

# Functional distance and establishment of non-native species with complex life cycles

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Received: 4 April 2017 / Accepted: 24 January 2018 / Published online: 31 January 2018  
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**Abstract** More than 80% of animals have complex life cycles and undergo distinct changes in ecology and morphology during development. The strength and type of factors regulating each life-stage may differ as an organism may occupy different niches during ontogeny. We examined the functional distance at larval and adult life-stages of two non-native anurans (Green Tree Frog [*Hyla cinerea*] and Bullfrog [*Lithobates catesbeianus*]) that have established in a Chihuahuan Desert anuran assemblage in Big Bend National Park. Both life stages of both non-native species occupied niche space outside of the native assemblage. At the larval stage, the ability of the tadpoles to utilize permanent aquatic habitats and coexist with predatory fishes differentiated the non-

native species from the majority of the native species that are restricted to temporary pools. At the post-metamorphic life stage, each species appears to have established by exploiting unoccupied habitat and trophic niches in the recipient community. The arboreal habits of *H. cinerea* may enable it to utilize resources in microhabitats that are otherwise not used by native species because arboreal frogs are absent from this native assemblage. The large body size of post-metamorphic *L. catesbeianus* may enable it to utilize larger food resources that are otherwise unavailable to the smaller-bodied natives. Separate comparison of larval and adult functional traits between non-natives and the native community may help predict their potential establishment or invasion success as well as aid in the development of stage-specific control or eradication efforts.

**Electronic supplementary material** The online version of this article (<https://doi.org/10.1007/s10530-018-1678-3>) contains supplementary material, which is available to authorized users.

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**Keywords** Amphibians · Larva · Life history · Morphospace · Functional traits · Ontogenetic niche shift

## Introduction

Introductions of non-native species are a driver of global change and can have detrimental impacts on ecological communities (Simberloff et al. 2013). The likelihood of successful establishment and the magnitude of their subsequent impacts of non-native species

is linked to their functional traits (i.e., traits that influence an organism's performance) and the novelty or position of their functional niche relative to the species in the recipient community (Azzurro et al. 2014; Escoriza and Ruhí 2016). Identification of the traits linked with establishment and spread of non-native species has long been a central goal for ecologists (Simberloff et al. 2013). A priori, this information can be used to categorize the potential harm of a newly introduced species on the recipient community and aid in the design and implementation of control and management strategies (Escoriza and Ruhí 2016).

More than 80% of animals possess a complex life cycle (CLC) where larval and adult life stages undergo a distinct change in ecology and morphology (Wilbur 1980). Because the larval and adult stages are discrete, the factors and interactions regulating their population dynamics differ in strength and importance for each life stage (Wilbur 1980; Ruis et al. 2014). When these organisms invade a novel community, each life-stage may be differentially vulnerable to different suites of abiotic factors and antagonistic interactions, thereby affecting the likelihood of successful establishment (Ruis et al. 2014). In several experiments, Ruis et al. (2014) found that biotic resistance mechanisms were acting across multiple life stages with an invasive sea squirt; during early life stages, predation limited abundance of this invasive, whereas competition limited their abundance at adult life stages. Demographic modelling can also identify the life-stage that has the strongest influence on population dynamics to help design management strategies for invasive species with CLCs (Govindarajulu et al. 2005). Yet, few studies have examined the degree of functional trait similarity across multiple life stages of invasive species relative to the native communities they invade.

Anurans possess one of the most distinctive and well-known CLCs, generally characterized by an aquatic larva that metamorphoses into a carnivorous, terrestrial adult (Wilbur 1980). As invasive species, anurans have had detrimental impacts to native biodiversity in recipient communities (Shine 2010). In their examination of the global invasion patterns of Bullfrogs (*Lithobates catesbeianus*) and Cane Toads (*Rhinella marina*), Escoriza and Ruhí (2016) found that both species were functionally distant in recipient communities. However, the authors highlighted several shortcomings that are common with large-scale

macroecological studies, specifically their method may produce an inaccurate description of a local recipient community because they aggregated species' distributions as a proxy for community composition, which is prone to imperfect sampling (Escoriza and Ruhí 2016). In this study, we sought to examine the functional distance of the larval and post-metamorphic life stages of two non-native species in a local assemblage with a known community composition. Specifically, we sought to test if the non-native species exhibited greater phenotypic dissimilarities at one or both life stages relative to members of the recipient community. Because the native and non-native species have been well-studied, we were able to create a functional trait matrix that incorporated detailed life stage-specific traits. We predicted that the non-native species would exhibit greater functional distance compared to the members of the recipient community at both the larval and post-metamorphic life stages and would utilize unoccupied or peripheral niche space relative to of the recipient assemblage.

## Methods

### Study system

Within the last 40 years, breeding populations of two non-native anurans (Bullfrog [*Lithobates catesbeianus*] and Green Treefrog [*Hyla cinerea*]) have established in Big Bend National Park (BBNP) in the Chihuahuan Desert (Dayton et al. 2007; Leavitt and Fitzgerald, 2009; see Supplementary materials for a general site description). Little is known about the establishment of *L. catesbeianus* in BBNP. It was first detected in the mid-1970s, but it is unclear if it naturally expanded from its native range in the lower Rio Grande, expanded from the upper Rio Grande where it has also been introduced, or was a direct introduction in the park (Dayton et al. 2007). A breeding population of *H. cinerea* was first documented in September 2006 (Leavitt et al. 2007). The *H. cinerea* BBNP population is over 500 km outside of its previous range (Conant and Collins 1998; Leavitt et al. 2007) and because of the harsh abiotic conditions between BBNP and the closest native site, natural range expansion seems unlikely and is believed to be human-aided (Leavitt and Fitzgerald, 2009).

Both non-native species first established at the Beaver Pond, a warm spring-fed pond that borders the popular campground in Rio Grande Village. The pond holds water year-round and contains many non-native fish (e.g., Green Sunfish [*Lepomis cyanellus*], Blue Tilapia [*Oreochromis aureus*], and Western Mosquitofish [*Gambusia affinis*]). The site is surrounded by reed stands comprised of Giant Reed (*Arundo donax*) and Common Reed (*Phragmites australis*). The native anuran assemblage around Rio Grande Village is comprised of six species: Rio Grande Leopard Frog (*Lithobates berlandieri*), Texas Toad (*Anaxyrus speciosus*), Red-spotted Toad (*Anaxyrus punctatus*), Couch's Spadefoot Toad (*Scaphiopus couchii*), Great Plains Narrowmouth Toad (*Gastrophylax olivacea*), and Spotted Chirping Frog (*Syrrophus guttillatus*) (Leavitt, unpubl. data).

### Functional traits

We assessed the degree of functional trait resemblance of the adult and larval stages of *L. catesbeianus* and *H. cinerea* relative to the native frog assemblage. For larvae, we selected traits based on the ability to occupy certain breeding habitats (based on their susceptibility to pond drying vs predation; Wellborn et al. 1996), instead of focusing solely on morphology, as tadpoles can exhibit context-dependent morphological plasticity (Schalk 2016). We considered the following tadpole traits: body size (maximum tadpole length), activity level (low, moderate, high), breeding habitat lability (temporary, permanent, or both types), length of larval period (days), habitat guild (benthic or nektonic), feeding strategy (rasping or suspension feeder), palatability to predators (palatable or unpalatable), and thermal tolerance (critical thermal maxima,  $T_{max}$ ) (Table 1; Electronic Supplementary Materials of Appendix 1). Note that *Syrrophus guttillatus* is a direct developer and lacks an aquatic larval stage, therefore it was not included in these analyses. We built distance matrices using these larval traits using Gower's dissimilarity, which can integrate categorical and continuous variables (Anderson 2006). We reduced the variable dimensions with a principal coordinate analysis (PCoA) using the Gower matrices (after Buisson et al. 2013).

For the post-metamorphic life-stage, previous studies have revealed strong relationships between morphology and function (see Schalk et al. 2015 and

references therein). Therefore, we selected 13 external morphological traits associated with the foraging ability and ability to occupy different habitats (Table 2). Traits were measured using a caliper (precision = 0.1 mm) in a standardized manner on specimens collected from the northern Chihuahuan Desert (Electronic Supplementary Materials of Appendix 2). The original measurements were natural log-transformed prior to analysis. We removed the effect of size by calculating residuals based on a generalized least squares linear regression of each measurement against snout-vent-length (SVL; Schalk et al. 2015). We used principal components analysis (PCA) to describe the functional trait space of the recipient assemblage and the non-native species using the 12 size-adjusted traits and SVL. Using PC 1 and 2, Voronoi polygons were created to visualize the functional trait space of the recipient assemblage and the non-native species (Azzurro et al. 2014).

We calculated the functional trait index of originality, which describes the position of the non-native species in the functional space relative to the entire recipient community and is calculated as the distance between the non-native species and the centroid of the recipient community (Buisson et al. 2013). We also calculated the functional uniqueness, which describes how distinctive the non-native species functional traits are compared with other species in the recipient community and is calculated as the nearest neighbor distance between a non-native species and a native species (Buisson et al. 2013). Euclidean distances were used to calculate these functional indices. We tested for mean differences in functional traits between non-native and recipient frog assemblage for both the larval and post-metamorphic life-stages using PERMANOVA with 9999 unrestricted permutations of the normalized predictor data to assess significance (Anderson 2001).

## Results

### Larval life stage

Larvae were differentiated by traits associated with breeding habitat and ecomorphological guild. PCoA resulted in two main axes explaining 80.9% of the total variance (Fig. 1a). PCoA 1 described a gradient that reflected variation along the pond permanence

**Table 1** Traits used to measure tadpole functional diversity of the native species and non-native species (designated by an asterisk [\*])

Species	Activity level	Breeding habitat lability	Length of larval period (days)	Habitat guild	Feeding strategy	Max total tadpole length (mm)	Palatability	T <sub>max</sub> (°C)	References
<i>Lithobates berlandieri</i>	Low	Permanent pools	120	Benthic	Raspers	90	Palatable	31	Altig and McDiarmid (1999), Dayton et al. (2007), Dodd (2013)
<i>Anaxyrus speciosus</i>	Moderate	Temporary pools	18	Benthic	Raspers	28	Unpalatable	34	Wright and Wright (1949), Moore (1976), Altig and McDiarmid (1999), Dayton and Fitzgerald (2001)
<i>Anaxyrus punctatus</i>	Moderate	Temporary pools	56	Benthic	Raspers	30	Unpalatable	30	Altig et al. (1998), Altig and McDiarmid (1999), Dayton and Fitzgerald (2001)
<i>Scaphiophrynus couchii</i>	High	Temporary pools	8	Benthic	Raspers	40	Palatable	42	Newman (1987), (1989), Altig and McDiarmid (1999), Dayton and Fitzgerald (2001)
<i>Gastrophryne olivacea</i>	Moderate	Both	28	Benthic	Suspension feeder	35	Unpalatable	35	Bragg (1947), Wright and Wright (1949), Duellman and Trueb (1986), Altig and McDiarmid (1999)
<i>Lithobates catesbeianus</i> *	Low	Permanent pools	240	Benthic	Raspers	197	Palatable	30	Brattstrom and Lawrence (1962), Woodward (1982, 1983), Altig and McDiarmid (1999), Schooley and Schwemm (2008), Adams et al. (2011)
<i>Hyla cinerea</i> *	Moderate	Both	28	Nektonic	Raspers	60	Palatable	34	Orton (1947), Wright and Wright (1949), Garton and Brandon (1975), Turnipseed and Altig (1975), Blouin (1990), Blouin and Loeb (1991), Altig and McDiarmid (1999), Adams et al. (2011)

The references used to compile the tadpole trait matrix are listed in Appendix 1 (Electronic Supplementary Materials)

**Table 2** Thirteen morphological traits measured on each frog specimen and used for functional distance analyses of the post-metamorphic life stage

Morphological trait	Trait code	Definition of trait
Snout-to-vent length	SVL	Maximum distance from tip of the snout to behind the vent
Mouth width	MW	Horizontal distance measured outside of mouth at its widest point at the dorsal view
Head length	HL	Horizontal distance from the tip the snout to the posterior margin of tympanum
Head width	HW	Horizontal distance measured passing through the tympanum
Head height	HH	Vertical distance from dorsum to ventrum passing through pupil
Forelimb length	FL	Maximum distance of the ulna/radius to the to the tip of the third digit on the hand
Thigh length	TL	Maximum distance of femur while leg is held in a Z pattern at perpendicular angle to vertebral column
Shank length	SL	Maximum distance of tibiofibula while leg is held in a Z pattern
Tarsus-and-foot length	TFL	Maximum distance from beginning of tarsus to the tip of the third digit on the foot while leg is held in a Z pattern
Inter-orbital width	IW	The shortest distance between upper eye lids
Eye diameter	ED	Horizontal distance from eye margin to eye margin
Inter-narial distance	IN	The distance between the midpoints of naris
Narial-to-mouth distance	ND	Vertical distance from bottom of naris to upper lip of the mouth

gradient. Species with positive scores on PCoA 1 tended to inhabit more ephemeral ponds, whereas negative scores were species associated with permanent ponds. Species with lower or negative scores on PCoA 2 tended to be benthic tadpoles with rasping mouthparts, whereas species with higher scores tended to be species that were either suspension feeders (*G. olivacea*) or a nektonic guild member (*H. cinerea*).

Comparing the larvae of the two non-native species relative to the recipient assemblage, *L. catesbeianus* exhibited greater functional originality (centroid distance = 0.7 vs 0.5, respectively) and functional uniqueness (nearest neighbor = 0.2 vs 0.05, respectively) compared to *H. cinerea*. However, larvae of both *H. cinerea* and *L. catesbeianus* were not significantly different in their functional traits compared to the recipient assemblage (PERMANOVA;  $F = 1.849$ ,  $P$  [perm] < 0.1499).

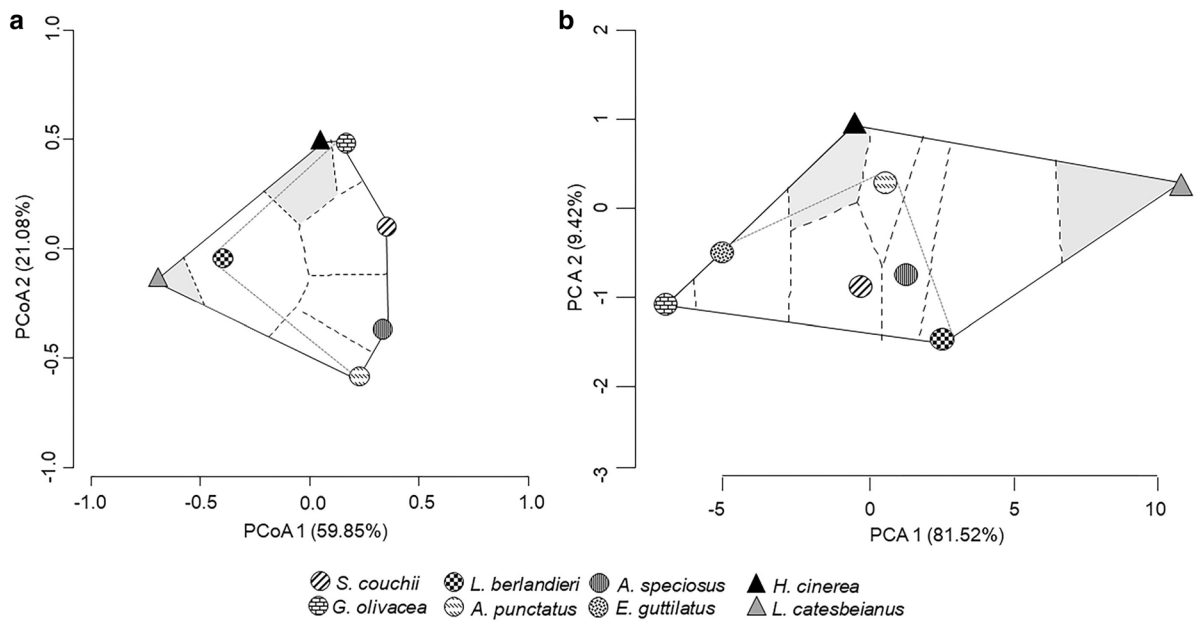
#### Post-metamorphic life stage

Adults were differentiated by traits associated with body size, habitat use and feeding. PCA resulted in two main axes explaining 89.1% of the total variance (Fig. 1b). PCA 1 described a gradient that reflected body size with large-bodied species having positive

scores (Fig. 1b). PCA 2 described a gradient that reflected habitat use and feeding with species with lower or negative scores possessing shorter limbs and narrower mouths, whereas species with higher scores tended to possess longer limbs and wider mouths (Fig. 1b). Post-metamorphic *L. catesbeianus* exhibited greater functional originality (centroid distance = 13.2 vs 1.2, respectively) and functional uniqueness (nearest-neighbor = 7.9 vs 0.2, respectively) from the recipient assemblage compared to *H. cinerea*. The post-metamorphic life stage of *H. cinerea* and *L. catesbeianus* were significantly different in their functional traits compared to the recipient assemblage (PERMANOVA;  $F = 36.48$ ,  $P$  [perm] < 0.0001).

#### Discussion

*Hyla cinerea* and *L. catesbeianus* were functionally divergent relative to native species, and occupied niche space outside or peripheral to the recipient assemblage. The strong environmental filters of arid environments impose constraints on the number and diversity of amphibians that can persist in these environments (Schalk et al. 2015). Because of the



**Fig. 1** Functional position of native (represented by circles) and non-native (represented by triangles) anuran species in the **a** tadpole life stage, and **b** post-metamorphic life stage. The gray

shaded polygons represent the niche space occupied by the non-native species. The solid gray lines represent functional space of the native species assemblage

relatively depauperate regional and local species pools in this system, the recipient assemblage is likely not saturated with species, enabling *H. cinerea* and *L. catesbeianus* to establish and to occupy niches unexploited or underexploited by natives and minimize antagonistic interactions with native species (Azzurro et al. 2014). Similar patterns have been observed with fish invasions where the most abundant non-native species or those most likely to invade successfully were added to the outside or the margins of the morphospace of the recipient assemblage (Azzurro et al. 2014). However, our independent examination of each life stage suggests that functional distance at both life stages may facilitate the establishment of species with CLCs.

Both non-native species were on the periphery or outside of the recipient larval assemblage trait space because they possess traits that enable them to utilize permanent aquatic habitats. Only two native species (*L. berlandieri* and *G. olivacea*) can utilize permanent ponds, whereas the other three native species (*S. couchii*, *A. punctatus*, and *A. speciosus*) occur in ephemeral ponds (Dayton et al. 2007). Experiments have shown that *S. couchii* has a higher activity level and is competitively dominant over those species that occupy longer hydroperiod ponds, but their high

activity level makes *S. couchii* vulnerable to predation and are restricted ephemeral ponds that contain the fewest predators (Dayton and Fitzgerald 2001). The longer larval periods of the non-native species restrict their occurrence to more permanent aquatic habitats and are unlikely to co-occur with *S. couchii*. In the permanent aquatic habitats, larval *L. catesbeianus* have been documented as being superior competitors to larval Green Frogs (*Lithobates clamitans*) and larval Red-legged Frogs (*Rana aurora*) (Werner 1991; Kiesecker et al. 2001). In Florida, larval *H. cinerea* have been shown to be poor competitors when reared in the presence of non-native larval amphibians (Smith 2005). Further, tadpoles that occur in permanent aquatic habitats in this region may not be food limited as recent studies have found that tadpoles tend to be trophic generalists that exhibit trophic plasticity across environmental gradients (Schalk et al. 2017). For example, in their native range, *L. catesbeianus* tadpoles, traditionally thought to be detritivorous or herbivorous, display high degrees of omnivory, and in some cases, may even be carnivorous (Schiesari et al. 2009). Due to a generalized and plastic feeding strategy, the non-native tadpoles may not have experienced limitation of food resources, further enabling their establishment.



Post-metamorphic *H. cinerea* and *L. catesbeianus* appear to be exploiting different niche opportunities that were unoccupied by members of the recipient assemblage. Chihuahuan Desert anurans are functionally redundant due to limited water availability that impose strong environmental filters as coexisting species exhibit high trait overlap (Schalk et al. 2015). In their native range, post-metamorphic *H. cinerea* and *L. catesbeianus* have strong ties to aquatic habitats (Conant and Collins 1998), whereas in the recipient assemblage only *L. berlandieri* is restricted to permanent aquatic habitats (Hillis 1981). Arboreal anurans are absent in native Chihuahuan Desert assemblages (Schalk et al. 2015) and the longer limbs of *H. cinerea* enable it to exploit more arboreal microhabitats not utilized by native species. Leavitt and Fitzgerald (2009) frequently encountered *H. cinerea* in reed microhabitats that encircled the Beaver Pond and they observed that this species has a generalized invertebrate diet with a high proportion of arboreal-dwelling prey. Their generalist diet, coupled with their wider mouth, enables them to exploit a broad range of prey, including novel prey resources occurring outside of their natural range (Leavitt and Fitzgerald 2009). The maximum body size of *L. catesbeianus* (20.3 cm) is nearly double than the largest native species (*L. berlandieri* maximum size = 11.4 cm; Conant and Collins 1998). Ecological implications of body size affects an individual's access to resources and vulnerability to predators (Werner 1986). *Lithobates catesbeianus* have a generalized diet, which is comprised of both invertebrates and vertebrates (Werner et al. 1995). The larger-bodied *L. catesbeianus* have the ability to exploit novel prey resources (i.e., large-bodied prey) that are unavailable to the smaller-bodied native anurans.

Functionally redundant native communities may not be impacted by functionally divergent non-native species because niche overlap and therefore antagonistic interactions (e.g., competition), may be minimized (Escoriza and Ruhí 2016). However, the two non-natives are occupying niche space that is normally unoccupied in this system. From a functional perspective, they may have stronger, and more negative effects on ecosystem processes, such as nutrient cycling, or other native biodiversity as novel sources of predation or competition. Recognizing that each life stage occupies an ecologically distinct niche can be used a priori to understand not only if a species is

potentially harmful (sensu Escoriza and Ruhí, 2016), but also if eradication or control efforts would be more effective by targeting one life stage over another. We suggest that these results should be further investigated of both successful and failed invasions of species with CLCs. Understanding if successful or failed invasions are linked to trait divergence, or a lack thereof, respectively, at a single or at multiple life stages, could provide information to determine the likelihood of establishment and spread of species with CLCs.

**Acknowledgements** We thank L.A. Fitzgerald and T.J. Hibbitts for access to specimens, and L.E. Springer and A. Fields for measuring specimens. We also thank N.F. Angeli, E. Buchholtz, K. Chyn, E. Cunha, J. Kolbe, and D. Walkup and two anonymous reviewers for their constructive comments on the manuscript.

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