



# Red herring or low illumination? The peninsula effect revisited

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## ABSTRACT

**Aim** The peninsula effect is the prediction that the number of species declines from a peninsula's base to its tip. We evaluated evidence for and against the peninsula effect, and conducted a field study designed to test alternative hypotheses for that effect.

**Location** The Florida peninsula, USA.

**Methods** First, we critically reviewed the accumulated literature on peninsula effects; second, we sampled microcrustaceans in palustrine wetlands on the ridges of peninsular Florida. Site selection in our field study accounted for historical effects and partially controlled for habitat effects. Statistical analyses further accounted for habitat effects, leaving peninsular geometry as the remaining causative mechanism for residual variation in species richness regression analyses.

**Results** Our literature review found mixed evidence (49% of cases) for a peninsula effect. However, most study designs did not control for alternative hypotheses, most comparisons of alternative hypotheses were qualitative, and most studies focused on vertebrate animals. Our field study found that freshwater microcrustaceans inhabiting isolated wetlands on Florida's peninsular ridges do not exhibit a peninsula effect. Essentially, no variation in microcrustacean species richness could be attributed to peninsular geometry, but 82.5% of variation in species richness was attributed to habitat and sampling effort.

**Main conclusions** Although our research results support the 'red herring' label for the peninsula effect, our literature review leads us to argue that more illumination (in the form of study design and quantitative analysis) is needed if mechanisms causing the peninsula effect hypothesis are to be resolved. Future studies of peninsula effects need to control for alternative causative hypotheses (geometry, habitat or history) in study design, and compare quantitatively the effects of hypothesized mechanisms on peninsular diversity patterns. Additionally, studies of taxa other than vertebrate animals need to be conducted for generality. Our study may serve as an example of such an approach.

## Keywords

Crustacea, Florida, geometry, habitat, history, North America, peninsula effect, species richness, wetland, zooplankton.

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A comparison of species ranges, population densities and structures, and related factors in peninsular and nonpeninsular species should cast some light on this problem. George Gaylord Simpson, 1964, p. 73

## INTRODUCTION

The peninsula effect is the prediction that the number of species declines from a peninsula's base to its tip (Simpson,

1964). Means & Simberloff (1987) identified three hypotheses (history, habitat, and geometry) that seek to explain species diversity patterns on peninsulas.

The history hypothesis (Means & Simberloff, 1987) proposes that past climatic or geological events caused species distributions, and can cause either a peninsula effect or the lack of one. History may leave its mark because species are still colonizing a geologically young peninsula (Orr, 1960), or because distributions continue to reflect past sea-level or tectonic shifts (Seib, 1980; Lawlor, 1983). This hypothesis assumes that species' distributions continue to bear the mark of past events, and thus more recent environmental changes are relatively inconsequential for species' distributions.

In contrast, the habitat hypothesis argues that current climatic and habitat conditions determine species diversity patterns, and can either cause or prevent a peninsula effect. This hypothesis assumes that considered habitat variables are consistently important to all recorded species, and that species shift their biogeographical distributions rapidly enough to track current habitat patterns.

The geometry hypothesis (or immigration–extinction equilibrium hypothesis) states that species diversity patterns result from an immigration : extinction ratio that decreases at greater distances along a peninsula from the base (the 'mainland'), because immigration originates from the mainland and declines with distance (Simpson, 1964). This hypothesis assumes that immigration rates are scaled to peninsular dimensions so that immigration does not swamp out extinction towards the tip, and that no other immigration sources exert an influence. The geometry hypothesis can only lead to a peninsula effect (or a reverse or dual effect if colonization also occurs from the peninsular tip and is assessed).

Four decades of peninsula-effect research have yielded a mixed record that reflects diverse peninsulas, taxa studied, and methods used. Our review of all relevant papers showed that the peninsula effect was observed in 18 of 37 cases (49%; Table 1). Study authors considered habitat important to species richness pattern for 22 of 37 (59%) peninsular studies, but history (18 of 37; 49%) and geometry (9 of 37; 24%) have also been commonly considered important. In the midst of this history, Busack & Hedges (1984) considered the peninsula effect to be a 'red herring' (a distraction) because they considered habitat to drive species richness, as it does on mainlands. Means & Simberloff (1987) agreed, though the subject remains the focus of continuing discussion. For 11 of the peninsular study cases reported since 1987 (Table 1), habitat was considered important to species richness pattern in 10, while history and geometry were considered important in four and two cases, respectively.

Is the peninsula effect a red herring, or does the record of peninsula-effect research suffer from low illumination? Just as the human eye struggles in dim light, it may be argued that more light needs to be focused on the peninsula effect before its colour and form can be judged. Here, we report on a study with two goals. First, we reviewed the accrued evidence to judge the illumination to date. For clarity, we focused on

geological peninsulas and excluded studies of habitat peninsulas (e.g. Tubelis *et al.*, 2007) because habitat peninsulas are typically smaller in spatial scale and less distinct than geographical peninsulas. Our review is intended to provide context for our effort to address peninsula-effect study design, but it is not a meta-analysis (*sensu* Gurevitch *et al.*, 2001). Second, we report on a study that controlled for the effects of habitat and history and tested for the effects of geometry on microcrustacean assemblages of the Florida peninsula. Microcrustaceans have not been evaluated for peninsula effects, perhaps because they have been assumed to disperse readily (Bohonak & Jenkins, 2003). Biogeographical evidence for microcrustaceans does not clearly predict the presence or absence of a peninsula effect: while microcrustaceans can be carried long distances by waterfowl (Green & Figuerola, 2005), long-distance community assembly may require thousands of years (Stemberger, 1995).

## Peninsulas

Peninsula-effect studies have focused primarily on Baja California (14 studies; 38%) and Florida (seven studies; 19%). Choice of a peninsula, and the application of prior knowledge about that peninsula, are important to studies of peninsula effects: immigrant sources other than a mainland or geological history of the peninsula potentially confuse patterns, as does strong habitat heterogeneity on the peninsula. For example, the Baja California peninsula is derived from a southern-oriented promontory plus a tectonic fragment of the Mexico mainland (Seib, 1980) and is parallel to that coast. Biota that existed on the tectonic fragment, or that disperse across the relatively narrow Gulf of California, may nullify a peninsula effect or generate a dual effect (e.g. Seib, 1980; Brown, 1987; Table 1). Florida has simpler geological origins, but also exhibits dual peninsula effects for some taxa, reflecting immigration from Caribbean or South America sites (Schwartz, 1988; Brown & Opler, 1990; Peck *et al.*, 2005). Florida has also changed in size with Quaternary sea level changes, and its habitats vary from the mainland to the tip (Means & Simberloff, 1987). In contrast, the Iberian peninsula lies across the narrow Strait of Gibraltar from North Africa, but peninsula effects remain important to species density patterns of butterflies and passerine birds (Martin & Gurrea, 1990; González-Taboada *et al.*, 2007). Clearly, biogeographical history varies among peninsulas: no single hypothesis should be expected to fit all peninsulas equally well, and hypotheses are not mutually exclusive. The goal of peninsula-effect studies should be to discern the relative importance of the different causative hypotheses summarized above while accounting for the biogeographical context of the peninsula and taxa in the study design.

## Taxa

A peninsula effect has been observed for some taxonomic groups on some peninsulas, but it is not a general pattern. Are

**Table 1** Summary of previous empirical research on the peninsula effect.

Peninsulas	Organisms studied	Species density units or richness	Peninsula effect?	History	Habitat	Geometry	Method to discern mechanism	Reference
North America	Mammals	58,275 km <sup>2</sup>	Yes			•	Reasoning	Simpson, 1964
Baja California	Birds	64,750 km <sup>2</sup>	Yes			•	Reasoning	MacArthur & Wilson, 1967
Florida	Birds	64,750 km <sup>2</sup>	Yes			•	Reasoning	MacArthur & Wilson, 1967
Yucatan	Birds	64,750 km <sup>2</sup>	Yes			•	Reasoning	MacArthur & Wilson, 1967
North America	Breeding birds	60,606 km <sup>2</sup>	Yes	•	•		Reasoning	Cook, 1969
Contiguous USA (Florida)	Amphibians, reptiles	25,900 km <sup>2</sup>	Yes				None*	Kiester, 1971
Baja California	Heteromyid rodents	Richness	Yes			•	Model	Taylor & Regal, 1978a,b
Baja California	Reptiles	c. 16 km <sup>2</sup>	Dual	•	•		Reasoning	Seib, 1980
Lake Winniepeg	Carabid beetles	Richness	No				Reasoning	Taylor & Pfannmüller, 1981
Lake Winniepeg	Mammals	Richness	No				Reasoning	Taylor & Pfannmüller, 1981
Baja California	Artiodactyl mammals	Richness	Yes	•	•	•	Reasoning	Lawlor, 1983
Baja California	Carnivore mammals	Richness	No	•	•	•	Reasoning	Lawlor, 1983
Baja California	Geomyid rodents	Richness	No	•	•	•	Reasoning	Lawlor, 1983
Baja California	Heteromyid rodents	Richness	Yes	•	•	•	Reasoning	Lawlor, 1983
Baja California	Insectivore mammals	Richness	No	•	•	•	Reasoning	Lawlor, 1983
Baja California	Lagomorph mammals	Richness	No	•	•	•	Reasoning	Lawlor, 1983
Baja California	Lizards	100 km <sup>2</sup>	No	•	•	•	Reasoning	Lawlor, 1983
Florida	Lizards	100 km <sup>2</sup>	Yes	•	•		Reasoning	Busack & Hedges, 1984
Iberian	Lizards	100 km <sup>2</sup>	No	•	•		Reasoning	Busack & Hedges, 1984
Yucatan	Lizards	100 km <sup>2</sup>	No	•	•		Reasoning	Busack & Hedges, 1984
Baja California	Scorpions	Richness	No	•	•		Reasoning	Busack & Hedges, 1984
Florida	Scorpions	Richness	No			•	Reasoning	Due & Polis, 1986
Italy	Scorpions	Richness	Yes			•	Reasoning	Due & Polis, 1986
Maine, USA	Forest vegetation	Richness	Yes			•	Reasoning	Due & Polis, 1986
Baja California	Butterflies	1° latitude	Yes	•	•		DCA, regression†	Milne & Forman, 1986
Florida	Amphibians, reptiles	Richness	Dual	•	•		Reasoning	Brown, 1987
Aleutian	Woody plants	52-km-wide transects	Yes	•	•		Reasoning	Means & Simberloff, 1987
Florida	Woody plants	64.5-km-wide transects	No	•	•		Reasoning	Schwartz, 1988
Seward	Woody plants	52-km-wide transects	Dual	•	•		Reasoning	Schwartz, 1988
Florida	Butterflies	60-km-wide transects	No	•	•		Reasoning	Schwartz, 1988
Iberian	Butterflies	1° lat × 1° long	Dual	•	•	•	Reasoning	Brown & Opler, 1990
Baja California	Birds	2° lat	Yes	•	•		Multiple regression‡	Martin & Gurrea, 1990
Europe	Mammals	Richness	Yes	•	•		Reasoning	Wiggins, 1999
Baja California	Ants	1.9° lat	Yes	•	•		Reasoning	Baquero & Telleria, 2001
Korea	Butterflies	0.5° lat × 0.5° long	No			•	Reasoning	Johnson & Ward, 2002
			Yes			•	Multiple regression§	Choi, 2004

Table 1 Continued

Peninsulas	Organisms studied	Species density units or richness	Peninsula effect?	History	Habitat	Geometry	Method to discern mechanism	Reference
Florida	Carabid beetle guilds	0.5° lat	Dual	•	•		Reasoning	Peck <i>et al.</i> , 2005
Spain	Passerine birds	100, 900 & 2500 km <sup>2</sup>	Yes	•	•	•	SA, CAR, AIC	González-Taboada <i>et al.</i> , 2007

Papers are listed chronologically; studies of habitat peninsulas (e.g. forests) are not listed. Some authors concluded that dual peninsula effects occurred (species richness of two assemblages decline along the peninsula in opposing directions), and that the mechanisms of history, habitat and/or geometry were important to species richness pattern.

SA, spatial autocorrelation; CAR, conditional autoregressive models; AIC, Akaike information criterion.

\*Focused on broader latitudinal patterns.

†Detrended correspondence analysis of nine peninsulas.

‡Forward stepwise multiple regression, where species density was a function of position and topography variables; no collinearity analysis.

§Forward stepwise multiple regression, where species density was a function of position and altitude, with area as a covariate.

some taxa more likely than others to exhibit an effect? Of the 33 animal cases (Table 1), studies of volant taxa (primarily birds and insects,  $n = 13$ ) were more likely to conclude that a peninsula effect (including dual effects) existed than were studies of non-volant taxa ( $\chi^2$ -test,  $P = 0.043$ ). For example, six out of six studies on birds observed a peninsula effect (or dual effect), whereas five of 10 studies on mammals observed that pattern. Otherwise, no other significant differences among taxa or dispersal modes were apparent. Relatively few (four of 37) peninsula-effect studies have been conducted on vegetation, and studies of animal taxa have been biased towards vertebrates (23 of 33 animal cases). More studies of plants and invertebrates are needed to test for cross-taxon generality.

## Methods applied

Beyond differences in the peninsulas and taxa studied, the methods applied have varied over four decades, especially in terms of the units of species diversity measured and the means to discern between competing hypotheses. The peninsula-effect concept was originally proposed by Simpson (1964) as an accessory to his analysis of mammalian species density (species per large quadrat) throughout North America. Since then, peninsula-effect studies have been based on species density (22 of 37 studies; Table 1) or species richness (species per locality; 15 of 37 studies). This difference is important because the two methods assay species diversity patterns differently (Gotelli & Colwell, 2001). Species density may be considered equivalent to gamma diversity or total diversity for a region (Kiester, 1971), especially when quadrats are large and habitats that are patchy within a quadrat have been censused thoroughly. Species density calculations are based on species richness plus an assumption that population densities are comparable among quadrats (Gotelli & Colwell, 2001). On the other hand, species richness is simpler in its assumptions, and may be considered equivalent to alpha diversity because samples are local (Whittaker *et al.*, 2001).

Should a study of mechanisms causing species diversity patterns on a peninsula be based on species density or species richness? The answer depends on one's goals, the data at hand, and the method to discern potential mechanisms. Species density may be appropriate if one wishes to test for a peninsula effect in its original terms (Simpson, 1964), extract data from existing compendia (e.g. county records), and then express those data for large units of area without collecting local data on habitat and history. However, that approach is not optimal for all cases, and may not shed sufficient light without sophisticated analyses (e.g. those employed by González-Taboada *et al.*, 2007). A peninsula effect need not be studied using species density given the continent-scale focus of its origin (Simpson, 1964) and the assumption of equal population densities among quadrats (Gotelli & Colwell, 2001). If species diversity is sampled from localities that are distinct from the surrounding matrix, and if habitat and history are analysed for those localities to test hypothesized mechanisms, then species richness is most appropriate. Regardless of the

path chosen, peninsula-effect studies should address this decision explicitly and consider the relative merits of species density and species richness (Gotelli & Colwell, 2001; Whittaker *et al.*, 2001). We chose to measure species richness for the study reported here because: (1) we sampled palustrine wetlands of limited spatial extent and embedded in a terrestrial matrix; (2) we considered it important to assess habitat effects on local assemblages directly; and (3) we attempted to control for potential history effects by site selection.

An especially striking pattern from the peninsula-effect literature is that most analyses (32 of 37) have employed only verbal arguments regarding the importance of history, habitat or geometry in shaping species diversity patterns. Reasoned, verbal arguments may be wise, but their evidence remains unquantified, which frustrates the assessment of relative contributions of the three hypothesized mechanisms and retrospective assessment of accrued evidence. Studies designed *a priori* to control for or quantify the effects of history or habitat are rare, so analyses of the three hypotheses have typically been *post hoc*. The result is a continuing need for greater illumination on the problem, although this criticism is tempered by recognition that computational statistics and study design methods have advanced markedly over the four decades since a peninsula effect was hypothesized.

Our study controlled for history by sample design, and for habitat by statistical analysis: hypothesized mechanisms that can either cause or obscure a peninsula effect. We then tested for the potential effects of peninsular geometry, which can only cause a peninsula effect, and compared the relative importance of habitat and geometry.

## MATERIALS AND METHODS

We studied microcrustacean species richness in 31 palustrine wetlands spanning four degrees of latitude on ancient ridges of Florida. The four major ridges (Fig. 1) were shaped by rising and receding sea levels and have been exposed for *c.* 100,000 years (Myers & Ewel, 1990). Historical differences among sites on the peninsula could be controlled for by focusing the study on these ridges, and habitat differences were also partially controlled for because the ridges have similar elevations and soils. The ridges have been subject to some human modification, but we selected wetlands within protected areas to minimize the potential effects of disturbance.

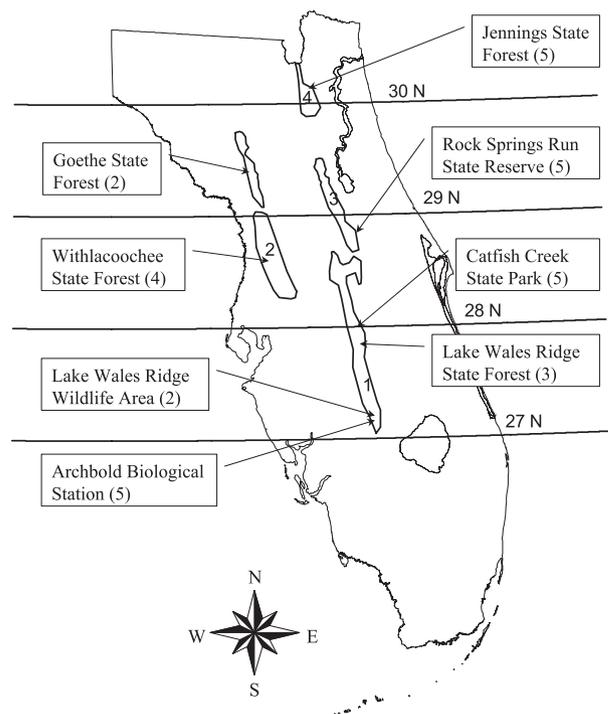
Freshwater microcrustaceans disperse passively among discrete habitats (Green & Figuerola, 2005; Havel & Medley, 2006). Unlike active dispersers, microcrustacean distributions cannot be confused by behavioural habitat selection upon arrival, assuming that phoretic dispersal is diffuse and frequent enough in geological history to generate broad distributions.

Multiple wetlands were sampled within sites on the ridges (e.g. within a state preserve). All wetlands were dry during spring and summer of 2004, but filled with a succession of three hurricanes (Charlie, Frances and Jeanne) that made landfall between 13 August and 21 September. Thus, wetlands filled nearly simultaneously, which aided sampling design. On

the other hand, sampling was delayed until November 2004 because sites were inaccessible (fallen trees, etc.). Sampling was conducted monthly through the wet season, ending in April 2005 or earlier if a wetland had dried. Repeated sampling is customary for microcrustaceans to obtain a full census of species richness for short-lived organisms (e.g. Schneider & Frost, 1996; Jenkins *et al.*, 2003).

Wetland locations were recorded on-site using a Garmin global positioning system (GPSMAP 76). Area (ha) and centre-to-centre distance to the nearest water body (km) were calculated using ArcMap (ArcGIS ver. 9.0; ESRI, Redlands, CA, USA) based on polygons created from digital orthographic quarterquad (DOQQ) aerial photographs. Geographical information system (GIS) datalayers (DOQQs, digital elevation models and National Wetland Inventory maps) plus *in situ* observations were used to classify ponds as hydrologically connected or isolated.

Organisms were sampled using 64- $\mu$ m mesh dipnets swept *c.* 1 m in each habitat type within a wetland at each sampling event. Samples were collected and preserved with Lugol's solution (Pennak, 1989) for identification in the laboratory. Microcrustaceans were identified to species (or lowest taxonomic level) using several taxonomic keys (Edmondson, 1959; Pennak, 1989; Thorp & Covich, 2001), and data were recorded as species presence/absence. Fish presence or absence was



**Figure 1** Florida peninsula with sampled ridges of similar history. Ridge numbers: 1, Lake Wales Ridge; 2, Brooksville Ridge; 3, Mount Dora Ridge; 4, Trail Ridge. Multiple wetlands were sampled at each named place on a ridge (e.g. Jennings State Forest on the Trail Ridge included five sampled wetlands).

recorded at each site based on net samples and visual observations made during sampling. Given different hydroperiods among wetlands, microcrustacean species–sample curves were used to evaluate sampling adequacy, and the number of samples collected per wetland (hereafter, sampling effort) was used as a variable in analyses.

Field observations and information gathered from park biologists were used to classify wetlands as having subannual or superannual hydroperiods. Mean canopy openness (%) and total transmitted light ( $\text{MJ m}^{-2} \text{day}^{-1}$ ) were estimated using triplicate digital photographs of canopy (using a 180° fisheye lens) with GAP LIGHT ANALYZER ver. 2.0 (Frazer *et al.*, 1999). Canopy photographs of two wetlands were unsuitable for analysis: mean values for openness and transmitted light from nine similar wetlands were substituted in statistical analyses. Water temperature (°C), dissolved oxygen ( $\text{mg L}^{-1}$ ), pH and conductivity (mS) were recorded at each site with a YSI portable meter (model 556; Yellow Springs Instruments, Yellow Springs, OH, USA). A 500-mL water sample was collected at each site by combining four subsamples from varying locations at each wetland. Samples were transported on ice to the laboratory, where each sample was analysed for chlorophyll *a* ( $\text{mg L}^{-1}$ ), pheophytin ( $\text{mg L}^{-1}$ ), total phosphorus ( $\text{mg L}^{-1}$ ) and water hardness ( $\text{mg L}^{-1}$ ) as in Clesceri *et al.* (1989), and total nitrogen ( $\text{mg L}^{-1}$ ) as in Crumpton *et al.* (1992). Minimum, mean and maximum values of each water quality variable were computed for statistical analyses. Environmental variables were transformed for normality if needed (based on Shapiro–Wilk tests) prior to analyses. Precipitation and temperature data were also obtained per site from state climatologist records.

Because some wetlands dried before others, sample number varied among wetlands. We evaluated the effect of sampling effort on species richness by linear regression of species richness against number of samples. Next, species richness vs. habitat variables (plus sampling effort) was analysed by multiple regression to test for the effect of habitat heterogeneity among wetlands on species richness. Five alternative regression models were developed *a priori* to test hypotheses that species richness was related to habitat variables: (1) mean limnological conditions in each wetland; (2) extremes of limnological conditions in each wetland; (3) local landscape conditions (distance to nearest wetland, presence of surficial hydrological connection to another water body, temporary or permanent hydrology, canopy cover variables); (4) regional conditions (e.g. total wet season precipitation); and (5) a combination of the variables retained in all prior models. We used backward elimination multiple regression (SPSS ver. 11.5; SPSS Inc., Chicago, IL, USA) to select environmental variables that regressed with species richness and that were not strongly collinear. Backward elimination regression is more robust to multicollinearity than forward selection (Zar, 1999). Multicollinearity among retained environmental variables was further evaluated using tolerance indices, where a value  $\geq 0.1$  indicated that collinearity had been sufficiently reduced (Quinn & Keough, 2002). Alternative models were compared

using adjusted  $R^2$ , the modified Akaike information criterion ( $\text{AIC}_c$ ) and AIC model weights ( $w_i$ ; Anderson *et al.*, 2000).

Residuals of the resulting best model (variation in species richness not predicted by retained habitat variables) were then regressed against latitudinal position on the Florida peninsula, to test the hypothesis that any variation in species richness not explained by habitat (and sampling effort) would be explained by peninsular position. If both habitat and peninsular position accounted for species richness, the relative importance of each could then be evaluated by comparing regressions. We also tested our ability to account for historical effects by including ridges as an independent factor in regressions: if species richness varied among ridges, then ridges were not actually equivalent.

Finally, a nestedness analysis was conducted based on 500 null matrices and recommended settings of the BINMATNEST program (Rodríguez-Gironés & Santamaría, 2006). This analysis evaluated the pattern of assemblage structure among all wetlands sampled to test the prediction that assemblages further from the mainland should be nested subsets of assemblages closer to the mainland, as would be the case if a peninsula effect occurred. Alternatively, assemblages may be nested, but the pattern may not correspond to peninsular position: this possibility was tested by also examining the regression of species richness and latitude.

## RESULTS

Species richness ranged from two to 18 microcrustaceans per wetland. Overall, 53 different species of microcrustacean were identified, including 41 cladocerans, 10 copepods and two ostracods (see Appendix S1 in Supporting Information). Due to differences in wetland hydroperiod and hurricane-related inaccessibility, sites were sampled one to six times. Species–sample curves indicated that species richness was not fully inventoried in most wetlands, and species richness was significantly related to the number of samples ( $R^2 = 0.362$ ,  $P < 0.001$ ), so we used the number of samples collected as a variable in all multiple regressions discussed below. Species richness did not vary significantly among ridges ( $P = 0.803$ ), indicating no effect of historical or habitat differences among ridges.

Species richness was significantly related to sampling effort and latitudinal position on the Florida peninsula (adjusted  $R^2 = 0.353$ ,  $P = 0.001$ ), but latitude was not a significant predictor of species richness ( $P = 0.219$ ) in this multiple regression or alone in a simple regression ( $R^2 = 0.028$ ,  $P = 0.369$ ; Table 2). Therefore, an initial assessment comparable with most peninsula-effect studies indicated that no peninsula effect existed for microcrustaceans in isolated wetlands of Florida. Species distributions were significantly nested (matrix temperature = 19.3,  $P < 0.001$ ), but the least species-rich wetlands were not nearest the peninsular tip, as evidenced by the lack of a significant regression with latitude.

Wetlands varied in habitat conditions (Appendix S2). Total wet season precipitation ranged from 94 to 127 cm, reflecting

the active 2004 hurricane season. Wetland surface areas ranged from 0.07 to 6.45 ha and mean temperature ranged from 12 to 27°C, with more northerly wetlands generally reaching cooler temperatures (minimum = 7°C) and southerly wetlands reaching hotter temperatures (maximum = 26°C). All wetlands were acidic (mean pH = 3.92 ± 0.44 SD), and generally low in nutrients and chlorophyll *a* (a measure of phytoplankton biomass), although chlorophyll *a* and conductivity varied among wetlands.

Multiple regressions of species richness vs. habitat variables (plus sampling effort) were all significant ( $P < 0.001$ ) but varied in adjusted  $R^2$ ,  $AIC_c$  and  $w_i$  (Table 2). The best model applied a combination of limnological, local and regional habitat variables plus sampling effort to predict microcrustacean species richness ( $R^2 = 0.825$ ; Table 2).

Linear regression of residuals from that best habitat model against latitude did not account for any variation in residual species richness and was not significant (model E, Table 2). Thus the strong majority of variation in microcrustacean species richness in palustrine wetlands on the ridges of the Florida peninsula was due to habitat effects that did not correspond to peninsular position, and virtually no evidence existed for a peninsula effect caused by an immigration–extinction equilibrium. Also, there was no evidence for a dual peninsula effect: all species observed are commonly observed in North America and no species were Caribbean-centered.

## DISCUSSION

We found no evidence that microcrustaceans inhabiting palustrine wetlands of Florida's ridges exhibit a peninsula effect. Instead, our conclusion is similar to that of Busack & Hedges (1984) and Means & Simberloff (1987): habitat variation primarily determined microcrustacean species richness pattern among palustrine wetlands of Florida's ridges. We can confidently assign primary credit to habitat because we controlled for variation in history among wetlands, collected habitat variables and accounted statistically for habitat to permit a test of the third hypothesis, peninsular geometry. In addition, we expect that habitat was important for the nested pattern of species richness observed, though other mechanisms may also apply (Wright & Reeves, 1992; Ulrich & Gotelli, 2007).

The lack of a peninsula effect in this study suggests that freshwater microcrustaceans have fully colonized the c. 100,000-year-old Florida peninsula. In contrast, some copepod species have not yet extended their post-glacial distribution (c. 10,000 years) in the north-eastern USA (Stemberger, 1995). Based on these two studies, the time for microcrustacean assemblages fully to accrue species over large geographical areas may be estimated as ranging up to tens of thousands of years. The ecological literature is replete with colonization experiments (e.g. Maguire, 1963; Jenkins & Buikema, 1998; Cohen & Shurin, 2003; Allen, 2007), but these short-term and local experiments cannot help answer ques-

tions of 'how long?' or 'how far?' at biogeographical scales. Clearly, the answers to questions of microcrustacean dispersal, including invasions and community assembly, require analyses at multiple scales beyond those customary in ecological experiments (e.g. Havel & Medley, 2006).

We think an important difference between this study and most prior studies of peninsula effects is our approach to study design and statistical analyses. Several other studies have applied similar statistical analyses (Martin & Gurrea, 1990; Choi, 2004; González-Taboada *et al.*, 2007), but these examples are notably rare in the history of peninsula-effect studies. Thus, our study supports the argument that the peninsula effect is a red herring (Busack & Hedges, 1984), but we think that this label was assigned prematurely: a peninsula effect and its potential causes have not been fully tested for multiple taxa on multiple peninsulas. Habitat may yet be shown to consistently serve as a red herring for the peninsula effect among multiple peninsulas and taxa, but too little light has been cast on the subject to discern a general pattern. In the hope that more studies conducted like ours will help illuminate the topic, we offer a recipe for better tests of peninsula effects, as follows:

- (1) Learn about the biogeographical context of your peninsula. Select sites with similar geological and environmental history along a peninsula. This process controls for the effects of history.
- (2) Predict patterns to be observed, given the taxa and peninsula to be studied. Develop alternative predictions to test and steer data collection. Decide on species density vs. species richness and justify that decision.
- (3) Sample thoroughly and collect quantitative habitat data relevant to the study assemblage.
- (4) Conduct multiple regression (use backward elimination and judiciously eliminate multicollinearities) for species richness as a function of habitat variables. Include sampling effort as an independent variable if it varied among sites (alternatively, use rarefaction to estimate species richness; Gotelli & Colwell, 2001). Retain regression residuals. If comparing alternative regression models, employ  $AIC_c$  and AIC model weights (Anderson *et al.*, 2000).
- (5) Regress residuals (from step 4) against peninsular position. A significant negative slope indicates an immigration–extinction effect and the  $R^2$  relative to that of habitat compares the two effects.
- (6) Optional: select sites with similar habitats but different histories in step 1 above, substitute 'history' for 'habitat' in steps 2–5, and conduct steps 1–5 above to test for a history effect. Also collect habitat data to test your *a priori* assumption of habitat similarity.

Of course, other approaches (e.g. González-Taboada *et al.*, 2007) also provide quantitative tests of alternative hypotheses. Our hope is that quantitative analyses of competing hypotheses will help illuminate an important biogeographical concept that has lingered in shadow for over 40 years and has been likened to a fishy distraction (Busack & Hedges, 1984).

**Table 2** Results of regressions to predict species richness among 31 wetlands over c. 4° latitude.

Model description	$R^2$	F	P-value	$w_i$
A Species richness: sampling effort	0.362	16.466	< 0.001	
B Species richness: latitude	0.028	0.833	0.369	
C Species richness: latitude + sampling effort	0.353*	9.190	0.001	
Habitat multiple regressions sorted by $w_i$	Adjusted $R^2$	F	P-value	$w_i$
D (1) Species richness: combination of 2–5	0.825	16.707	< 0.001	55.84
(2) Species richness: aquatic extremes + canopy + fish	0.741	10.559	< 0.001	67.92
(3) Species richness: aquatic means + canopy + fish	0.542	12.833	< 0.001	71.98
(4) Species richness: local landscape, including temporary/permanent, area, connected, distance	0.413	11.559	< 0.001	78.14
(5) Species richness: regional conditions	0.432	8.614	< 0.001	78.64
E Residuals of regression D1 (above): latitude	$R^2$	F	P-value	
	0.000	0.011	0.918	

A, B and E were bivariate linear regressions; C and D were backward-elimination multiple regressions with additional evaluation of multicollinearity. Listed transformations (e.g.  $\log_{10}$ ) were applied to improve normality and homogeneity of variance (see Appendix S2 for untransformed variables).

min., minimum; max., maximum; avg., average; sqrt, square root; DO, dissolved oxygen; TP, total phosphorus; conduct., conductivity; chl $a$ , chlorophyll  $a$ .

\*Adjusted  $R^2$  is reported for model C because it is a multiple regression.

Finally, we note that Simpson (1964; see opening quote) suggested that peninsular species diversity patterns be compared with those elsewhere. In our study, we did what so many have done before us: we sampled on the Florida peninsula, but did not sample further afield on the continent. Future peninsula-effect studies would do well to sample beyond the peninsula for comparison.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Species recorded, sorted in decreasing order of the number of wetlands in which each species was recorded.

**Appendix S2** Wetland locations and physicochemical data.

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## BIOSKETCHES

**Dave Jenkins** is interested in the role of dispersal in ecology and biogeography, and thinks ‘isolated’ wetlands are great ecosystems in which to test related concepts.

**Deb Rinne** was a graduate student in the UCF Wetland Ecology Lab; this paper is based on her MSc thesis.

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