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Topology of syngameons

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Abstract

Syngameons are sets of species linked by interspecific hybridization. Common observations regarding the structure of syngameons are that hybridization propensity is not uniform across species and that patterns of hybridization are dominated by a few species. I use computer simulations to test these claims in naturally occurring syngameons selected from the literature and from personal observation. Natural syngameons, especially those involving plants, typically exhibit nonrandom structure: The first three order statistics for the number of hybrid partners and the variance in the number of hybrid partners are larger than chance alone would predict. The structure of two insect syngameons examined is not significantly different from random. To test a hypothesis that variation in hybridization propensity across species in natural syngameons is simply an artifact of hybridization opportunity, I examine the structure of four artificial syngameons (fertility relationships) produced by full diallel crosses. Three of four artificial syngameons exhibit nonrandom structure, as the observed variation in number of successful crosses is larger than chance alone would predict. In general, there are no significant results involving the order statistics. Finally, I discuss biogeographic, ecological, and phylogenetic hypotheses for variation in hybridization propensity across species in natural syngameons.

KEYWORDS
hybridization propensity, hybridization rate, interspecific hybridization, syngameon

1 | INTRODUCTION

Interspecific hybridization is a common feature in eukaryotic evolution and it has important consequences to cladogenesis, species interactions, invasion dynamics, and conservation biology. Recent evidence suggests that it has played a role in human evolution, as modern humans hybridized with both Denisovans and Neanderthals (Sankararaman, Mallick, Patterson, & Reich, 2016). In addition, interspecific hybridization has played a central role in the development of evolutionary theory, as early interest in interspecific hybrids (reviewed by Focke (1913) and Marza & Cerchez (1967)) contributed to the development of species concepts (Linnaeus, 1744; Lotsy, 1925), genetics (Mendel & Bateson, 1925; Naudin, 1862), plant reproductive biology (Gärtner, 1849; Roberts, 1919), and speciation (Linnaeus, 1760). More

recently, introgressive hybridization has been examined with respect to adaptive radiation (Seehausen, 2004) and invasion dynamics (Blair, Blumenthal, & Hufbauer, 2012; Ellstrand & Schierenbeck, 2000). In addition, plant hybrid zones have become important model systems to examine tritrophic interactions involving plants, herbivorous insects, and parasitoids (Aguilar & Boecklen, 1992; Preszler & Boecklen, 1994). There continues to be much interest among evolutionary biologists in interspecific hybridization, particularly with respect to speciation in animals (Dowling & Secor, 1997; Seehausen, 2004; Willis, van Oppen, Miller, Vollmer, & Ayre, 2006; Zinenko, Sovic, Joger, & Gibbs, 2016), fungi (Giraud, Refrégier, Le Gac, de Vienne, & Hood, 2008; Restrepo, Tabima, Mideros, Grünwald, & Matute, 2014), and plants (Grant, 1981; Rieseberg, 1997; Soltis & Soltis, 2009). There has been an exponential increase in the number of publications on interspecific hybridization

over the last 30 years (Schwenk, Brede, & Streit, 2008), and the topic has been the subject of many recent reviews (Abbott et al., 2013; Mallet, 2005; Seehausen, 2004; Soltis & Soltis, 2009; Whitney, Ahern, Campbell, Albert, & King, 2010; Willis et al., 2006).

Patterns of interspecific hybridization exhibit several emergent properties. For animals, the probability of hybridization between species may be inversely related to their phylogenetic distances (Coyne & Orr, 1989; Tubaro & Lijtmaer, 2002). For plants, the probability of homoploid versus polyploid hybrid speciation appears to be positively associated with the extent of genetic divergence of hybridizing species (Buggs, Soltis, & Soltis, 2011; Chapman & Burke, 2007; Paun, Forest, Fay, & Chase, 2009). In addition, the occurrence of hybrids varies by taxonomic group, with approximately 25% of plant species and 10% animal species producing natural hybrids (Mallet, 2005; Rieseberg, 1997). Lastly, there may be a strong phylogenetic signal to hybridization propensity, as natural hybrids are not equally distributed among families and genera of vascular plants (Ellstrand, Whitkus, & Rieseberg, 1996; Whitney et al., 2010).

A syngameon is produced when a group of closely related species forms a complex set of hybrid combinations (Lotsy, 1925). Classic examples include irises of the California Pacific Coast (Lenz, 1959), white oaks of the Eastern United States (Hardin, 1975), and British species of *Potamogeton* (Clapham, Tutin, & Warburg, 1962). Syngameons also exhibit emergent properties; a common observation is that hybridization events are not equally distributed among species and that a few species dominate the pattern of hybridization. Consider the pattern of hybridization between southwestern white oaks as depicted by a network graph (Figure 1) – the set of hybridizations is dominated by three species: *Quercus gambelli*, *Q. arizonica*, and *Q. grisea*; and the number of hybrid partners ranges from 8 (*Q. grisea*) to 1 (*Q. striatula*).

Variation between species within a syngameon in hybridization propensity may be due to a number of factors related to biogeography, ecology, phylogeny, reproductive biology, and genetics. Alternatively, the pattern may be due to chance alone. The appearance of a structured pattern of hybridization within a given syngameon may simply be an artifact of the number of species involved and the number of hybrid combinations. Nonrandom structure in the pattern of interspecific

hybridization among closely related species addresses a fundamental question in interspecific hybridization, namely "Why do some species readily hybridize, while others do not." The first step in answering this question is to demonstrate that there are, in fact, nonrandom patterns of hybridization. To date, this has not been done.

To reject chance in favor of more biologically interesting mechanisms producing patterns of hybridization within syngameons, it is necessary to enumerate all possible network graphs constrained by the observed number of species and hybrid combinations. The observed structure of a given syngameon can then be compared to the sample space of possible network graphs. I use computer simulations to determine whether syngameons, as represented by network graphs, exhibit nonrandom structure. In particular, I examine order statistics and variation in the number of hybridization partners to determine whether hybridizations events are significantly concentrated in a few species and whether the variation in hybrid propensity is greater than chance alone would predict. The objective was to place observations regarding the structure of syngameons on a sound probabilistic foundation.

2 | MATERIALS AND METHODS

I examined eight naturally occurring syngameons (Table 1). Two of these involve insects (carabid beetles and heliconiine butterflies) (Kubota & Sota, 1998; Mallet, Beltrán, Neukirchen, & Linares, 2007); the rest involve plants. Four of the plant syngameons were selected from the literature (Clayberg, 1968; den Nijs & Visser, 1985; Raamsdonk, Wietsma, & Vries, 1992; Sorensson & Brewbaker, 1994); two are unpublished (Southwestern White Oaks and *Boechera*). I have extensive experience with the Southwestern White Oak syngameon, having examined plant-herbivore interactions (Gaylord, Preszler, & Boecklen, 1996; Yarnes & Boecklen, 2005), reproductive biology (Williams, Boecklen, & Howard, 2001), and plant photochemistry (Yarnes, Boecklen, & Salminen, 2007; Yarnes, Boecklen, Tuominen, & Salminen, 2006). The *Boechera* syngameon represents an ongoing collaboration to examine hybridization propensity as a function of genetic distance (D. Bailey, pers. com.). For the *Boechera* syngameon, I examined a set of species that could potentially hybridize and a subset of species that actually do hybridize (*Boechera* subset). For the Heliconius Butterflies syngameon, I considered naturally occurring hybrids alone and then supplemented with artificial hybrids (Mallet et al., 2007).

To test a hypothesis that structure in natural syngameons is simply a function of variation among species in the opportunity to hybridize, I conducted two separate analyses. First, I examined four artificial syngameons (fertility diagrams) selected from the literature and produced by full diallel crosses. Because each species was mated to all other species, hybridization opportunity was equal for all species. The structure of these artificial syngameons was analyzed as described below. Second, I examined the relationship between geographic range and hybridization propensity in the *Boechera* syngameon. I assumed, all other things being equal, that geographic range is related to the opportunity to hybridize. I examined county-level species occurrences for *Boechera* species throughout the Southwestern United States
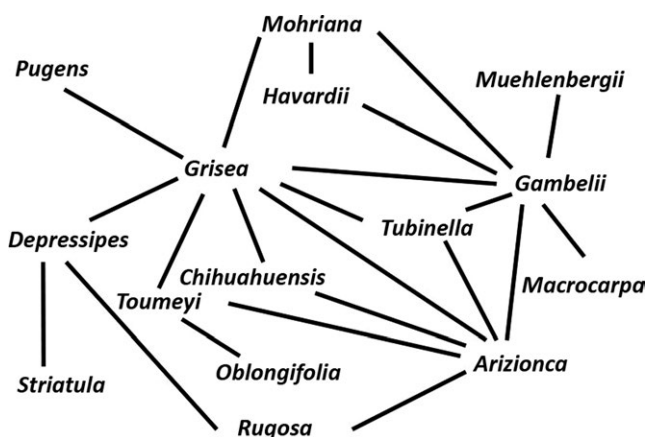

FIGURE 1 Pattern of hybridization between white oaks of the Southwestern United States and Northern Mexico

TABLE 1 Natural and artificial syngameons examined for nonrandom structure based on order statistics and standard deviations of observed numbers of hybrid combinations

Taxa	Species	Hybrid combinations	Hybridization rate	Order statistics				Hybrids	Reference
				1 Observed Expected p-value	2 Observed Expected p-value	3 Observed Expected p-value	SD Observed Expected p-value		
Eastern White Oaks	16	38	0.317	11	11	8	3.357	Natural	Hardin (1975)
				7.9	7.0	6.5	1.721		
				.012	<.001	.024	<.001		
Southwestern White Oaks	15	22	0.210	8	7	6	2.282	Natural	R. Spellenberg (pers. com.)
				5.6	4.8	4.3	1.451		
				.022	.004	.006	.001		
Boechera	58	42	0.025	8	7	5	1.789	Natural	Alexander et al. (2015)
				4.7	4.0	3.7	1.172		D. Bailey (pers. com.)
				.002	<.001	<.001	<.001		
Boechera (subset)	35	42	0.071	8	7	5	1.735	Natural	Alexander et al. (2015)
				5.9	5.1	4.7	1.462		D. Bailey (pers. com.)
				.045	.014	.616	.059		
Asplenium	16	19	0.158	7	6	4	2.062	Natural	Brownsey (1977)
				5.0	4.2	3.7	1.347		
				.039	.009	.710	.002		
Potamogeton	19	18	0.105	6	5	4	1.792	Natural	Clapham et al. (1962)
				4.5	3.7	3.3	1.253		Grant (1981)
				.093	.063	.274	.006		
California Irises	12	14	0.211	5	4	3	1.371	Natural	Lenz (1959)
				4.5	3.8	3.3	1.277		Grant (1981)
				.469	.736	.998	.397		Young (1998)
Carabid Beetles	16	9	0.075	3	3	2	0.957	Natural	Kubota and Sota (1998)
				3.1	2.4	2.1	0.974		
				.846	.409	.995	.616		
Heliconius Butterflies	9	9	0.250	5	3	2	1.323	Natural	Mallet et al. (2007)
				3.8	3.1	2.6	1.127		
				.111	.954	1.000	.277		
Heliconius Butterflies	11	13	0.236	6	4	3	1.567	Natural + Artificial	Mallet et al. (2007)
				4.5	3.7	3.2	1.258		
				.082	.685	.995	.142		
Sinningia Rechsteineria	15	32	0.305	8	8	6	2.282	Artificial	Clayberg (1968)
				7.3	6.4	5.9	1.651		
				.349	.035	.778	.020		
Leucaena	12	47	0.712	11	10	10	1.946	Artificial	Sorensson and Brewbaker (1994)
				10.0	9.4	9.0	1.418		
				.191	.390	.081	.034		

(Continues)

TABLE 1 (Continued)

Taxa	Species	Hybrid combinations	Hybridization rate	Order statistics				Hybrids	Reference
				1 Observed Expected *p*-value	2 Observed Expected *p*-value	3 Observed Expected *p*-value	SD Observed Expected *p*-value		
Allium	7	16	0.761	6	6	5	1.272	Artificial	Van Raamsdonk et al. (1992)
				5.8	5.2	5.0	0.946		
				.777	.248	.987	.146		
Cucumis	11	23	0.418	8	6	6	2.183	Artificial	den Nijs and Visser (1985)
				6.6	5.8	5.2	1.456		
				.106	.691	.249	.008		

(Alexander et al., 2015). I used nonparametric regression to determine whether the number of hybrid partners was related to the number of counties occupied by a species.

I recorded from each natural and artificial syngameon the total number of species, the total number of hybrid combinations, and the number of hybrid combinations for each species. I calculated the hybridization rate for a syngameon as the number of hybrid combinations observed relative to the number possible. I then calculated the order statistics for each syngameon. The first-order statistic is the number of hybrid combinations exhibited by the species with the most hybrid combinations, the second-order statistic is the number of hybrid combinations exhibited by the species with the next most hybrid combinations, and so on. For example, the first-order statistic for the Southwestern White Oak syngameon is 8, while the second-order statistic is 7 (Figure 1). To examine aggregate patterns of hybridization within syngameons, I calculated the standard deviation in the number of hybrid partners across all species in the syngameon.

For each syngameon, I used computer simulations to randomly assign the observed total number hybridization events between the observed total numbers of species. I then calculated all order statistics and the standard deviation in hybrid partners. I repeated each simulation 5,000 times and developed a sampling distribution for each order statistic and for the standard deviation in hybrid partners. I used the sampling distributions to determine the statistical significance of the observed order statistics and standard deviations.

3 | RESULTS

There was considerable variation in the structure of natural syngameons (Table 1). Numbers of species participating in a syngameon ranged from 9 (California Irises syngameon) to 58 (*Boechera* syngameon), while hybridization rates ranged from 0.024 (*Boechera* syngameon) to 0.317 (Eastern White Oak syngameon). Syngameons involving plants typically were more complex than were those involving insects; plant syngameons generally contained more species and more hybrid combinations.

Computer simulations indicated that significant nonrandom structure was a general feature of the natural syngameons, at least for those involving plants. The results are exemplified by the Southwestern White Oak syngameon (Figure 1). The first several order statistics for the number of hybrid combinations by species were significantly larger than were those expected by chance alone (Figure 2). This pattern held for all but one of the natural plant syngameons (California Iris syngameon). Observed values of the order statistics and observed values of the standard deviations in number of hybrid partners were significantly larger than chance alone would predict (Table 1). (The first two order statistics for the *Potamogeton* syngameon were weakly significant, while the standard deviation in number of hybrid partners was highly significant.) The two insect syngameons did not exhibit nonrandom structure; none of the order statistics or standard deviations in the number of hybrid partners were significantly different from that expected by chance alone. Adding artificial hybrids to the Heliconius Butterflies, syngameon did not produce significant nonrandom structure.

As expected, the four artificial syngameons exhibited higher hybridization rates than did the natural syngameons. However, in no
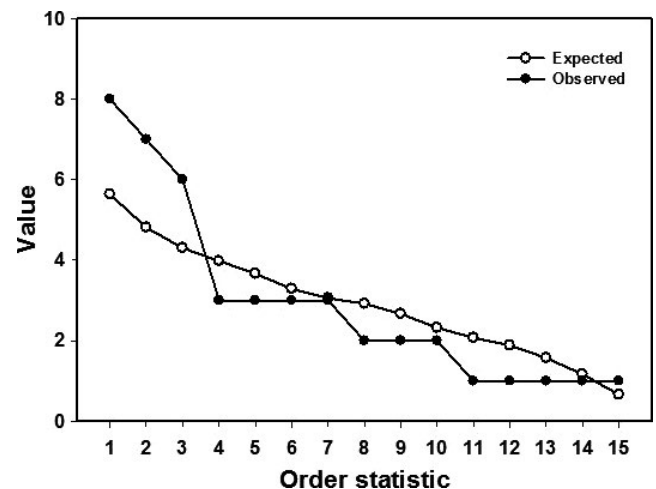

FIGURE 2 Observed and expected order statistics for the number of hybrid combinations between species in the Southwestern White Oak syngameon

case were all possible hybrid combinations realized. Hybridization rates for the artificial syngameons averaged 0.549 and ranged from 0.305 (_Sinningia_ and _Rechsteineria_ syngameon) to 0.761 (_Allium_ syngameon). A Mann–Whitney U-test indicated a highly significant difference between artificial and natural syngameons in hybridization rates (_p_ = .009).

Computer simulations indicated significant nonrandom structure in three of the four artificial syngameons. While the order statistics generally were not significantly different from that expected by chance alone, the standard deviations in the number of hybrid partners were. Only the _Allium_ syngameon did not exhibit nonrandom structure (Table 1).

Nonparametric regression indicated a marginally significant relationship (_p_ = .052) between the number of hybrid partners and number of counties occupied for species in the _Boechera_ syngameon. Geographic distribution explained roughly 26% of the variation in hybridization propensity.

4 | DISCUSSION

I have demonstrated that artificial and natural syngameons, at least for those involving plants, exhibit nonrandom structure with respect to variation in hybridization propensity. I also have demonstrated that patterns of hybridization within these syngameons are typically dominated by a few species. I found no evidence that syngameons involving animals, in this case insects, exhibited patterns of hybridization that differed from those that chance alone would predict. Of course, the sample size for animal syngameons was quite small, and an adequate determination of nonrandom structure in animal syngameons must await a larger compendium of case studies.

Unresolved is the mechanism that produces nonrandom structure in syngameons. For natural syngameons, differences in the geographic distributions of species are a compelling candidate mechanism. Geographically widespread species simply have more opportunities for hybridization than do geographically restricted species. I found partial support for this hypothesis in the _Boechera_ syngameon, as there was a marginally significant positive relationship between a species' geographic range and number of hybrid-producing mating combinations. I recognize that the measure of geographic range, the number of counties occupied, is not optimal. A rigorous test regarding the relationship between geographic range and hybridization propensity must await a more thorough analysis.

Analysis of the artificial syngameons suggests that patterns of hybridization within syngameons are not wholly a function of mating opportunity. The fertility diagrams that I analyzed were produced by full diellel crosses – every species had equal opportunity to hybridize. Nevertheless, I detected significant variation between species in hybridization propensities. This suggests that there are factors intrinsic to species that make them greater or lesser hybridizers. Exactly what these factors are is an open question. Possible factors include plasticity in habitat requirements, timing, and duration of reproductive episodes, ploidy levels (plants), strength of species recognition, and intricacies of mating displays (animals), specificity

of sperm-egg interactions, and cytoplasmic incompatibility (animals). This list is not exhaustive, nor is it mutually exclusive. Of course, the opportunity hypothesis and the intrinsic-factors hypothesis are not mutually exclusive either.

One potential intrinsic factor that deserves greater investigation is phylogenetic position. It is known at a gross level that there is a phylogenetic signature to hybridization propensities. Plants produce natural hybrids more readily than do animals (Mallet, 2005), and production of natural hybrids is not equally distributed across orders of vascular plants (Ellstrand et al., 1996; Whitney et al., 2010). At a finer level, the probability of interspecific hybridization may be related to genetic distance (Chapman & Burke, 2007; Coyne & Orr, 1989). Avid hybridizers may be those species with many close neighbors in genetic space, or they may typically occupy basal or distal positions within their respective clades. A robust test of this hypothesis will require a large compendium of case studies with detailed phylogenies that include all members of a syngameon.

CONFLICT OF INTEREST

None declared.

AUTHOR CONTRIBUTION

WJB analyzed and interpreted all literature and unpublished data, wrote the computer code for the simulations, and drafted and revised the article.

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