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Article

The Importance of Scaling for Detecting Community Patterns: Success and Failure in Assemblages of Introduced Species

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Abstract: Community saturation can help to explain why biological invasions fail. However, previous research has documented inconsistent relationships between failed invasions (*i.e.*, an invasive species colonizes but goes extinct) and the number of species present in the invaded community. We use data from bird communities of the Hawaiian island of Oahu, which supports a community of 38 successfully established introduced birds and where 37 species were introduced but went extinct (failed invasions). We develop a modified approach to evaluate the effects of community saturation on invasion failure. Our method accounts (1) for the number of species present (NSP) when the species goes extinct rather than during its introduction; and (2) scaling patterns in bird body mass distributions that accounts for the hierarchical organization of ecosystems and the fact that interaction strength amongst species varies with scale. We found that when using NSP at the time of extinction, NSP was higher for failed introductions as compared to successful introductions, supporting the idea that increasing species richness and putative community saturation mediate invasion resistance. Accounting for scale-specific patterns in body size distributions further improved the relationship between NSP and introduction failure. Results show that a better understanding

of invasion outcomes can be obtained when scale-specific community structure is accounted for in the analysis.

Keywords: body size; community assembly; community structure; competition; Hawaii; Introduced; Oahu

1. Introduction

Biological invasions provide an opportunity for testing ecological theory, including assessments of the role of competition in community assembly and structure. Invasion biologists have suggested that invasion resistance increases in strongly interacting communities as community saturation is approached [1–3]. Previous analysis used the numbers of invasive species present (NSP) as a surrogate of potential community saturation and compared NSP for failed *versus* successful introductions [4,5]. Because invasive and remaining native species are strongly segregated by habitat and altitude, the outcome of invasion success or failure in ecosystems is most likely associated with the structural and functional attributes of communities, and interactions between, species [6,7]. Supporting the idea that the structure of the existing community influences the relative success of invasions, Moulton [4] found higher NSP values for failed introductions in the lowland avifauna of the Hawaiian island of Oahu. A higher failure rate for introductions when more introduced species were present suggested that the bird community was approaching saturation. However, NSP values were significantly higher for failed introductions on Oahu only for introductions up to the year 1960, but when the species list was updated through 1981 [4], NSP values were not-significantly ($p < 0.235$) higher for failed introductions, despite the number of invasive species having increased. This finding is counterintuitive because if competition and invasion resistance increase as communities become saturated, then differences in NSP between failed and successful introductions should be even more pronounced following additional introductions.

The approach based on NSP by Moulton and colleagues [4,8,9] is useful to evaluate the role of community saturation on invasion success or failure. A recent study of successful *versus* unsuccessful vertebrate introductions in Florida, USA, supported a NSP effect for mammals, herpetofauna and fish but not for birds [5]. Refinements of the method are needed to explore its full potential and for testing current theories about mechanisms conferring resistance to invasions. Here we advance an alternative that allows for improved inference. This is achieved by using NSP at the time a species goes extinct (NSP_e) to evaluate unsuccessful establishment instead of NSP at the time a species is introduced (NSP_i). NSP_e considers that introduction is not equivalent to establishment, meaning that a species can be introduced in a first stage to an ecosystem which then can, but must not necessarily, become established in a second stage [10]. Second, although NSP may serve as a surrogate of relative invasion resistance [11], the quantitative evaluation of competitive interactions is impossible with census data, which is a potentially severe limitation in any analysis of competitive effects, and thus the importance of community saturation. We therefore take an indirect approach to assess competitive interactions qualitatively within the community of introduced birds. We use techniques and theory which account for scale-specific structures and processes in the environment and which is mirrored in the structure of ecological communities [12–14], particularly birds [15,16].

Peterson *et al.* [17] suggested that groups of species operating at the same range of scale may represent strongly competitive units regardless of their taxonomic or functional similarity. Exploiting resources at different spatiotemporal scales in the environment reduces the strength of interactions between differently sized species relative to interactions among animals that operate at similar scales [18]. Consider the hypothetical invasion of a bird community by a raven that weighs 1000 g and occupies a large home range. The addition of the raven to the community increases the NSP by one, but it is unlikely that it interacts with the extant small-bodied birds as intensely as another small-bodied bird would. It may be ecologically more relevant to assess how the raven interacts with other species of similar body mass.

Animal body mass is a useful index for linking animal community structure with scales of resource use (see [19]). The average adult body mass of a species strongly correlates with many ecological attributes, including energy use, movement, home range size, and foraging [20,21]. The ecological scales at which a species operates corresponds with average species body mass, making body mass a useful index of the scale at which an animal perceives and exploits its environment [12,22].

Here we assess the importance of scale-specific patterns and NSP_e of introduction outcomes. We test the hypothesis that relationships between introduction success and failures as a function of NSP become better discernable in analyses that account for scale *versus* approaches that do not.

2. Experimental Section

Study Site and Analyses

The Hawaiian island of Oahu has lost nearly its entire native avifauna in lowland habitats (<1000 m elevation) since European colonization [23]. A diverse community of introduced birds has replaced the native avifauna. The development of this introduced community has been well documented, and the fate of species introductions is relatively well known [4,24–28]. These species represent a community distinct from that of the surviving native species. Native species are mostly restricted to native forests at high elevations [23,24,29]. Non-indigenous species are mostly restricted to lower elevation landscapes with a high degree of anthropogenic transformation [30]. The present introduced bird community includes approximately 38 successfully established species, primarily passeriformes (26 species), but also four Galliformes, three Columbiformes, two Psittacidae, one Tytonidae, one Apodidae, and one Ciconidae. Thirty-seven species from the same families have been introduced but subsequently failed to establish breeding populations or went extinct after a period of establishment in the island.

We used the species list of Moulton [4] for passeriform introductions with the addition of all other families of introduced birds [23,27,31]. This list includes all known avian introductions to Oahu, both successful and unsuccessful, since European colonization through the year 1993. Although introduction effort was not available for most species, limiting an assessment of propagule size on introduction success [32], we highlight that we were interested in the consequences of community assembly processes when invaders have become established for some time in the ecosystem rather than in the factors that potentially mediate their establishment *per se*.

Introductions were ranked by year of introduction, and the number of other introduced species (NSP) present in the community was calculated for each successful or failed introduction (Table 1). The NSP values for the successfully introduced and unsuccessfully introduced species were then compared using

a 1-tailed t-test (if the data were normally distributed and variance homogenous) or using a 1-tailed Mann-Whitney U-test. In our analysis we compared NSP for successful introductions with both the NSP at the time of introduction and NSP at the time of extinction for failed introductions. This comparison is appropriate because if competition is one of the factors driving species success or failure, it is the number of species present in the community at the time of extinction that is most relevant. For species that failed immediately, NSP at the time of introduction and extinction are identical.

Table 1. Order and fate of introductions of birds introduced to Oahu. Numbers in parentheses after the birds' names indicate membership of the body size group revealed by the discontinuity analysis.

Species	Year of Introduction	Year of Extinction	NSP _i	NSP _e
<i>Gallus gallus</i> (3)	1000	1935	0	31
<i>Columba livia</i> (2)	1850		1	
<i>Callipepla californica</i> (3)	1855	1941	2	28
<i>Alauda arvensis</i> (2)	1870		3	
<i>Numida meleagris</i> (3)	1874	1908	4	15
<i>Phasianus colchicus</i> (3)	1875		5	
<i>Passer domesticus</i> (2)	1879		8	
<i>Acridotheres tristis</i> (3)	1879		8	
<i>Streptopelia chinensis</i> (3)	1879		8	
<i>Lonchura punctulata</i> (1)	1883		10	
<i>Carpodacus mexicanus</i> (2)	1883		10	
<i>Pavo cristatus</i> (3)	1896		11	
<i>Amandava amandava</i> (1)	1900		13	
<i>Garrulax canorus</i> (2)	1900		13	
<i>Colinus virginianus</i> (3)	1906	1926	14	23
<i>Syrnaticus soemmerringii</i> (3)	1907	1920	15	14
<i>Coturnix chinensis</i> (2)	1921	1927	14	22
<i>Geopelia striata</i> (2)	1922		19	
<i>Grallina cyanoleuca</i> (3)	1922	1936	19	31
<i>Geopelia humeralis</i> (3)	1922	1938	19	27
<i>Geophaps lophotes</i> (3)	1922	1927	19	22
<i>Phaps chalcoptera</i> (3)	1922	1927	19	22
<i>Alectoris chukar</i> (3)	1923	1928	20	23
<i>Chalcophaps indica</i> (3)	1924	1928	22	23
<i>Rollulus rouloul</i> (3)	1924	1930	22	27
<i>Rhipidura leucophrys</i> (2)	1926	1937	23	29
<i>Parus varius</i> (2)	1928	1963	23	30
<i>Leiothrix lutea</i> (2)	1928		23	
<i>Geopelia cuneata</i> (2)	1928	1931	23	28
<i>Paroaria coronata</i> (2)	1928		23	
<i>Mimus polyglottos</i> (2)	1928		23	
<i>Streptopelia decaocto</i> (3)	1928	1944	23	24
<i>Zosterops japonica</i> (1)	1929		27	
<i>Cettia diphone</i> (1)	1929		27	

Table 1. Cont.

Species	Year of Introduction	Year of Extinction	NSP _i	NSP _e
<i>Cyanoptila cyanomelana</i> (2)	1929	1958	27	24
<i>Cardinalis cardinalis</i> (2)	1929		27	
<i>Paroaria dominicana</i> (2)	1931	1932	29	31
<i>Sturnella neglecta</i> (3)	1931	1937	29	29
<i>Copsychus saularis</i> (2)	1932	1976	31	40
<i>Chrysolophus pictus</i> (3)	1932	1941	31	28
<i>Chrysolophus amherstiae</i> (3)	1932	1941	31	28
<i>Lophura nycthemera</i> (3)	1932		31	28
<i>Passerina cyanea</i> (1)	1934		31	31
<i>Lonchura malacca</i> (1)	1936		31	
<i>Copsychus malabaricus</i> (2)	1940		26	
<i>Passerina leclancherii</i> (1)	1941		28	24
<i>Garrulax caerulatus</i> (3)	1947		24	
<i>Syrnaticus reevesii</i> (3)	1957		24	39
<i>Francolinus pondicerianus</i> (3)	1959		25	
<i>Bubulcus ibis</i> (3)	1959		25	
<i>Gracula religiosa</i> (3)	1960		26	
<i>Tyto alba</i> (3)	1961		27	
<i>Vidua macroura</i> (1)	1962		30	38
<i>Gallus sonneratii</i> (3)	1962		30	41
<i>Meleagris gallopavo</i> (3)	1962		30	40
<i>Serinus mozambicus</i> (1)	1964		31	
<i>Lonchura oryzivora</i> (2)	1964		31	
<i>Estrilda troglodytes</i> (1)	1965		39	38
<i>Estrilda melpoda</i> (1)	1965		39	
<i>Lagonosticta senagala</i> (1)	1965		39	41
<i>Estrilda caerulescens</i> (1)	1965		39	
<i>Uraeginthus angolensis</i> (1)	1965		39	42
<i>Uraeginthus bengalus</i> (1)	1965		39	38
<i>Sicalis flaveola</i> (2)	1965		39	
<i>Pycnonotus jocosus</i> (2)	1965		39	
<i>Pycnonotus cafer</i> (2)	1966		39	
<i>Francolinus erckelii</i> (3)	1967		40	
<i>Uraeginthus cycnocephala</i> (1)	1969		40	42
<i>Myiopsitta monachus</i> (3)	1970		41	38
<i>Nandayus nenday</i> (3)	1971		41	40
<i>Tiaris olivacea</i> (1)	1974		41	
<i>Amazona viridigenalis</i> (3)	1975		42	
<i>Estrilda astrild</i> (1)	1981		38	
<i>Psittacula krameri</i> (3)	1982		36	
<i>Lonchura malabarica</i> (1)	1984		37	

We also determined NSP values among species operating at the same range of scale to account for strong interactions among those species as compared to interactions among species operating at different

scales. We used the methods similar to those described in [33] to objectively determine scaling patterns in the established bird community, based on their body mass distributions, which reflects the hierarchical organization of ecosystems [12,22].

Body mass estimates were obtained from [34] and body mass distributions were analyzed using simulations that compared the observed data with a null distribution established by estimating a continuous unimodal kernel distribution of the log-transformed data [35]. Significance of discontinuities in the data (significantly large gaps between adjacent body masses that represent transitions between scaling regimes [22]) was determined by calculating the probability that the observed discontinuities were randomly generated by comparing observed values with the output of 1000 simulations from the null distribution. Groups of species of similar body mass (body mass aggregations) are defined by the discontinuities detected. Species within a body mass aggregation are assumed to exploit their environment at the same range of scale [12,17,36]. After determining the significant discontinuities in the successfully introduced Oahu bird community, we proceeded to compare NSP values as described above, but comparisons were made within body mass aggregations to take into account the strong interactions among species operating at the same scale as compared to relatively weak interactions among species operating at different scales. Body mass estimates for three failed species (*Serinus leucopygius*, *Luscinia akahige* and *Erithacus komadori*) were unavailable so these species were omitted from our analysis.

Finally, we used correlation analysis to test the hypothesis that the strength of association between the number of extinctions and the NSP at the time of extinction becomes stronger when scale is accounted for in the analyses. We also examined whether extinction rates show non-linear patterns, *i.e.*, whether extinctions are increased upon a threshold in the number of species composing the invaded community. These relationships were examined for the unscaled data and for each body mass aggregation group identified by the discontinuity analysis.

3. Results and Discussion

Of the 75 bird species that have been introduced to Oahu as of 1991, 38 introductions were successful and 37 failed [4,27]. The mean NSP value for the successful introductions was 24.6 and for unsuccessful introductions the mean NSP_i was 25.4 (Table 2). There was no difference between these two groups ($p = 0.374$, 1 tailed t-test). However, when we considered NSP_e for unsuccessful introductions median values for successful introductions (26) and for unsuccessful introductions (29) were significantly different ($p = 0.026$, 1 tailed Mann-Whitney U-test; Table 2).

The body mass distribution of the introduced bird community of Oahu was significantly discontinuous; that is, we identified birds operating in different scaling regimes. Two very distinct breaks in the body mass distribution were detected, leading to the conclusion that there were three distinct body mass aggregations or scales (Figure 1). From an ecological perspective the bird species composing these body mass aggregations presumably exploit the environment at small, meso and large scales, respectively. The first aggregation of species had body masses ranging from 7.5 to 14 g (11 successful and 8 unsuccessful species; Table 1). Body masses of the second aggregation of birds ranged from 20 to 56 g (15 successful and 7 unsuccessful; Table 1). The third aggregation included birds that weighed more than 86 g; contrary to patterns observed in body mass aggregations 1 and 2, we observed almost double

the number of unsuccessful *vs.* successful introductions in this third body mass group (12 successful and 22 unsuccessful; Table 1).

Table 2. Mean or median NSP_i or NSP_e values for Oahu birds in three different body mass categories, with body mass data pooled, and for unscaled data. Number of observations is given in parentheses.

	Number of Species Present (NSP)		
	Successful	Failed	<i>p</i> -value
Body mass aggregation 1 NSP _i	6.27(11)	8.88(8)**	0.090
Body mass aggregation 1 NSP _e	6.27(11)	10.5(8)**	0.020
Body mass aggregation 2 NSP _i *	11(15)	11(7)**	0.137
Body mass aggregation 2 NSP _e	8.33(15)	12.57(7)**	0.026
Body mass aggregation 3 NSP _i *	8(12)	9.5(22)**	0.144
Body mass aggregation 3 NSP _e	8(12)	9.77(22)**	0.047
Pooled data NSP _i *	8(38)	11(37)	0.051
Pooled data NSP _e *	8(38)	12(37)	0.002
Unscaled data NSP _i	24.58(38)	25.43(37)	0.374
Unscaled data NSP _e *	26(38)	29(37)	0.026

* Comparisons made with the Mann-Whitney Rank Sum Test because either the data were not normally distributed or variances were not equal. Otherwise, comparisons represent t-tests.

** Numbers in parentheses indicate the number of observations that are specific to each scale.

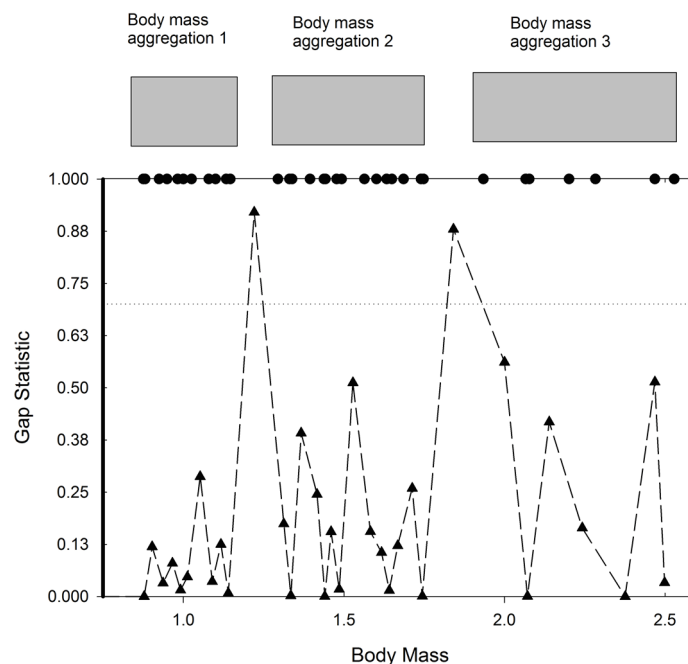


Figure 1. Body mass structure of the Oahu introduced bird community. The upper axis shows the location (black circles) of successfully introduced bird species along a log body mass axis. Gray rectangles represent the three identified body mass aggregations. Gap Statistic is a measure of the deviation of the observed body mass distribution from the unimodal null model.

Comparing the NSP_i values of successful *versus* unsuccessful species, probability values were marginally significant (*p* = 0.09) for small-scale species in the first body mass category, and

nonsignificant for the other two body mass categories ($p > 0.10$; Table 2). Comparison of NSP_e values for failed species yielded significant results for all three body mass aggregations ($p < 0.05$; Table 2). When data were pooled across body mass aggregations, the comparison between successful and failed species was either marginal ($p = 0.05$), using NSP_i or highly significant ($p < 0.01$), using NSP_e .

Correlations between NSP at the time of extinction and the number of extinctions were positive and significant when conducted with both unscaled data and for the data segregated into three scales. These correlations were higher for the scaled data in all three body mass categories ($r = 0.540, 0.683, \text{ and } 0.507$, respectively) than for the unscaled data ($r = 0.467$). Comparing the number of failed invasions *versus* the NSP at the time of extinction suggests that a threshold may be present (Figure 2 upper panel). Only two species were lost from the community when there were fewer than 20 species present, but when more than 20 species were present the number of extinctions dramatically increased. Similar nonlinear patterns were found when examining the same relationships within body mass groups with the number of extinctions increasing upon thresholds of 12 species for body mass aggregations 1 and 2 and 9 species for body mass aggregation 3 (Figure 2 lower panel).

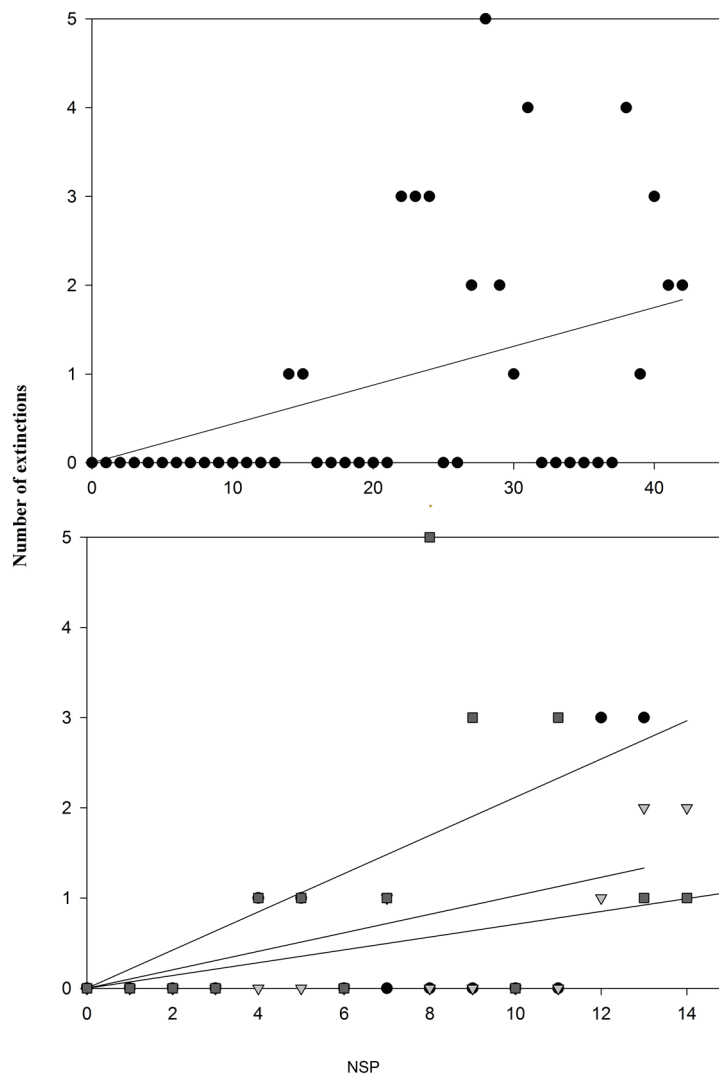


Figure 2. Plots of the number of extinctions *versus* the number of species present at the time of extinction. Upper panel, all species; Lower panel, species segregated into three body mass categories.

Our results indicate that calculating NSP at the time of extinction, rather than at the time of introduction, and scaling the community to account for differences in interaction strength between species in different size classes both represent improvements over earlier analyses of introduced bird communities [4,5]. For species that went extinct, calculating NSP at the time of extinction rather than at the time of introduction is less conservative and assays patterns of invasion resistance in the community more realistically. Scaling communities prior to such an analysis also represents an improvement, because of the strong interaction among species operating over the same or similar ranges of scale relative to species operating at grossly different scales.

If competition is one of the forces in the community assembly process [37], we would expect that to be manifested at the time of extinction rather than the time of introduction. For example, *Callipepla californica* was introduced in 1855, when only one other species was present. However, it went extinct in 1941 when 28 species were present. Clearly the consideration of NSP at the time of introduction is less appropriate than NSP at the time of extinction. For species that went extinct immediately following introduction, NSP_e and NSP_i are identical.

Correlations between NSP at the time of extinction and the number of extinctions were positive and significant but higher for the scaled data in all three body mass categories than for the unscaled data. We also found that thresholds exist when comparing the number of failed introductions with the NSP at the time of extinction, and also these patterns were consistently found for unscaled data or data scaled into body mass aggregations. This finding of thresholds is consistent with the conclusions derived from computer models [1,2] and suggests that if competitive interactions are indeed the ultimate factor shaping the island bird community, they do not become significant in producing community structure until saturation is approached. Most importantly, and supporting our hypothesis, this relationship is strengthened when the community is segregated into body size categories, accounting for scaling relationships in ecosystems.

Scaling interactions within communities is one of many different approaches that have been taken to compartmentalize biological interactions in communities. However, most efforts are based on phylogeny and thus ignore an often substantial portion of the community. The model of Peterson *et al.* [17] accounts for both phylogeny and scale. We used that model to guide our analysis based on segregating the community based on species body size. The two breaks in scale (discontinuities) we identified and used to guide our aggregation of the community into three body mass categories are prominent, unmistakable, and based on an objective identification of scaling patterns in ecological communities. Our results support the model of Peterson *et al.* [17] that suggests the importance of scaling species interactions and conclusions suggesting the prominent role of competition in structuring animal communities [8,24,38–41]. However, it should be noted that differences in taxonomic and guild diversity exist among the three body size categories. Specifically, all species in the first body mass category are passeriformes, and all except two (*Cettia diphone* and *Zosterops japonica*) are primarily seed eaters [42]. There is more taxonomic and guild diversity among species in the second body mass category, which consists of both Passeriformes and Columbiformes. The largest body mass category consists of six different families with a greater diversity of feeding strategies. Additionally, the size range of members of the largest body size category is greater than the body size range of species in the first two body size categories.

Despite this higher variability in the third body mass aggregation, we found that the number of failed invasions is comparatively higher in this aggregation (22 species or 65% of all species found in this

aggregation) compared to aggregations 1 (8 species; 42%) and 2 (7 species; 31%). Previous research has shown that establishment success is more likely in large-bodied birds [43], but our analysis suggests that larger-bodied species also fail more often to persist in the bird communities. That extinction risk is higher in birds with higher body masses is consistent with patterns found for large mammals [44] and other bird communities [45]. Single or combined effects related to small population sizes, lower reproductive rates and larger home or geographic ranges have been suggested to increase the extinction risk in large-bodied birds [45]. Although the causes mediating the patterns observed for birds in the largest body mass aggregation on Oahu Island, cannot be ascertained with the data at hand, the pattern itself is consistent with a large body of theory and empirical findings.

4. Conclusions

Our study underscores the usefulness of body mass as a predictor of ecological processes [12,19,22,46,47]. Our results particularly underscore the benefit for elucidating clearer patterns of invasion outcomes when body mass is partitioned into scale-specific patterns. Further research is warranted to assess the generality of pattern found in this study also for other organism groups.

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Author Contributions

Craig R. Allen developed and wrote the first draft of the paper. David G. Angeler, Michael P. Moulton, and Crawford S. Holling contributed to writing and idea development.

Conflicts of Interest

The authors declare no conflict of interest.

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