are commonly used to manage ranch lands, and in turn affect wetlands embedded in those pastures. Based on our results, prescribed fire should be used judiciously in wetlands, including the use of a heterogeneous spatial and temporal schedule across a landscape to maintain biodiversity. Prescribed fires are often applied on a regular schedule, but more varied schedules and spatial distributions are likely to better maintain diversity among wetlands (Driscoll et al. 2010). This balance may make prescribed fire coordination more complicated than a routine schedule, but could better boost local and regional biodiversity relative to a more homogeneous approach, and thus improve ecosystem services for a set of managed lands. In a similar manner, a heterogeneous spatiotemporal schedule of rotational grazing, including flash grazing, may promote biodiversity while also providing high forage quality and quantity for cattle. Careful coordination of current management practices in grazing lands can help conserve natural diversity and partially mitigate undesired conservation outcomes of some other long-term management practices.

For example, based on our results alone, occasional prescribed fire in unfenced, seminatural pastures should boost aquatic beetle diversity and improve phylogenetic dispersion in an assemblage. This general conclusion is consistent with a general understanding of pyrogenic landscapes of Florida (Myers and Ewel 1990). In addition, ranchers may mitigate (in part) the effects of long-term pasture intensification by fencing wetlands to exclude cattle. We hypothesize that brief "flash" grazing would enable ranchers to take advantage of subsequent high-quality forage and control woody plants but mitigate grazing effects in wetlands. After several years, prescribed fire could be applied to those fenced wetlands, but earlier fire would only depress desired effects. Because no one expects ranchers to manage their lands for the sake of aquatic beetle diversity, similar experimental results need to be tested with vegetation that more directly affects a ranch budget and that are likely to respond differently from expectations above. Nonetheless, this study points the way for such research, helps address knowledge gaps in disturbance ecology, and is relevant to ecosystem services based on biological diversity.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A and B are available online: http://dx.doi.org/10.1890/14-1225.1.sm