Authors for correspondence:
Xingfeng Si
e-mail: sixf@des.ecnu.edu.cn
Eben Goodale
e-mail: eben.goodale@outlook.com

†These authors contributed equally to the study.

‡Present address: Department of Biological Sciences, California State University, Long Beach, 1250 Bellflower Boulevard, Long Beach, CA 90840, USA.

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Interspecific sociality alters the colonization and extinction rates of birds on subtropical reservoir islands

Ari E. Martínez[1,†,‡], Xingfeng Si[2,†], Liping Zhou[1,3], Di Zeng[2], Ping Ding[4] and Eben Goodale[1,5]

[1]Guangxi Key Laboratory of Forest Ecology and Conservation, College of Forestry, Guangxi University, 100 DaXue Road, Nanning, Guangxi 530004, People's Republic of China
[2]Zhejiang Zhoushan Archipelago Observation and Research Station, Institute of Eco-Chongming, Zhejiang Tiantong Forest Ecosystem National Observation and Research Station, School of Ecological and Environmental Sciences, East China Normal University, Shanghai 200241, People's Republic of China
[3]Kunming Natural History Museum of Zoology, Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming, Yunnan 650223, People's Republic of China
[4]MOE Key Laboratory of Biosystems Homeostasis and Protection, College of Life Sciences, Zhejiang University, Hangzhou, Zhejiang 310058, People's Republic of China
[5]Department of Health and Environmental Sciences, Xi'an Jiaotong-Liverpool University, Suzhou, Jiangsu 215123, People's Republic of China

AEM, 0000-0001-9711-4669; XS, 0000-0003-4465-2759; LZ, 0000-0001-7750-7262; DZ, 0000-0003-2780-3738; PD, 0000-0001-5825-0932; EG, 0000-0003-3403-2847

Island biogeography theory has proved a robust approach to predicting island biodiversity on the assumption of species equivalency. However, species differ in their grouping behaviour and are entangled by complex interactions in island communities, such as competition and mutualism. We here investigated whether intra- and/or interspecific sociality may influence biogeographic patterns, by affecting movement between islands or persistence on them. We classified bird species in a subtropical reservoir island system into subcommunities based on their propensity to join monospecific and mixed-species flocks. We found that subcommunities which had high propensity to flock interspecifically had higher colonization rates and lower extinction rates over a 10-year period. Intraspecific sociality increased colonization in the same analysis. A phylogenetically corrected analysis confirmed the importance of interspecific sociality, but not intraspecific sociality. Group-living could enable higher risk crossings, with greater vigilance also linked to higher foraging efficiency, enabling colonization or long-term persistence on islands. Further, if group members are other species, competition can be minimized. Future studies should investigate different kinds of island systems, considering positive species interactions driven by social behaviour as potential drivers of community assembly on islands.

This article is part of the theme issue 'Mixed-species groups and aggregations: shaping ecological and behavioural patterns and processes'.

1. Introduction

The equilibrium theory of island biogeography (ETIB) posits that island area and isolation from a mainland source influences community dynamics [1], and has led to a proliferation of empirical and theoretical developments since its inception [2,3], including the application to the conservation of fragmented landscapes [4]. A major tenet of ETIB is that increasing island area lowers extinction rates (i.e. the area effect) as larger islands will have more resources, which lowers competition among species and allows larger population sizes. In addition, larger areas may increase colonization rates because of their higher chance of detection by dispersing species (the target effect [5]). Conversely, ETIB also states that increasing isolation lowers colonization rates (i.e. the distance effect), and further could reduce the chance that extinction may be offset within the same sampling

period by recolonization from the mainland (the rescue effect; [6]). These factors, as well as speciation on larger islands or archipelagos [7], interact to produce a dynamic equilibrium of the number of species on islands [8]. A large amount of empirical evidence has generally supported patterns of colonization and extinction rates across various animal and plant taxa consistent with ETIB [9,10]. Island size and isolation can also be incorporated into more complex modelling such as metacommunity dynamics, which explores dispersal between multiple populations living in different patches [11].

As ETIB is focused on the number of species, it cannot explain the composition of communities, limiting its usage for some applications such as evaluating species responses to fragmentation [4]. More recent studies have taken into account the extent to which different functional traits that underlie species interactions may influence colonization and extinction rates. For example, Jacquet et al. [12] examined the trait distribution of reef fishes and found that small and isolated reefs support a higher proportion of large-sized fishes. Si et al. [13] integrated species traits and the evolutionary history of birds into the framework of ETIB for islands in man-made lakes, and in a global analysis Triantis et al. [14] recently found oceanic island bird communities to be similar to each other in traits such as body plan, as well as phylogeny. Functional traits in these studies have been used to investigate competitive processes or habitat filtering that may underlie or influence colonization and extinction rates, and further affect community structure [15–17]. However, functional traits may also contribute to, or be influenced by, alternative ecological processes such as facilitation or mutualism [18,19].

An expanded model of ETIB that integrates species traits could include the influence of facilitation, an often-overlooked process, on colonization and extinction rates. For example, variation in dispersal ability is a fundamental factor explaining the distribution of species in island systems [20]. Yet the dispersal of some species may be influenced by other species: some species may facilitate the colonization of islands for other species, or preclude the establishment of other species (priority effects; [21]). Facilitation among groups of invasive species has been posited to also be likely in explaining patterns of establishment, as an alternative to competition [22]. Nonetheless, while the inclusion of facilitation in ecological theory has become more widespread, empirical tests still lag behind investigations of competition.

Facilitation among individuals of the same species or among individuals of different species may manifest itself in terms of increased dispersal, as monospecific or mixed-species groups may help species travel farther and more efficiently when flying together, or dispersal may manifest itself more frequently as travelling in groups may be less risky [23,24]. Further, the presence of such groups on the island could enhance foraging or reduce predation risk there [25–27], allowing the colonization of species that subsequently arrive [21]. Longer-term persistence and extinction of species on islands, too, may be influenced by the presence of other species already on the island, and not just in competitive ways. For example, social information could be increased by heterospecifics, particularly gregarious species that must provide information for conspecifics [28–30].

Thousand Island Lake (TIL; Zhejiang Province, China) provides an ideal study system in which to test these hypotheses. A series of land-bridge islands formed in 1959 by dam construction, it provides a unique opportunity to explore patterns of community assembly in a fragmented system [31,32]. As mixed-species flocks have been previously studied in fragments (e.g. [33,34]), but not in island systems, we originally selected TIL as a site to determine how ETIB could be related to such flocks. On the other hand, the islands at TIL are very close to each other, suggesting that this system may have more in common with fragmented patches than with systems where movement is very limited, like oceanic islands. In this sense, these islands may be viewed as patches within a metacommunity, whereby the proximity to the nearest island might have a greater influence on colonization and extinction rates than the degree of isolation from the mainland.

We tested how sociality influences colonization and extinction rates, by categorizing birds into subcommunities by their flocking propensities, and also understanding the effect of island size, isolation from the mainland and distance to the closest neighbouring island. We predicted that both high interspecific and intraspecific flocking propensities would have higher colonization rates and lower extinction rates than subcommunities with lower flocking propensities. We particularly anticipated a strong effect of interspecific sociality, because mixed-species groups are able to provide benefits without as much competition as monospecific groups, since the niches of different individual participants are more varied [35,36]. Because the trait of sociality may be influenced by evolutionary history, we also conducted phylogenetically controlled analyses [37].

2. Methods

(a) Study site

The TIL system (29°22′–29°50′ N, 118°34′–119°15′ E), is a series of islands formed by the creation of a man-made lake in 1959, harbouring patches of generally homogeneous sub-temperate coniferous and deciduous secondary forest. A subset of these islands ($n = 36$; fig. 2 in Si et al. [13]) were selected that encompass as much variation in area and isolation as possible, to conduct long-term studies of bird community dynamics. These islands range from 0.57 ha to ca 1300 ha (mean = 49 ± 215 (s.d.) ha), from about a 20 m separation from the nearest shore of the mainland to over 3.71 km (mean = 1470 ± 868 m), and from a 9 m separation from the nearest island to 103 m (mean = 42 ± 22 m) [38].

(b) Bird surveys

Bird communities were surveyed based on permanent transects on the set of 36 study islands annually from 2007 to 2016. The number of these transects on each island was proportional to the logarithm of island area, and the length of each transect was maximally 400 m, but was allowed to be less than 400 m on small islands (table S1 in Si et al. [13]). These permanent transects were visited 30 times per year from 2007 to 2010, and 18 times per year from 2011 to 2016, a total of 228 times for each transect over the 10 year surveys, in order to census bird communities in both summer (April to June) and winter (November to January) seasons sufficiently. During the field survey, we counted a species as present when a species was seen or heard on a given transect on the island for that year, excluding high-flying individuals passing overhead, and individuals not identified with confidence to species [38]. We also excluded from the analyses infrequently recorded species (less than five observations during the course of the 10 year survey), resulting in a total of 79 species. From that total, we removed all migrant species to reach a sample size of 46 species (one species, Parus minor, had a colonization rate that could not be calculated because it was always present, and so $n = 45$ for analyses of colonization).

Table 1. The subcommunities for which colonization and extinction rates were measured based on flocking propensity, and the total number of species that were represented in them.

flocking category	interspecific grouping	intraspecific grouping	number of total species
S0	species never in mixed-species flocks	usually solitary	11
S1	species never in mixed-species flocks	usually in monospecific groups	9
F0	species participates in mixed-species flocks	species in pairs or solitary in mixed-species flocks	9
F1	species participates in mixed-species flocks	monospecific groups that join mixed-species flocks	17

(c) Evaluation of flocking propensities

We surveyed the group of study islands from 26 February to 8 March 2017, 25 September to 15 October 2020 and 3–9 October 2021, walking the same permanent transects on the islands described above, to quantify flocking propensity (per cent of individuals in flocks) of the species in the TIL bird community. These two times of year are representative of winter mixed-species flocks (February, March) and flocks that include migrant species (September, October). A mixed-species flock was defined as two or more individuals that moved in the same direction for at least 5 min. We spent a similar sampling effort to quantify flocking propensity along multiple 400–1000 m transects on the mainland; flocking propensity was similar on the mainland as on islands and was not affected by island size or isolation. We derived flocking propensities with direct field observations for 34 of the 46 species and supplemented these data for the remaining species from the literature [39]. In total, we saw 218 flocks and 8647 individual birds for this part of the fieldwork. Note that it is possible that imperfect detection could influence the exact values of these rates, but because colonization and extinction rates are transitions between absence and presence (and thus should be independent of the overall number of absences or presences; see calculations below), the relationships between these rates, flocking propensity and island size/isolation should not be altered.

Given that monospecific and mixed-species flocks may have different dynamics, we evaluated flocking propensities based on a combination of species tendencies to be in monospecific and/or mixed-species flocks, grouping bird species into one of four mutually exclusive subcommunities by their propensities (table 1). Any species that was ever seen in mixed-species flocks was considered to be interspecifically gregarious, and species with monospecific group sizes of 2.5 individuals (close to a natural divide in the data, larger than a pair of birds) or more were considered to be intraspecifically gregarious.

(d) Data analysis

We calculated species-specific annual colonization and extinction rates on each island using metapopulation models developed by Gotelli & Taylor [40]. In this study, we thus defined the *colonization rate* (Pc) as the probability that a species present on an island in one year was absent in the previous year, and the *extinction rate* (Pe) as the probability that a species present on an island was absent in the next year. Note that this is a measure of 'local (to the island) extinction rate', which we refer to as 'extinction rate' for simplicity. During two consecutive years, four possible transitions can be observed (AA, AP, PA and PP) where A is the absence and P is the presence. Thus, the colonization and extinction rates were calculated as:

$$Pc_{i,j} = \frac{N_{i,j}(\mathrm{AP})}{[N_{i,j}(\mathrm{AP}) + N_{i,j}(\mathrm{AA})]}$$
$$Pe_{i,j} = \frac{N_{i,j}(\mathrm{PA})}{[N_{i,j}(\mathrm{PA}) + N_{i,j}(\mathrm{PP})]}.$$

Where $N_{i,j}$ (AP), $N_{i,j}$ (AA), $N_{i,j}$ (PA) and $N_{i,j}$ (PP) are the number of observed transitions (AP, AA, PA and PP) for species i on island j, and with species equally weighted. Rosenzweig & Clark [41] originally proposed this method; a limitation is that it does not incorporate rescue effects [40]. However, previous studies did not observe rescue effects to be an important factor for birds at TIL because all islands are quite close to each other [38]. For island-level rates, colonization (Pc_j) and local extinction (Pe_j) rates for each island were then averaged across all species in the subcommunity [42,43].

We modelled the island-level colonization and extinction rates of species as responding to flocking propensity, island area and island isolation. For isolation, we tested the influence of the distance to the mainland from any island, and the distance to the nearest island. We conducted three sets of separate analyses based on different classifications of flocking propensity. In the first set of analyses, we grouped species into four levels of flocking propensities (table 1), with S0 set as the reference category. In subsequent analyses, we used a simpler classification scheme where species were classified as either mixed-species flocking or solitary species (F versus S in the terminology of table 1), or monospecific flocking or solitary species (1 versus 0). Given that colonization and extinction rates were measured as proportions, we modelled the response using a beta regression, using the package 'betareg' in the R statistical environment. We used an information theoretic approach to compare nested models (in which subsets of the predictors are compared in separate models from the global model), considering all candidate models within difference in Akaike information criterion corrected for small sample size (ΔAIC_c) of 2 of the best model. We then plotted parameter estimates and 95% confidence intervals, estimated using a parametric bootstrap, to evaluate the relevance of the predictor variables for the candidate set of models.

(e) Tests of phylogenetic independence

To evaluate whether the results were driven by phylogenetic relationships, we downloaded the phylogenetic tree from BirdTree (http://birdtree.org) by pruning the global tree to include only the 46 recorded bird species from this study for extinction analyses, or 45 for colonization, under the option of 'Hackett All Species: a set of 10 000 trees with 9993 OTUs each' [44]. We then sampled 1000 pseudo-posterior distributions and constructed the maximum clade credibility tree using mean node heights by the software TreeAnnonator v.1.8.2 of the BEAST package [45].

We did not have enough data on colonization and extinction rates per species per island to compare rates between species as a function of island size (the colonization data had many zeros, and the extinction data many datapoints that were not calculable (NA)). Instead, we pooled overall colonization and extinction rates for each species across all islands to look for evidence of phylogenetic independence in the patterns we observed. In these phylogenetical generalized least square (PGLS) models, conducted with the 'caper' package, we followed the same process as above, first running models that had four
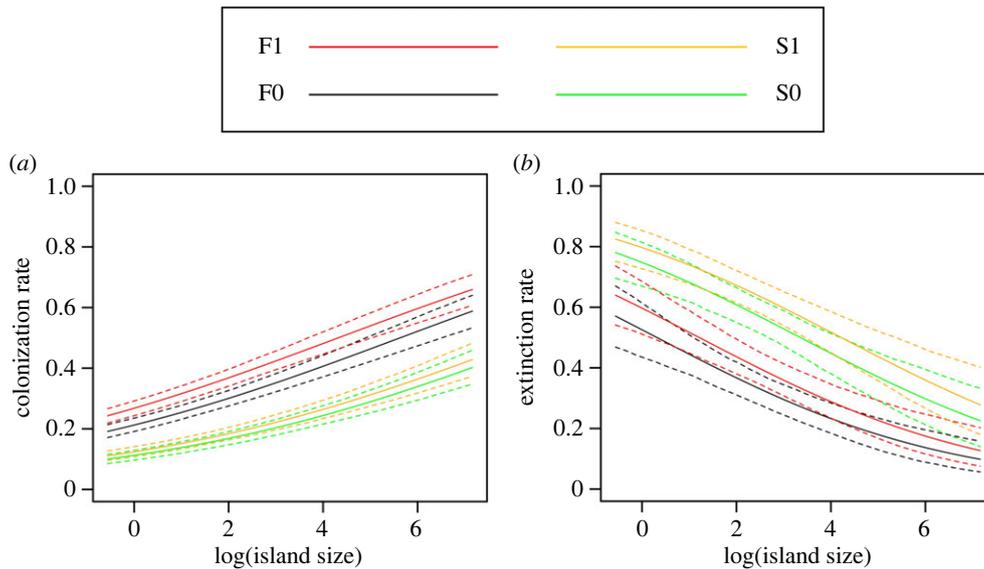
Figure 1. Colonization rates (*a*) and extinction rates (*b*) of four categories of sociality, across a gradient of island area. F1 (red), both interspecifically and intraspecifically social; F0 (black), interspecifically social, but not intraspecifically social; S1 (orange), not interspecifically social, but intraspecifically social; S0 (green), neither interspecifically nor intraspecifically social. The curves shown are the top models in table 2. Broken lines represent 95% confidence intervals around the solid line.

Table 2. Model selection results for the influence of mixed/mono species flocking propensity (four categories; table 1) on (*a*) colonization rates and (*b*) extinction rates. (Candidate variables also included island area, and island isolation (either distance to mainland or distance to nearest island). This table is abbreviated to include all the models with $\text{AIC}_c < 2$, and the null model. For the full table with all possible combinations of variables, see the electronic supplementary material, table S1.)

model no.	model terms	d.f.	logLik	AIC_c	delta	weight
(*a*) colonization rates						
1	log(area) + propensity	6	195.6	−378.5	0.0	0.43
2	log(area) + propensity + log(distance to the mainland)	7	196.5	−378.2	0.3	0.37
3	log(area) + propensity + log(distance to nearest island)	7	195.9	−377.0	1.6	0.20
4	null	2	107.2	−210.4	168.1	0.00
(*b*) extinction rates						
1	log(area) + propensity + log(distance to nearest island)	7	81.9	−148.9	0.0	0.61
2	log(area) + propensity	6	80.0	−147.4	1.6	0.28
3	null	2	26.2	−48.3	100.7	0.00

levels of sociality, and then running models that had two levels of sociality (either interspecific or intraspecific).

3. Results

Consistent with previous work in this system, island area increased colonization rates and decreased extinction rates (figure 1), but in addition, flocking propensity was also an influential predictor of colonization and extinction rates across all three approaches to categorizing flocking and non-flocking species. Flocking propensity and island area were consistently found in all models with $\Delta\text{AIC}_c < 2$, with one exception (the model contrasting extinction between intraspecifically flocking and non-flocking species; table 2; electronic supplementary material, tables S1, S2 and S4), and the coefficient for propensity was always influential (i.e. had 95% confidence intervals that did not cross zero; table 3; electronic

supplementary material, tables S3 and S5; not including the one exception discussed above). By contrast, neither measurement of isolation (distance to the mainland or distance to the nearest island) was influential in any model.

When considering the four subcommunities with different levels of monospecific and interspecific sociality, colonization rates were highest for interspecific flocking species (F1 and F0), and substantially lower for purely monospecific flocking and solitary species (S1 and S0; figure 1*a*; table 3*a*). Extinction rates showed the opposite pattern to colonization, being lower for interspecifically flocking species than for monospecific flocking and solitary species (figure 1*b*; table 3*b*).

Results were similar when we analysed only the two categories of interspecific flocking. The subcommunity with the higher interspecific flocking propensity (F) had strongly higher colonization rates (electronic supplementary material, figure S1 and table S3A) and lower extinction rates (electronic supplementary material, figure S2 and table S3B).

Table 3. Parameter estimates for top candidate models from table 2 ($\Delta AIC_c < 2$), and their 95% confidence intervals (CIs), as estimated by a parametric bootstrap. (For flocking propensity, the reference category is S0, and a positive number means that the category has a higher value of (a) colonization or (b) extinction rates.)

model no.	model term	estimate	95% CI
(a) colonization rates			
1	intercept	−2.06	(−2.21,−1.92)
1	log(area)	0.23	(0.20,0.27)
1	propensity F0	0.75	(0.57,0.95)
1	propensity F1	1.06	(0.87,1.25)
1	propensity S1	0.11	(−0.11,0.31)
1	phi	36.9	(31.2,48.7)
2	intercept	−1.74	(−2.21,−1.28)
2	log(area)	0.23	(0.20,0.26)
2	log(distance to mainland)	−0.05	(−0.11,0.02)
2	propensity F0	0.75	(0.58,0.94)
2	propensity F1	1.06	(0.88,1.24)
2	propensity S1	0.11	(−0.09,0.32)
2	phi	37.5	(31.5,49.1)
3	intercept	−1.85	(−2.42,−1.32)
3	log(area)	0.22	(0.19,0.27)
3	log(distance to nearest island)	−0.06	(−0.19,0.09)
3	propensity F0	0.75	(0.57,0.95)
3	propensity F1	1.06	(0.87,1.26)
3	propensity S1	0.11	(−0.09,0.33)
3	phi	37.1	(31.1,50.1)
(b) extinction rates			
1	intercept	1.61	(0.77,2.51)
1	log(area)	−0.25	(−0.32,−0.19)
1	propensity F0	−0.98	(−1.29,−0.71)
1	propensity F1	−0.69	(−0.99,−0.42)
1	propensity S1	0.28	(−0.01,0.54)
1	log(distance to nearest island)	−0.22	(−0.01,−0.45)
1	phi	10.2	(8.54,13.5)
2	intercept	0.77	(0.57,1.00)
2	log(area)	−0.22	(−0.28,−0.17)
2	propensity F0	−0.98	(−1.30,−0.70)
2	propensity F1	−0.69	(−0.97,−0.39)
2	propensity S1	0.29	(0.0,0.60)
2	phi	9.97	(8.40,13.3)

When comparing between monospecific flocking and non-flocking species, monospecific flocking species had significantly higher colonization rates (electronic supplementary material, figure S3 and table S5A). However, for extinction, three of four models with $\Delta AIC_c < 2$ did not

Table 4. Coefficients for phylogenetic generalized least squares (PGLS) models relating species' (a) colonization rates, or (b) extinction rates to flocking propensity (four categories; table 1). (Again, the reference category is S0.)

model term	estimate	95% CI
(a) colonization rates		
intercept	0.15	(0.01,0.30)
propensity F0	0.12	(−0.12,0.35)
propensity F1	0.24	(0.05,0.43)
propensity S1	0.01	(−0.21,0.23)
(b) extinction rates		
intercept	0.72	(0.57,0.87)
propensity F0	−0.27	(−0.50,−0.03)
propensity F1	−0.20	(−0.40,−0.01)
propensity S1	0.06	(−0.17,0.29)

include flocking propensity (electronic supplementary material, table S4B), and there was no significant effect for flocking propensity on extinction rates (electronic supplementary material, figure S4 and table S5B).

In the PGLS analysis, we found effects of sociality (four levels) on colonization were significant, with F1 having higher colonization rates than S0 (ANOVA, $F_{3,41} = 2.96$, $p = 0.043$; table 4a). We similarly found effects of sociality (four levels) on extinction were significant, with S0 having higher extinction rates than both F0 and F1 (ANOVA, $F_{3,42} = 3.78$, $p = 0.017$; table 4b). There was an effect of interspecific sociality (two levels) on colonization rates (ANOVA, $F_{1,43} = 7.02$, $p = 0.011$; electronic supplementary material, table S6A) and extinction rates (ANOVA, $F_{1,44} = 9.58$, $p = 0.0034$; electronic supplementary material, table S6B). However, when we compared monospecific flocking to solitary species there was no influence on colonization (ANOVA, $F_{1,43} = 2.29$, $p = 0.14$; electronic supplementary material, table S7A) nor on extinction rates (ANOVA, $F_{1,44} = 0.19$, $p = 0.66$; electronic supplementary material, table S7B). For all models, phylogenetic signal (λ) was estimated to be zero by maximum likelihood, except for the model for intraspecific sociality and extinction, for which it was 0.28.

4. Discussion

In a general sense, these results are consistent with previous work in the TIL system that found higher colonization rates and lower extinction rates with increasing island area, whereas island isolation showed little influence on metrics of community assembly, owing to the small distances between the islands and the mainland [38] and the relatively high mobility of birds. For any given island area, we found the subcommunities that were interspecifially social exhibited higher colonization rates, and lower extinction rates, as compared to those that were purely intraspecifically social or solitary. In both the main analysis and the phylogenetically controlled one, the interspecific aspect of sociality was more influential than the intraspecific one. Overall, our findings reinforce the suggestion of moving beyond species equivalency in colonization and extinction rates at TIL [13].

Individuals colonizing or persisting on islands are not all equivalent to one another, since they have species-specific traits that influence the probability of these processes on islands, traits that are in this case related to their degree of sociality.

From a colonization perspective, our work is consistent with previous work which has shown that multiple arriving species may mutually benefit each other (see Simberloff & Von Holle [22], in the context of invasive species). Indeed, facilitation has been increasingly recognized as a mechanism that influences community organization (e.g. [46]) and the ability of species to help each other become established on islands is no exception. Interspecific interactions that facilitate recruitment have been observed in a variety of communities [18,47], and analogously individuals newly arrived on an island might be at less risk if they could join a mixed-species flock.

Alternatively, higher colonization rates may not be a result of increased benefits while in a habitat but rather facilitation of movement through a matrix of uninhabitable or 'risky' areas [48]. Grouping may offer a simple dilution of risk in dangerous habitats [25,26]. In birds, titmice have been shown to facilitate the movement of other passerines across forest boundaries and into open areas [23,49]. Similarly, species of passerines have been shown to facilitate movement through Mediterranean type forest patches by minimizing predation risk when in larger intraspecific groups [50]. This is interesting because our main finding for colonization included an intraspecific component, although the phylogenetically corrected one did not. The functional traits implicated in this study, variation in group-living tendencies, are quite distinct from those that underlie dispersal ability based on mobility among species that have previously been argued to be important to predicting which species colonize islands [20,51].

Longer-term persistence on islands could be closely linked to colonization, or could involve additional mechanisms. Flocks that arrive at small islands might not persist there but rather move frequently among a number of small islands, as these sized islands have little habitat or locations to escape or hide from predators [52]. In this case, the colonization event also produces the lack of extinction, similar to a rescue effect. Conversely, on larger islands, we hypothesize that both lower predation risk and augmented ability to find food resources in mixed-species flocks may be the mechanism behind lower extinction rates, with the degree of benefit dependent on the overlap among species in their diets and foraging techniques [36]. Here there is a trade-off between intraspecific and interspecific sociality: individuals of different species compete less because their niches are different, yet at the same time individuals of the same species might be more efficient at finding food resources of interest to the members of the group.

Why would the effect of interspecific sociality be stronger than that for intraspecific sociality? Species in bird flocks have been shown to exhibit 'activity matching', overlapping their niches along some aspects such as diet and body size, so that they find the same sort of food and can travel at the same rate [53–55]. Yet they can remain divergent in other aspects, such as foraging technique and microhabitat to avoid competition [36,54,55]. Further, mixed-species flocks might allow the creation of niches for certain species. For example, mixed-species flocks might create niches for birds that capture insects beaten into the air by other species'

gleaning activities [56,57], or by allowing species to lower predation risk in otherwise unsafe habitats [58]. Overall, our results support the idea that interspecific mutualisms such as mixed-species groups can strongly affect ecological processes at the population and community level [36,59].

We should acknowledge that some of the features of TIL may limit generalizations to other island systems, such as oceanic islands that are far from the mainland. The proximity of the mainland and closeness of the islands to each other mean that there may be much movement among the islands and the mainland within a year, especially in nonbreeding seasons. What we refer to as 'extinction' (or 'local extinction') may well be represent simply movement from that island (e.g. all individuals of a species vacate the island, rather than perish). More generally, in such an environment of rapid inter-island movements of individuals, extinction and colonization rates could represent behaviourally mediated, short-term processes compared to more movement-constrained systems that are driven by slower demographic processes, such as what might be found on oceanic islands. Nevertheless, long-distance migrant birds do travel in mixed-species flocks [60], and birds even in remote islands can participate in mixed-species flocks [61]. Our study may not be able to be generalized to oceanic island systems, but it can raise the question of how interspecific sociality might affect dispersal and subsequent colonization and extinction dynamics for such systems.

5. Conclusion

ETIB and subsequent theoretical developments have been evaluated in the context of competitive interactions of species. Our work suggests that sociality, and interspecific sociality in particular, can enhance the ability of species to colonize land-bridge islands and persist on them. Additional work should consider the exact mechanisms of how interspecific groups affect these processes: whether it occurs owing to movements between islands, during facilitation as a species arrives on an island, or because of increased foraging efficiency and reduced predation long-term. Increased colonization rates and lowered extinction rates of subcommunities of birds categorized by their sociality highlights the potential for mutualism to structure avian communities. This phenomenon may potentially be observed across other taxonomic groups where social organization is present, and so we encourage studies on different taxa and on other kinds of island systems, such as oceanic islands.

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