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Snake co-occurrence patterns are best explained by habitat and hypothesized effects of interspecific interactions

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Summary

1. Snakes often occur in species-rich assemblages, and sympatry is thought to be facilitated primarily by low diet overlap, not interspecific interactions.

2. We selected, *a priori*, three species pairs consisting of species that are morphologically and taxonomically similar and may therefore be likely to engage in interspecific, consumptive competition. We then examined a large-scale database of snake detection/nondetection data and used occupancy modelling to determine whether these species occur together more or less frequently than expected by chance while accounting for variation in detection probability among species and incorporating important habitat categories in the models.

3. For some snakes, we obtained evidence that the probabilities that habitat patches are used are influenced by the presence of potentially competing congeneric species. Specifically, timber rattlesnakes (*Crotalus horridus*) were less likely than expected by chance to use areas that also contained eastern diamond-backed rattlesnakes (*Crotalus adamanteus*) when the proportion of evergreen forest was relatively high. Otherwise, they occurred together more often than expected by chance. Complex relationships were revealed between habitat use, detection probabilities and occupancy probabilities of North American racers (*Coluber constrictor*) and coachwhips (*Coluber flagellum*) that indicated the probability of competitive exclusion increased with increasing area of grassland habitat, although there was some model uncertainty. Cornsnakes (*Pantherophis guttatus* or *Pantherophis slowinskii*) and ratsnakes (*Pantherophis alleghaniensis*, *Pantherophis spiloides*, or *Pantherophis obsoletus*) exhibited differences in habitat selection, but we obtained no evidence that patterns of use for this species pair were influenced by current interspecific interactions.

4. Overall, our results are consistent with the hypothesis that competitive interactions influence snake assemblage composition; the strength of these effects was affected by landscape-scale habitat features. Furthermore, we suggest that current interspecific interactions may influence snake occupancy, challenging the paradigm that contemporary patterns of snake co-occurrence are largely a function of diet partitioning that arose over evolutionary time.

Key-words: co-existence, *Coluber*, competition, *Crotalus*, detection probability, *Elaphe*, occupancy modelling, *Pantherophis*, reptile, sympatry

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Introduction

Interspecific competition is thought to have an important influence on the composition and structure of species assemblages. Within studies on the topic, interspecific competition is suggested to occur more often than not (Connell 1983; Schoener 1983); however, determining its role and relative importance in structuring ecological assemblages is contentious (Ferson *et al.* 1986). Simple, elegant studies have documented that a species' presence (Connell 1968) or abundance (Hairston 1980, 1981) may influence the abundance and distribution of sympatric species, which implies that competitive interactions may influence the probability of occurrence of each species. Although the observed strength of interspecific competition can be measured in experimental studies (Gurevitch *et al.* 1992), such experiments are often impractical at large scales (Sih *et al.* 1985).

If two species rarely co-occur, a potential interpretation is that the species that is a superior competitor has limited the distribution of the inferior competitor (Diamond 1975). Generally, four primary criticisms have arisen regarding this interpretation: (i) it is not congruent with the scientific method to infer ecological processes from observed patterns (Ulrich 2004), (ii) observed patterns often are not tested against a null hypothesis based on patterns apparent in randomly structured assemblages (Connor & Simberloff 1979), (iii) a '0' to denote a species' absence may actually reflect nondetection rather than absence (Cam *et al.* 2000; MacKenzie, Bailey & Nichols 2004) and (iv) species that occur together less frequently than expected by chance may be responding to differences in habitat, or other unmeasured variables, rather than each other (MacKenzie, Bailey & Nichols 2004).

The development of models that allow for estimation of detection probability and species occupancy (MacKenzie *et al.* 2002, 2006) allows one to evaluate multiple competing hypotheses while determining whether co-occurrence of species happens more or less often than expected by chance (MacKenzie, Bailey & Nichols 2004). These analyses require at least two surveys for species at multiple sites and estimate the probability of observing the detection/nondetection data under various models. From these probabilities, maximum likelihood estimators are used to generate a probability of occupancy (MacKenzie, Bailey & Nichols 2004). Other explanatory variables, such as habitat type, may be incorporated into models as covariates to determine the influence of these factors on co-occurrence patterns. By ranking models, it is possible to determine whether there is evidence for nonrandom co-occurrence above and beyond other variables that may influence occupancy. Consequently, of the criticisms relevant to prior investigations of co-occurrence patterns (above), occupancy modelling may address 2–4.

Snakes may be found in species-rich assemblages (e.g. Guyer 1994; Akani *et al.* 1999), as compared to assemblages of some other predatory animals (e.g. mammalian carnivores; Wang & Macdonald 2009; Davis, Kelly & Stauffer 2010), and snakes, emerging model organisms in ecology (Shine & Bonnet 2000), possess diverse life-history strategies (Greene 1997). Thus, this taxonomic group is useful for investigating co-occurrence patterns (e.g. Luiselli & Filippi 2006; França & Araújo 2007; Luiselli *et al.* 2012). A recent review of resource partitioning among snakes demonstrated that resource use was consistent with what may be expected if interspecific competition was occurring (Luiselli 2006a), but the link between resource use, competition, and co-occurrence was tenuous. Past interspecific interactions (i.e. the ghost of competition past; Connell 1980) may have played a role in snake co-evolution, and evolutionary lineages are thought to be a major influence of current patterns of resource use (Vitt & Pianka 2005). However, there is evidence that resource use has some degree of plasticity and that current interspecific interactions have the potential to influence co-occurrence patterns (Luiselli 2003; Steen *et al.* 2013).

Sympatry between potentially competing snakes may occur with greater frequency in North America than elsewhere (e.g. Australia, Shine 1977); this sympatry may be facilitated by a high diversity of prey resources to partition (Arnold 1972). By partitioning diet (e.g. Mushinsky & Hebrard 1977), multiple species can inhabit an area without substantial competition. However, this explanation is not completely supported, particularly for terrestrial snakes in temperate regions (Luiselli 2006a), and may not hold for species within the same genus (Toft 1985). For example, eastern diamond-backed rattlesnakes (*Crotalus adamanteus* Palisot de Beauvois) and timber rattlesnakes (*Crotalus horridus* Linnaeus) are morphologically and taxonomically similar, prey on similar resources by ambush foraging and occur sympatrically in portions of the south-eastern United States (Smith *et al.* 2006; Steen *et al.* 2007). The same sites may also contain additional congeneric pairs of species that (i) actively forage on the same prey base [e.g. red cornsnake (*Pantherophis guttatus* Linnaeus) and grey ratsnake (*Pantherophis spiloides* Duméril, Bibron and Duméril; Ernst & Ernst 2003; Stapleton 2005)] or (ii) actively forage on a wide variety of prey items [e.g. North American racer (*Coluber constrictor* Linnaeus) and coachwhip (*Coluber flagellum* Shaw; Halstead, Mushinsky & McCoy 2008)].

Occupancy modelling may offer a method of overcoming some of the logistic hurdles that have hindered previous investigations of co-occurrence while providing novel insights regarding co-occurrence patterns of a little-understood group of predators (e.g. Bailey *et al.* 2009). To this end, we used this technique to evaluate multiple working hypotheses explaining co-occurrence patterns of congeneric pairs of terrestrial snakes across the south-eastern United States while incorporating landscape-scale habitat preferences for each of the species. If models with considerable support suggested occupancy probabilities of species within a congeneric pair were independent, we interpreted this to mean that patterns of habitat use and selection were most likely due to evolutionary or random processes. If top models explaining occupancy for a species pair revealed a negative relationship between occupancy probabilities, we considered this as evidence consistent with competitive exclusion.

Materials and methods

SAMPLING

We based this study on a data set that was previously used to examine how terrestrial snake occupancy was influenced by land cover (Steen *et al.* 2012). Data were compiled from 449 passive traps from a number of different sites located across the southeastern United States, from North Carolina through eastern Texas. Traps were drift fence arrays with box traps and/or funnel traps (see Burgdorf *et al.* 2005; Steen, Smith & Bailey 2010; Sutton, Wang & Schweitzer 2010 for representative trap design). Sites included military installations, national forests and managed forestlands (Table 1 in Steen *et al.* 2012), and each site contained numerous traps. We considered traps independent, and there was no evidence that site-specific features influenced snake occupancy patterns (Steen *et al.* 2012). Sites were sampled for 2–7 years, and we treated each year of sampling as one sampling occasion.

We used 2001 National Land Cover Data (Homer *et al.* 2004) and ArcGIS to characterize the land cover surrounding each trap at multiple scales. These land cover data are coarse (30-m resolution) and do not consider microhabitat features, although snakes may also select habitat at this scale (e.g. Steen, Linehan & Smith 2010). More details are available in Steen *et al.* (2012).

SELECTION OF STUDY SPECIES

We selected congeneric pairs of species for study that we hypothesized a priori may interact, thus potentially influencing assemblage structure. These species pairs are similar morphologically, use comparable resources and co-occur throughout portions of their geographical ranges (e.g. Waldron *et al.* 2006a; Halstead, Mushinsky & McCoy 2008). Thus, they may be expected to have undergone evolutionary divergence in the past or engage in resource partitioning currently, to reduce competitive pressure.

Congeneric pairs selected for analyses were (i) eastern diamond-backed rattlesnake and timber rattlesnake (ii) North American racer and coachwhip, and (iii) ratsnakes (*Pantherophis alleghaniensis* Holbrook, *P. spiloides* Duméril, Bibron and Duméril, and *Pantherophis obsoletus* Say; Burbrink 2001) and cornsnakes (*P. guttatus* and *Pantherophis slowinskii*, Burbrink 2002).

ANALYSIS

We first modelled species co-occurrence using the psiBa parameterization in program PRESENCE (Hines 2006). This parameterization requires the *a priori* determination of which species is subordinate and thus chooses habitat based on the presence or absence of the other dominant species (Richmond, Hines & Beissinger 2010). This parameterization estimates the probability of occupancy for the dominant species (psiA) as well as occupancy of the subordinate species when the dominant species is present (psiBA) and absent (psiBa).

If sympatric snakes compete, this interaction is likely to occur over habitat and/or prey (Reinert 1984; Toft 1985). It is difficult to distinguish between the relative influence of habitat and prey availability in snake habitat selection because prey distribution at local and landscape scales has played an important role in the evolution of snake habitat selection (Reinert 1993). Within this study, we were able to explicitly incorporate landscape-scale habitat covariates into our analyses. There is limited evidence for interspecific resource defence in snakes, and space is unlikely to be limiting within our study sites. Therefore, we assume that if occupancy probabilities were not independent, then this lack of independence can be attributed to competitive exclusion arising from consumptive competition. Because a snake's body size is an important determinant of the size of prey, larger snakes can consume a wider range of prey (Arnold 1993). Therefore, for all congeneric species, we assumed that the largest species (based on total lengths reported in Ernst & Ernst 2003) was dominant.

We assumed that if competitive exclusion of a given area was occurring, the dominant species for each pair would select the area surrounding a given trap based on habitat (and the mechanism leading to exclusion of the subordinate species would be depletion of prey within that habitat). Thus, we modelled psiA for each species using habitat covariates identified as important by Steen *et al.* (2012). Consideration of appropriate scale is vital when interpreting ecological patterns (Wiens 1989). We used land cover within a 1000-m buffer surrounding each trap because this was the spatial scale that best explained occupancy for most species (i.e. all but *P. guttatus*; Steen *et al.* 2012). Although evergreen forest was not identified as important for either rattlesnake species in our previous study (Steen *et al.* 2012), we included this covariate when examining this species pair because eastern diamond-backed rattlesnakes are considered a pine forest and savanna specialist on a large spatial scale (Guyer & Bailey 1993; Means 2006; Waldron *et al.* 2006a; Waldron, Welch & Bennett 2008). We built models that assumed that occupancy of the subordinate species was influenced by (psiBA $\neq$ psiBa) or independent of (psiBA = psiBa) the dominant species. We also built models that tested for differences in habitat use based on the presence or absence of the dominant species.

We calculated the species interaction factor (SIF) according to Richmond, Hines & Beissinger (2010) if the competition model (psiBA $\neq$ psiBa) was the best model. A SIF <1 indicates that species co-occur less frequently than expected if occupancy probabilities were independent, while a SIF >1 indicates species co-occur more frequently than expected if occupancy probabilities were independent.

Detection can also be estimated based on the presence or absence of the subordinate and dominant species. To ensure that variation in detectability was not confounding our ability to identify competitive exclusion, we tested models that assumed detection of the subordinate was both independent of (rBA = RBa) and influenced by (rBA $\neq$ rBa) the presence and detection of the dominant species (Table 2). Within each model for a given species, we also included the factors identified by Steen *et al.* (2012) to influence the detection of that species.

Although the psiBa parameterization is often reliable with regard to model convergence (Richmond, Hines & Beissinger 2010), we encountered convergence problems when modelling co-occurrence for *Coluber* and *Pantherophis*. For these comparisons, we therefore modelled the occurrence of the subordinate species conditional on the occupancy of the dominant species.

We did so by adding the conditional probability of occupancy – given the detection history – of the dominant species (psiA) as a covariate in the single-season, single-species parameterization in program PRESENCE (Hines 2006). We calculated psiA at each trap using the best model for that species as identified by Steen *et al.* (2012). We then tested for species interactions by comparing models built with and without psiA and with interactions between psiA and habitat covariates. We also tested whether psiA affected the detection of the subordinate species by evaluating models with and without psiA as a covariate for detection.

We only analysed data from study sites within the geographical range of both species within a pair, based on range maps in Ernst & Ernst (2003). We also z-transformed all habitat covariates and arcsine-square-root-transformed psiA for use in single-species models to help improve convergence. For North American racers and for cornsnakes, we estimated model fit by calculating the overdispersion parameter ($\hat{c}$) using the most parameterized model (Burnham & Anderson 2002). We then used ($\hat{c}$) to correct Akaike Information Criterion for small sample size (AIC_c, Hurvich & Tsai 1989) and for overdispersion ($QAIC_c$, Burnham & Anderson 2002). Because no test of model fit exists for multispecies occupancy models, we did not correct AIC_c values for overdispersion within the *Crotalus* model set.

We considered a covariate as useful for inference if it was within a model that did not contain uninformative parameters (Arnold 2010), was within a model(s) $\leq 2\ \Delta QAIC_c$ from the highest ranked model and had 85% confidence intervals that did not include zero (Arnold 2010). We calculated confidence intervals for the SIF from the psiBa models and occupancy of the subordinate species from the single-season, single-species models using the 'deltamethod' function in the msm package within the R statistical programming environment (R Development Core Team 2011). We report weight (w_i) and number of parameters (k) in each model. Coefficient estimates are presented as $\beta \pm$ SE.

Traps included in analyses for *Coluber* and *Pantherophis* were monitored for 2–7 years (mean = 3·4 ± 0·06); and 2–4 years (mean = 2·7 ± 0·06) of monitoring was used for *Crotalus*. Our analyses assumed that each trap was closed to changes in occupancy status over these time periods. Regarding *Pantherophis* and *Coluber*, many individuals were often captured within a given trap over the course of the study and these snakes generally have established home ranges and may live 10–20 years (e.g. Plummer & Congdon 1994; Fitch 1999). *Crotalus*, on the other hand, were captured relatively infrequently but also have established and relatively small home ranges (Waldron, Lanham & Bennett 2006b; Hoss *et al.* 2010) and live long lives (Aldridge & Brown 1995; Brown, Kéry & Hines 2007). As a result, within this study, we consider the presence of a single individual of a species in a trap as representative of an extant population of that species using the area surrounding that trap. Given the length of time we trapped, we consider it highly unlikely that the area sampled by a given trap was either colonized by a population of snakes or experienced an extirpation of a population over the course of the study. Even if the closure assumption was violated, parameter estimates are likely still valid as long as the assumption was violated randomly, although we would need to interpret sites as being used rather than occupied (MacKenzie, Bailey & Nichols 2004). Further, violations of the closure assumption in occupancy models cause an overestimation of occupancy (MacKenzie *et al.* 2006; Rota *et al.* 2009). Therefore, violation of the closure assumption would likely cause the distributions of the two species to appear to overlap more than they actually do and thus make an effect of competition more difficult to detect. Any effects of competition we detect are therefore likely conservative estimates. To be further conservative and to reflect the reality that populations of different species may occur in the same site (but not necessarily in the area surrounding each trap), we interpret our occupancy probabilities as the probability of a species using the area sampled by a given trap.

Results

A total of 104, 431 and 449 traps were included in analysis for *Crotalus*, *Coluber* and *Pantherophis*, respectively (Table 1). All models $\leq 2\ \Delta AIC_c$ for *Crotalus* assumed that use of an area by timber rattlesnakes was influenced by the presence of eastern diamond-backed rattlesnakes ($psiBA \neq psiBa$) (Table 2). These models accounted for 80% of the AIC_c weight and assumed that use of evergreen forest by timber rattlesnakes was influenced by the presence of eastern diamond-backed rattlesnakes. The best model also assumed that detection of timber rattlesnakes was not influenced by the presence of eastern diamond-backed rattlesnakes ($rBA = rBa$). The only other model within $2\Delta AIC_c$ contained an uninformative parameter and was therefore not used for inference. The coefficient for use of evergreen forest by timber rattlesnakes in the best model was −2·78 ± 1·67 when eastern diamond-backed rattlesnakes were present, whereas the coefficient for use of evergreen forest in the absence of eastern diamond-backed rattlesnakes was 0·88 ± 1·30. In other words, timber rattlesnakes significantly avoided evergreen forests when eastern diamond-backed rattlesnakes were present, but exhibited a positive but nonsignificant association with evergreen forests when eastern diamond-backed rattlesnakes were absent. The SIF of eastern diamond-backed rattlesnakes and timber rattlesnakes in the near absence of evergreen forest was 1·94 ± 0·22, indicating co-occurrence. This value was 0·16 ± 0·22 when the area of evergreen forest within 1000 m of the trap was at its maximum (Fig. 1), indicating avoidance.

Table 1. Capture data for species of interest trapped throughout the south-eastern United States. The species we considered as dominant in each pairing is listed first; '*a*' denotes the number of traps at which the dominant species was detected and the subordinate species was not, '*b*' denotes the number of traps where the subordinate species was detected and the dominant was not, 'BA' is the number of traps where both species were detected, and '*n*' is the total number of traps used for analysis for each pairing

	a	*b*	BA	*n*
Eastern diamond-backed rattlesnake Timber rattlesnake	47	4	12	104
Ratsnake Cornsnake	119	73	162	449
Coachwhip North American racer	51	55	317	431

Table 2. Models used to evaluate whether interspecific interactions helped explain occupancy patterns between sympatric snakes in the south-eastern United States. All models for cornsnakes and North American racers included covariates for detection indicating the site in which a survey was performed, as this was identified as an important covariate for these species in Steen *et al.* 2012

Crotalus	$\mathrm{AIC_c}$	$\Delta\mathrm{AIC_c}$	wi	*k*
psiA (Mixed), psiBA ≠ psiba (Evergreen), rBA = rBa	409·92	0	0·53	8
psiA (Mixed), psiBA ≠ psiba (Evergreen), rBA ≠ rBa	411·38	1·46	0·26	9
psiA (Mixed), psiBA = psiba (Evergreen), rBA ≠ rBa	411·96	2·04	0·19	7
psiA (Mixed), psiBA = psiba (Evergreen), rBA = rBa	416·2	6·28	0·02	6
psiA, psiBA ≠ psiba, rBA = rBa	441·46	31·54	0·00	5
psiA, psiBA ≠ psiba, rBA ≠ rBa	443·19	33·27	0·00	6
psiA, psiBA = psiba, rBA ≠ rBa	445·56	35·64	0·00	5
psiA, psiBA = psiba, rBA = rBa	448·82	38·9	0·00	4
Pantherophis	$\mathrm{QAIC_c}$	$\Delta\mathrm{QAIC_c}$	wi	*k*
ψ(Mixed + Scrub + Grass), p(.)	1400·14	0	0·31	14
ψ(Mixed + Scrub + Grass + Water), p(.)	1401·13	0·99	0·19	15
ψ(Mixed + Scrub + Grass), p(Ratsnake)	1402·08	1·94	0·12	15
ψ(Mixed + Scrub + Grass + Ratsnake), p(.)	1402·28	2·14	0·11	15
ψ(Mixed + Scrub + Grass + Water), p(Ratsnake)	1403·14	3	0·07	16
ψ(Mixed + Scrub + Grass + Water + Ratsnake), p(.)	1403·27	3·13	0·07	16
ψ[(Mixed + Scrub + Grass)*Ratsnake], p(.)	1403·89	3·75	0·05	18
ψ(Mixed + Scrub + Grass + Ratsnake), p(Ratsnake)	1404·22	4·08	0·04	16
ψ(Mixed + Scrub + Grass + Water + Ratsnake), p(Ratsnake)	1405·21	5·07	0·02	17
ψ[(Mixed + Scrub + Grass)*Ratsnake], p(Ratsnake)	1405·33	5·19	0·02	19
ψ(.), p(Ratsnake)	1414·02	13·88	0·00	12
ψ(.), p(.)	1423·02	22·88	0·00	11
Coluber	$\mathrm{QAIC_c}$	$\Delta\mathrm{QAIC_c}$	wi	*k*
ψ(Scrub + Grass), p(Coachwhip)	1884·67	0	0·42	14
ψ[(Scrub + Grass)*Coachwhip], p(.)	1885·43	0·76	0·29	16
ψ[(Scrub + Grass)*Coachwhip], p(Coachwhip)	1886·25	1·58	0·19	17
ψ(Scrub + Grass + Coachwhip), p(.)	1888·85	4·18	0·05	14
ψ(Scrub + Grass), p(.)	1890·07	5·4	0·03	13
ψ(.), p(Coachwhip)	1891·15	6·48	0·02	12
ψ(.), p(.)	1895·43	10·76	0·00	11
ψ(Scrub + Grass + Coachwhip), p(Coachwhip)	Did not converge			

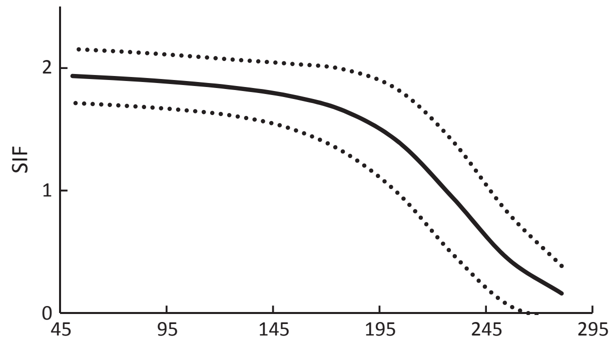

Fig. 1. Species interaction factor (and 85% confidence intervals) between eastern diamond-backed rattlesnakes, *Crotalus adamanteus*, and timber rattlesnakes, *Crotalus horridus*, within the south-eastern United States in relation to the amount of evergreen forest within 1000 m of traps.

The best models for cornsnakes did not include psiA (i.e. ratsnake occupancy) as a covariate for occupancy or detection, and all other models within $\Delta\mathrm{QAIC_c}$ <2 contained uninformative parameters (Table 2). Further, models that included psiA only accounted for 50% of the model weight (Table 2). The best model indicated that cornsnakes were positively associated with mixed forest (1·41 ± 0·54), scrub (0·30 ± 0·15) and grass (0·48 ± 0·22; this finding is different than what is reported in Steen *et al.* 2012, because cornsnakes were not grouped together in that independent work. The overdispersion parameter ($\hat{c}$) for the global model of cornsnake occupancy was 1·13.

The best model of occupancy of North American racers included the conditional occupancy of coachwhips (psiA) as a covariate for detection (Fig. 2, β = 0·64 ± 0·24) and revealed a negative effect of scrub (β = −1·13 ± 0·42) and grass (β = −0·71 ± 0·28) on occupancy. The only other model within $\Delta\mathrm{QAIC_c}$ <2 without uninformative parameters in the North American racer model set indicated a negative effect of psiA (β = −3·96 ± 1·19) and the interaction of psiA and grass (β = −13·16 ± 0·28), but a positive effect of grass in the absence of coachwhips (β = 20·0 ± 0·44, Table 2) on North American racer occupancy. These results indicate that the amount of grass surrounding a site perhaps mediates competition between these two species (Fig. 3). However, we interpret the

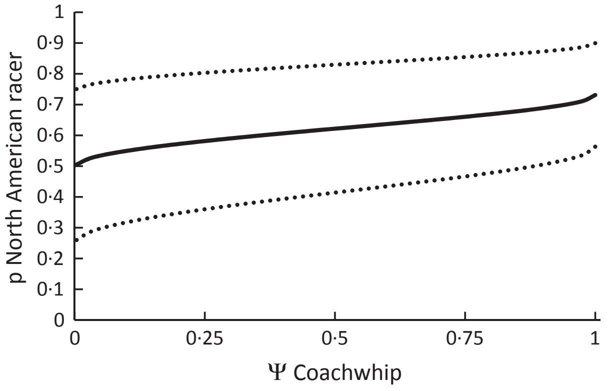

Fig. 2. Relationship between estimated detection probability (p) and 85% confidence intervals for North American racers (*Coluber constrictor*) and occupancy (Ψ) of coachwhips (*Coluber flagellum*) in the south-eastern United States.

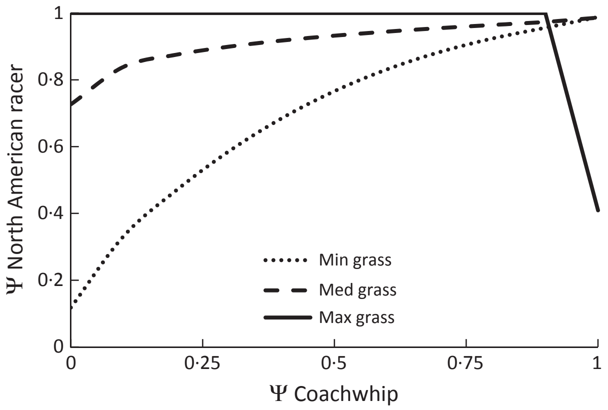

Fig. 3. Relationship between estimated occupancy (Ψ) for North American racers (*Coluber constrictor*) and occupancy of Coachwhips (*Coluber flagellum*) at sites surrounded by the minimum, median and maximum amount of grass surrounding traps within the south-eastern United States.

effects of coachwhips on North American racer occupancy and detection with caution because of substantial model uncertainty – models including psiA for occupancy only had a cumulative weight of 0·53 and models with psiA for detection had a cumulative weight of 0·63. The overdispersion parameter ($\hat{c}$) for the global model of North American racer occupancy was 1·03.

Discussion

When examining nonrandom species co-occurrence patterns, it is often difficult to determine whether observed patterns result from interspecific interactions, such as competitive exclusion, or simply from differences in habitat preference. In addition, low and varied detection probabilities may confound straightforward interpretation of occurrence data (Miller *et al.* 2012). We used occupancy modelling to explicitly incorporate habitat selection and varied detection probabilities into analysis of co-occurrence patterns (MacKenzie, Bailey & Nichols 2004); evidence generated from *Crotalus* and *Coluber* is consistent with the suggestion that (i) competitive exclusion may influence habitat use by subordinate competitors and (ii) snakes may interact with the potential to influence detection probabilities. Overall, we therefore suggest that competition may influence both the composition of diverse predator assemblages (through competitive exclusion) and our ability to characterize them (through alteration of detection probabilities). Furthermore, because we generated different results for each of the species pairs we examined, we find no general ecological phenomenon that explains snake co-occurrence patterns. Interestingly, though, evidence for competitive exclusion was associated with specific habitat types for both *Crotalus* and *Coluber*, suggesting that the strength of interspecific interactions is influenced by features of the landscape and perhaps mitigated by high habitat heterogeneity.

Experimental studies offer high inferential power; however, they are impractical or impossible to institute over large scales. By examining patterns of habitat use and co-occurrence in a large region (i.e. the south-eastern United States), over a long time frame and over a range of habitats comprising different snake assemblages, we took advantage of a natural experiment to gain novel insights regarding how predator assemblages are structured. However, observational techniques such as those we employed do not rule out alternative interpretations of any observed patterns (Sih *et al.* 1985). Thus, to justify our interpretation, it seems necessary to include some discussion of relevant natural history as well as speculation regarding how these natural histories may have influenced the patterns we observed.

Although reptiles have generally low metabolic rates, as compared to endotherms (Nagy 2005), their reproductive output may be heavily influenced by food availability (Ford & Seigel 1989). Snakes can reach high densities in suitable habitats; as a consequence, they may regulate prey populations (Nowak, Theimer & Schuett 2008; Campbell *et al.* 2012). The presence of a superior competitor in a given area could decrease prey availability for other species indefinitely. We suggest that the co-occurrence patterns we documented in *Crotalus* are consistent with what we would expect if consumptive competition was decreasing the probability that a population of inferior competitors would use a particular area or habitat (Schoener 1974).

Sympatric vipers in North America are thought to partition habitat (Reinert 1984; Luiselli 2006a), and habitat features may influence the degree of diet overlap, potentially resulting in competitive pressure (Luiselli 2006b). In our study, eastern diamond-backed rattlesnakes and timber rattlesnakes occurred together more frequently than expected by chance when evergreen forests were at relatively low levels. At relatively high levels of evergreen forest, we obtained evidence that timber rattlesnakes avoided areas that contained eastern diamond-backed rattlesnakes. Occupancy for the two species may be influenced by multiple habitat types (Steen *et al.* 2012), and their spatial ecology may be a function of habitat heterogeneity (Hoss *et al.* 2010). When evergreen forests are at low levels, there is a greater probability of a relatively high proportion of other habitats being present; this habitat diversity may facilitate co-occurrence of the two species, which exhibit different habitat preferences within a site (Waldron *et al.* 2006a; Steen *et al.* 2007).

When evergreen forests represented ≥72% (225/314 ha) of the landscape, this relative habitat homogeneity apparently resulted in timber rattlesnakes avoiding areas used by eastern diamond-backed rattlesnakes. Although occupancy of eastern diamond-backed rattlesnakes is positively associated with forests of mixed evergreen/hardwood trees on the spatial scale we examined (Steen *et al.* 2012), the species is thought to be a specialist of pine forests and savannas (Guyer & Bailey 1993; Means 2006; Waldron *et al.* 2006a; Waldron, Welch & Bennett 2008) and is likely associated with this habitat at a large scale (Steen *et al.* 2007). Therefore, eastern diamond-backed rattlesnake density, which can reach high levels in suitable habitat (Ernst & Ernst 2003), may be higher in pine forests and savannas than in other habitat types. This high density may result in increased competition with sympatric timber rattlesnakes.

Both rattlesnake species prey largely on rodents, although both may also take rabbits (Ernst & Ernst 2003). Forest fires result in short-term fluctuations in abundance of some small mammals because the loss of understory plants makes animals vulnerable to predation (Morris *et al.* 2011). For example, cotton rats (*Sigmodon hispidus* Say & Ord), a common prey item for *Crotalus* (Ernst & Ernst 2003), may experience significant decreases in survival following fire due to predation (Morris *et al.* 2011). In contrast to hardwood or mixed evergreen/hardwood forests, evergreen forests in the south-eastern United States are frequently burned (Mitchell *et al.* 2006). This burning likely benefits small mammal assemblages associated with the habitat over the long term, as this type of disturbance replicates the ancestral condition (Masters *et al.* 1998). However, due to higher overall predation rates by nonsnake predators (and potentially higher predation rates by snakes as well), frequently burned evergreen forests may represent habitats containing unstable food resources for snakes and fluctuating resource levels may influence the strength of interspecific interactions (Luiselli 2006c). In these conditions, eastern diamond-backed rattlesnakes, which share an evolutionary history with the longleaf pine (*Pinus palustris* Mill.) forest (Guyer & Bailey 1993), may be better suited to persist. Similarly, eastern diamond-backed rattlesnakes have a close association with another longleaf pine associate, the gopher tortoise (*Gopherus polyphemus* Daudin), and may use their burrows for refuge to a greater extent than timber rattlesnakes. This may allow for eastern diamond-backed rattlesnakes to have a competitive advantage in pine forests.

North American racers and coachwhips are sympatric throughout much of the south-eastern United States. These two closely related species exhibit complementary resource use; specifically, they have different habitat preferences on a large scale (Steen *et al.* 2012) and may consume different prey when they do co-occur in a given site (Halstead, Mushinsky & McCoy 2008). Interestingly, North American racers are generally smaller where they co-occur with coachwhips, compared with where coachwhips are absent, a phenomenon that may reduce competition for prey (Steen *et al.* 2013). Thus, differences in body size may facilitate co-occurrence between these species, lessening the likelihood that competitive exclusion would occur. The results of our current study indicate that patterns of co-occurrence may be more complicated. Specifically, top models suggested that large-scale habitat might mediate complex relationships between detection and occupancy probability of North American racers. At median and low levels of grassland habitat, there was a positive relationship between the occupancy probabilities of the two species. At high levels of grassland habitat, however, the probability that an area was occupied by North American racers was 100% except when the probability that coachwhips were also present exceeded 90%. The situation is therefore analogous to what we documented for *Crotalus* within evergreen forests. Perhaps resources are limiting in relatively homogenous grassland areas, and North American racers are competitively excluded by coachwhips.

Further, North American racers were more detectable when the probability of coachwhip occupancy was high. Because of the close relationship between abundance and detection probability (e.g. Royle & Nichols 2003; Chen *et al.* 2009; Delaney & Leung 2010), an increase in the abundance of North American racers is likely to make them more detectable via our passive traps. Thus, we suggest that this result is consistent with the hypothesis that the presence of coachwhips is reflective of some measure of habitat quality that benefits North American racer populations. An alternative explanation for the patterns we documented could be that North American racer behaviour is influenced by the presence of coachwhips such that, for example, they move more and are therefore more available to be detected but, based on our knowledge of snake biology, we can think of little corroborating information that would suggest this is the case. Clearly, controlled and experimental studies quantifying interactions between these two similar species will facilitate a greater understanding of how they persist in the same landscape.

We find no evidence consistent with competition between cornsnakes and ratsnakes. These two taxa select different habitats on large scales (Steen *et al.* 2012). Habitat selection by individual animals at a given site may also differ between the two species, a result that has been attributed to interspecific competition (Stapleton 2005). Our data suggest that patterns of habitat use by cornsnakes and ratsnakes are independent, indicating that any differences in habitat preference between the two species are due to either random processes or strong selection in the past to occupy divergent niches rather than strong ongoing interspecific interactions.

Generalizations are lacking regarding the role of interspecific competition in structuring predator assemblages, including those of temperate region snakes (Luiselli 2006a), perhaps due to the inherent difficulties in studying this group (Reichenbach & Dalrymple 1980; Vitt 1987). However, it is generally suggested that co-occurrence patterns are driven largely by overlap in diet (Luiselli 2006a) and diet is a function of a species' evolutionary lineage (Vitt & Pianka 2005). Using a large-scale database and analyses that explicitly incorporate the low detection probabilities that characterize many species of terrestrial snakes (Steen 2010; Steen, Guyer & Smith 2012), we obtain evidence that interspecific interactions may influence snake assemblage structure and detection probability and that these effects are dependent on habitat features. Because habitat alteration may influence the strength of competitive interactions (Luiselli 2006b), disturbance may alter snake co-occurrence patterns. Our study took place in relatively unfragmented and natural landscapes, so we were unable to evaluate this potential.

Together with other recent research (Luiselli 2003; Steen *et al.* 2013), we suggest that the composition of snake assemblages may be influenced by dynamic and ongoing interspecific interactions to a greater extent than previous studies of resource overlap and partitioning have indicated. However, we are inferring process from observed patterns. Further research, including investigations of how experimental manipulations of prey density influence snake spatial ecology, habitat selection, dietary overlap and population density, may help elucidate the mechanisms behind the patterns we identified, and this research, whether it occurs in temperate or tropical regions, will inform our knowledge of snake community ecology.

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