

Behavioural complementarity among frugivorous birds and lizards can promote plant diversity in island ecosystems

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Funding information

Consejo Superior de Investigaciones Científicas; Spanish Ministry of Science and Education; Consejo Nacional de Investigaciones Científicas y Técnicas; Cabildo de Tenerife; FEDER funds from the European Union; MEDI; FDCAN

Handling Editor: Matthias Schleuning

Abstract

1. The behavioural complementarity of fruit-eating animals is thought to exert a key role in plant community assembly. However, a mechanistic understanding of the causal links between the two processes is still lacking.
2. This study assesses whether complementarity between dispersers in feeding and microhabitat-use behaviour enhances community-scale dispersal services, resulting in a more diverse community of seedlings.
3. We used a Bayesian approach to connect a comprehensive database of seed dispersal effectiveness at a community scale with a transition probability model that accounts for behavioural complementarity. Our model system was the thermo-sclerophyllous shrubland of the Canary Islands. There, fleshy-fruited plants rely on two types of frugivores: lizards and birds.
4. Lizards consumed all plant species and preferentially used open areas, whereas birds foraged for small single-seeded fruits and dispersed their seeds beneath plants. Through feeding on different sets of plants, they generated a rich seed-rain community. By diversifying the microhabitat of deposition, more species could find suitable recruitment sites.
5. Distinct foraging and microhabitat-use choices led to complementary dispersal services. Lizards ensured that all plant species were present in the seedling community, while birds promoted a more even distribution of them. As a result, diversity in the community of seedlings was enhanced.
6. Overall, our work underscores that behavioural complementarity promotes diversity in the early-regenerating plant communities. These enhanced dispersal services rely on the presence of all functional groups. Thus, in communities where frugivores display unique behaviours, preserving a diverse community of dispersers should be a conservation target.

KEYWORDS

behavioural complementarity, diversity maintenance, fruit choice, microhabitat use, plant-frugivore assemblages, seed dispersal effectiveness

1 | INTRODUCTION

Mutualisms between plants and animals are considered among the most important interactions to promote biodiversity world-wide. Plant–animal encounters do not occur in isolation but are embedded within assemblages, where species interact with multiple partners (Bascompte & Jordano, 2007). In the case of plant–frugivore mutualisms, this implies that community-level seed dispersal services rely on multiple species (Jordano, 2000). Thus, if dispersers within communities are functionally redundant, high levels of generalization are expected to promote stability against extinctions (Bascompte, Jordano, Melián, & Olesen, 2003; Zamora, 2000). In contrast, if animals play irreplaceable roles, the loss of a single species may compromise the sustainability of plant populations (Traveset, Gonzalez-Varo, & Valido, 2012) or even community organization (Vidal et al., 2014). Complementarity is the mechanism by which species exploit different resources, resulting in an enhanced aggregate function of the species assemblage (Schleuning, Frund, & Garcia, 2015). Therefore, a critical question in basic and conservation ecology is whether animal species or groups provide complementary dispersal services to plants (Brodie, Helmy, Brockelman, & Maron, 2009).

Even though redundancy is thought to be widespread across ecosystems (Lawton & Brown, 1994; Schindler, Armstrong, & Reed, 2015), complementarity has been frequently observed in plant–frugivore assemblages (Schleuning et al., 2015). Lack of redundancy often responds to a decoupling between the quantity and the quality components of seed dispersal effectiveness (*sensu* Schupp, Jordano, & Gómez, 2010; Jacomassa & Pizo, 2010; Schleuning et al., 2015). It is common that frugivores showing the highest consumption rates deposit seeds locally or in unsuitable microhabitats for recruitment, whereas opportunistic consumers provide enhanced dispersal services (Brodie et al., 2009; Bueno et al., 2013; Calviño-Cancela & Martín-Herrero, 2009; McConkey & Brockelman, 2011). If plants are highly dependent on specific microhabitats to recruit, uncommon but efficient dispersers will disproportionately contribute to regeneration (Brodie et al., 2009; Calviño-Cancela & Martín-Herrero, 2009). In contrast, if plants are more generalists, both types of dispersers will play a key role. Short-distance dispersers that are avid consumers will drive local recruitment, while vagile opportunistic ones will promote landscape connectivity and colonization success (Escribano-Avila et al., 2014; Jordano, García, Godoy, & García-Castaño, 2007; Lehouck, Spanhove, Demeter, Groot, & Lens, 2009; McConkey & Brockelman, 2011). When focusing on plant communities, two sources of complementarity may operate—diet and microhabitat-use behaviour. In the former case, trait-matching constraints or digestive physiology can lead to distinct foraging behaviours, resulting in frugivores using different sets of plants (Bueno et al., 2013; Dehling, Jordano, Schaefer, Böhning-Gaese, & Schleuning, 2016; González-Castro, Yang, Nogales, & Carlo, 2015; Gorchov, Cornejo, Ascorra, & Jaramillo, 1995; Rother, Pizo, & Jordano, 2016; Tewksbury & Nabhan, 2001). In the latter, a wide range of movement behaviours can diversify the habitats of seed deposition (García & Martínez, 2012; Morales, García, Martínez, Rodríguez-Pérez, & Herrera, 2013;

Rehm, Fricke, Bender, Savidge, & Rogers, 2019). Either way, complementarity entails enhanced community-level seed dispersal services (Schleuning et al., 2015). Thus, understanding the causes and consequences of complementarity will provide new insights into the processes involved in diversity maintenance throughout recruitment.

Alongside studies showing that complementarity was widespread among plant–frugivore assemblages, the interest in quantifying it has grown steadily (Schleuning et al., 2015; Zamora, 2000). For instance, within the framework of network theory, Blüthgen's specialization index (Blüthgen, Menzel, & Blüthgen, 2006) and modularity analyses (Mello et al., 2011) have been proposed as appropriate tools to detect diet-driven complementarity. However, given that deposition patterns can strongly affect seed fates (Schupp et al., 2010), comprehensive estimates of functional complementarity should also account for differences in post-feeding behaviour (Escribano-Avila et al., 2014; Jordano et al., 2007). In fact, it has been claimed that quantifying seed dispersal effectiveness is the only way to assemble an accurate picture of complementarity (Calviño-Cancela & Martín-Herrero, 2009; McConkey & Brockelman, 2011). At the community level, this task is logistically challenging at the very least. Here, we use a comprehensive database with accurate estimates of seed dispersal effectiveness at the community scale to quantify complementarity effects on plant recruitment. Specifically, we tested whether (a) distinct fruit and microhabitat-use choices by frugivores result in a more diverse community of seedlings; and (b) frugivores showing contrasting behaviours also provide complementary community-level dispersal services.

To achieve these goals, we used the plant–frugivore assemblage of the thermosclerophyllous shrubland of the Canary Islands as a model system. The frugivore assemblage in this community includes two types of frugivores with different feeding and movement behaviours: lizards and birds. In general, lizards tend to consume plant material in a generalist way (Rodríguez, Nogales, Rumeu, & Rodríguez, 2008) and preferentially use open microhabitats. In contrast, birds select fruits and often feed on uncommon species (Carlo & Morales, 2016; González-Castro, Yang, & Carlo, 2019), tending to use covered areas (González-Castro, Calviño-Cancela, & Nogales, 2015). Therefore, we expected that the two types of dispersers would provide distinct community-level dispersal services. Lizards would facilitate richness maintenance due to their generalist foraging behaviour (Rodríguez et al., 2008), whereas birds would contribute to evenness thanks to rare-biased fruit choices (Carlo & Morales, 2016).

2 | MATERIALS AND METHODS

2.1 | Study site

Fieldwork was carried out in the northwest of the island of Tenerife (≈4 ha patch; Canary Islands, UTM: 28R 317523 E/3138253 N, 220 m a.s.l.) in one of the best-conserved thermosclerophyllous vegetation remnants. The climate is Mediterranean, with mean annual rainfall of 250–450 mm and mean temperature of 19°C

(Fernández-Palacios et al., 2008). The vegetation is a shrubland with some patches of woodland embedded within it. There, two microhabitats are clearly identifiable: open areas without vegetation cover and areas under vegetation canopy (hereafter open and covered, respectively). The fruit assemblage is mainly composed of 11 plant species (*Asparagus plocamoides*, *Bosea yervamora*, *Canarina canariensis*, *Heberdenia excelsa*, *Jasminum odoratissimum*, *Rhamnus crenulata*, *Rubia fruticosa*, *Ruta pinnata*, *Scilla haemorrhoidalis*, *Tamus edulis* and *Withania aristata*), with fruits of contrasting seed size (from 0.1 to 3.21 g) and nutrient content. Carbohydrates represent from 6% to 98% of pulp content (González-Castro, Yang, et al., 2015). The disperser assemblage consists of the endemic lizard (*Gallotia galloti*) and four highly frugivorous passerine birds (*Sylvia atricapilla*, *S. melanocephala*, *Turdus merula* and *Erithacus rubecula*) (Herrera, 1995). Both their movement patterns across microhabitats at the study site and their seed retention time are very similar (Herrera, 1984). In contrast, *Gallotia galloti* shows a generalist foraging behaviour long retention times and preferentially uses open areas (González-Castro, Calviño-Cancela, et al., 2015). For such a reason, this study is focused on comparison between two clearly different types of seed dispersers: lizards and birds.

2.2 | Model development

We adapted the model developed by González-Castro, Calviño-Cancela, et al. (2015), in order to parameterize the behavioural rules of frugivores based on the data available. The previous version was a stochastic transition probability model that connected all stages of plant recruitment, from fruit production to 1-year-old seedlings. It estimated seed dispersal effectiveness at the community scale by bootstrapping the observed transition probabilities. However, the behavioural mechanisms responsible for these probabilities were not parameterized. Thus, the effects of behavioural complementarity on recruitment patterns could not be quantified. Here, we use a Bayesian approach to parameterize behaviours driving transition probabilities. In particular, we consider two sources of complementarity: frugivorous diet (diet, hereafter) and microhabitat-use choices.

2.2.1 | Parameterization of behavioural rules

To estimate diet complementarity, we had data of the seed rain generated by each frugivore each month (y_{fm}), the number of fruits consumed per foraging bout in each plant-frugivore-type interaction (B_{fp}) and the number of seeds per fruit (N_p). It was parameterized as following:

$$y_{fm} \sim \text{Multinom} \left(D_{fm}, \sum_{p=1}^P Y_{fpm} \right), \quad (1)$$

$$D_{fpm} = F_{fpm} N_p B_{fp} / \sum_{p=1}^P F_{fpm} N_p B_{fp}, \quad (2)$$

$$F_{fpm} = e_{fpm} / \sum_{p=1}^P e_{fpm}, \quad (3)$$

$$\log(e_{fpm}) = \beta_{0f} + \beta_{1f} A_{pmm} + \beta_{2f} S_p + \beta_{3f} C_p + \beta_{4f} S_p C_p. \quad (4)$$

The composition of the seed rain obtained from the f -th frugivore in the m -th month (y_{fm}) is generated by a multinomial process. In Equation 1, y_{fm} is a vector of length equal to the number of species (11) that contains for each p -th plant species the observed number of seeds found in the seed rain from the f -th frugivore in the m -th month. D_{fpm} , in turn, contains for each plant species the expected probabilities according to our model. For each plant species, these probabilities (D_{fpm}) depended on the proportion of foraging bouts on their fruits (F_{fpm}), the number of fruits consumed per foraging bout (B_{fp}), and the number of seeds per fruit (N_p). In Equation 2, fruits consumed per bout (B_{fp}) and number of seeds per fruit (N_p) correspond to species-specific averages from field data (see below). In contrast, F_{fpm} depends on frugivores' fruit choices (Equations 3 and 4). The probability that the f -th frugivore chooses the p -th plant species during the m -th month depends on the relative abundance of its fruits (A_{pmm} , proportion) (Carlo & Morales, 2016), their size (S_p , fruit radial diameter), their non-structural carbohydrate content (C_p , percentage of pulp content, hereafter just carbohydrates) and their interaction (González-Castro, Yang, et al., 2015). In Equation 4, β_{1f} informs about frequency-dependent fruit selection by the f -th frugivore (Allen, Raison, & Weale, 1998). β_{2f} , β_{3f} and β_{4f} represent fruit choices driven by traits. To obtain a discrete probability distribution (F_{fpm}), we divided e_{fpm} by its sum. In the case of birds, the term $\beta_5 V_p$ was added to Equation 4. This term represents the effects of fruit accessibility on fruit choice by birds (Pizo, Batista, & Monteiro, 2019). V_p was set to 0 for *Withania* fruits, which hang down from branches covered by their calyx, limiting fruit removal by birds (A. González-Castro, personal observation). In the rest of species, V_p was set to 1.

To estimate complementarity on microhabitat use, for each frugivore and on monthly basis, we had data on the number of droppings found in each microhabitat (open vs. covered). For each frugivore type, microhabitat use was parameterized as following:

$$Y_{fm} \sim \text{Binom} \left(U_{fm}, \sum_h^H Y_{fhm} \right), \quad (5)$$

$$\log \text{it}(U_{fhm}) = \alpha_{0f} + \alpha_{1f} M_h + \alpha_{2f} M_h R_m + \alpha_{3f} M_h P_m. \quad (6)$$

The number of droppings of the f -th frugivore found on each type of microhabitat in the m -th month (Y_{fm}) is generated by a binomial process. In Equation 5, Y_{fm} is a vector of length 2 that contains on the observed number of droppings on each microhabitat. U_{fm} contains the expected probabilities according to our model. For each frugivore and month, the probability that a dropping is deposited in h -th microhabitat depends on whether it is covered ($M_h = 1$) or open ($M_h = 0$)

and on the interactive effects between cover and monthly availability of fruits (R_m) and precipitation (P_m). α_{1f} represents the attraction (or avoidance) of the f -th frugivore towards covered areas. α_{2f} models fruit tracking by dispersers (Blendinger et al., 2012). α_{3f} accounts for temporal variability in microhabitat choices. It was specially included to acknowledge that the dependency of lizards on open areas for thermoregulation may be more important in cool and cloudy periods.

To obtain scaled regression coefficients for each behaviour (β s and α s), all continuous explanatory variables were standardized previous to model parameterization (mean = 0, $SD = 1$). The above-mentioned formulation allowed us to build four behaviour models: diet choice by birds and lizards, and microhabitat use by birds and lizards. We parameterized them by performing Monte Carlo Markov Chain (MCMC) procedures with an adaptive Metropolis–Hasting sampling scheme implemented in R. Uninformative priors were used for model parameters, and 10,000 iterations confirmed convergence for all model parameters (β s and α s; $Rhat < 1.1$), by means of coda package (Plummer, Best, Cowles, & Vines, 2006).

2.2.2 | Routine for simulating seedling recruitment

In each repetition, 10,000 foraging events were simulated. These were distributed among months accounting for the temporal variability in the abundance of dispersers. In particular, the number of foraging events of the m -th month (E_m) was proportional to the number of frugivores present in that period. $E_m = \|E \times Rd_m\|$. Rd_m was calculated according to $Rd_m = Id_m / \sum_{m=1}^{12} Id_m$ with Id_m being the number of frugivores per ha in the m -th month. Once a certain number of foraging events were assigned to the m -th month, the identities of each frugivore type (lizards or birds) were sampled from their monthly relative abundances. Subsequently, each frugivore type foraged and deposited seeds in different microhabitats, following the behaviour rules sampled from

the posterior distributions of MCMC (β s and α s). This procedure was repeated until seed dispersal was simulated for all months, generating the seed-rain community. Once deposited, seeds were classified as healthy or not according to the probability of being dispersed undamaged after ingestion by animals (H_{pff}). Each healthy seed had a probability of emergence that depended on its identity, the identity of the dispersal vector and the microhabitat of deposition (E_{pff}). The probability of emergence was sampled from the empirical probability distributions obtained from seed sowing experiments (see below). Finally, each newly emerged seedling had a probability of surviving 1 year, which depended on its identity and the microhabitat where it was deposited. The probabilities of post-dispersal survival (S_{pff}) were sampled from the empirical distributions obtained from seedling survival surveys (see below). The model kept track of the composition of the seed rain, and of the early-emerged and 1-year-old seedling communities. In addition, it recorded the type of frugivore (bird or lizard) driving each dispersal event and the microhabitat where seeds were deposited. To evaluate the effects of the number of foraging events simulated (parameter E) on model outputs, we run simulations with 1,000 and 100,000 foraging events. The composition of the early-emerged and 1-year-old seedling communities was similar in all cases (Bray–Curtis distances between scenarios ranging between 0.005 and 0.013 for early-emerged seedlings, and between 0.008 and 0.014 for 1-year-old seedlings). Figure 1 summarizes the processes involved in our simulations.

2.3 | Data for model parameterization: field studies and greenhouse experiments

2.3.1 | Estimates of frugivore abundance

Densities of birds and lizards (individuals per ha) were estimated on monthly basis with a 500-m transect across the plot, where all

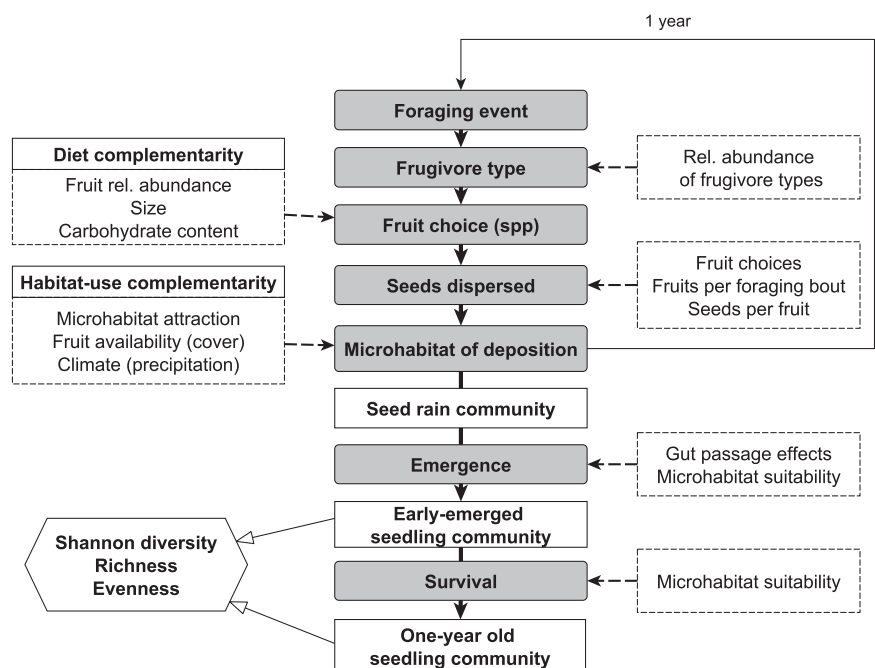


FIGURE 1 Flow chart summarizing our model. Grey boxes represent processes connecting frugivory with the community of seedlings. White boxes represent different stages during recruitment. Dashed white boxes contain the variables modulating recruitment processes. Those related to behavioural complementarity are on the left side of the panel. Model outputs are within the diamond

individuals (seen or heard) were counted. We used a 4- and 25-m bandwidth for lizards and birds, respectively (González-Castro, Calviño-Cancela, et al., 2015). For birds, we grouped all counts in one category (bird-type frugivore). We used the data of overall frugivore density to distribute the number of foraging events per month (Rd_m). Within each month, we distributed foraging events between frugivore types according to their relative abundance.

2.3.2 | Data for parameterization of behavioural rules

The animal-generated seed rain (y_{fm} , Equation 1; number of seeds found per plant species on monthly basis) was obtained from data of 55 seed traps randomly distributed across microhabitats (open vs. covered). Seed traps were square trays $1\text{ m}^2 \times 2\text{ cm}$ deep, made of green plastic mesh (1 mm aperture) to retain faeces (and regurgitations) and provide good drainage. Droppings from each frugivore type were easily distinguishable by their appearance. Seeds were collected and identified on a monthly basis for 1 year ($N_{\text{birds}} = 954$; $N_{\text{lizards}} = 1,524$) (González-Castro, Calviño-Cancela, et al., 2015). Number of seeds per fruit (N_p ; Equation 2) was estimated from 30 fruits per plant species. Low accessibility and visibility in our study area did not allow focal observations across the plot. Thus, number of fruits consumed per foraging bout (B_{fp}), was indirectly estimated through the seed content of faecal samples following González-Castro, Yang, et al. (2015). For birds, we collected faecal samples from individuals captured with mist nets ($N = 357$; González-Castro, Yang, et al., 2015). For each b -th bird species, the number of fruits of each plant species consumed in each i -th faecal sample was obtained by dividing the number of seeds found (S_{pi}) by the number of seeds per fruit (N_p). This value was rounded to the larger closest integer (ceiling function) ($B_{bpi} = \lceil S_{pi}/N_p \rceil$). Then, for each plant species we averaged B_{bpi} across faeces that contained its seeds ($C = \{i: B_{bpi} > 0\}$); $\widehat{B}_{bp} = \frac{1}{M} \sum_{i \in C} B_{bpi}$; M being the number of faeces with seeds from the p -th plant). Finally, to obtain the number of fruits consumed for the frugivore-type 'birds', we averaged this value across all bird species. In the case of lizards, 1,228 droppings were collected along three transects ($500 \times 2\text{ m}$) across the study site. The same calculations were performed (except for species averaging, as there was just one lizard species). Regarding the explanatory variables of fruit choice (Equation 4), relative abundance of fruits each month (A_{pm}) was estimated from data of landscape fruit production. We established 5-m^2 plots every 25 m along a 500-m transect running across the study area and counted fruits on a monthly basis (González-Castro, Calviño-Cancela, et al., 2015). We calculated relative abundances by dividing fruits of each species by the total fruit count. Fruit size (S_p) and carbohydrate content (C_p) were obtained from measurements on fruits of each plant species (González-Castro, Yang, et al., 2015).

From data for the number of droppings collected on seed traps on monthly basis, we characterized microhabitat use by each frugivore (Y_{fm} , Equation 5). Traps were classified according to the microhabitat where they were located (covered or not; M_h , Equation

6). Fruit availability in covered areas (R_m , Equation 6) was estimated from counts of landscape fruit availability (above) of plots located under cover (number of fruits per ha). Finally, we used WordClim (<https://www.worldclim.org/>) to obtain monthly precipitation (P_m).

2.3.3 | Data for post-dispersal processes

In our model, methods for parameterization of post-dispersal processes followed the procedures implemented by González-Castro, Yang, et al. (2015). First, for each of the p -th plant species we estimated the probability of being dispersed undamaged by each f -th frugivore type as the proportion of seeds defecated/regurgitated undamaged with respect to the total number of seeds found (H_{pf}). To estimate the probability of emergence of a seedling from the p -th species dispersed by the f -th frugivore and deposited in h -th microhabitat (E_{pffh}), we accounted for both gut passage effects and the suitability of the microhabitat. To estimate gut passage effects on emergence, for each plant species control seeds (taken directly from plants) and undamaged seeds defecated and/or regurgitated by both dispersers (birds and lizards) were sown in pots randomly distributed in a greenhouse and watered every 2 days for 6 months. Every 5 days seedling emergence was recorded. For every plant and frugivore type, our estimate of gut passage effects was equal to the ratio between ingested versus control seeds that emerged. To quantify for the suitability of microhabitat of deposition, we sowed control seeds taken from fruits of the 11 species in 1-m^2 plots located under cover and in open areas in the field (20 plots in total, $N_{\text{seeds}} = 5,218$). Newly emerged seedlings were surveyed every 15 days until the end of the rainy season (when natural emergence occurs in our system). To obtain the overall probability of emergence (E_{pffh}), the proportion of emerged seedlings in each microhabitat was multiplied by gut passage effects (ratio between ingested and control seeds that emerged). Finally, to quantify the effects of site on seedling survival (S_{ph}), 80 plots (2 m^2 , 40 in each microhabitat) were established. In each plot, recently emerged seedlings of plant species were counted and marked. The initial survey for seedlings was performed in March, before the dry season, and marked seedlings were recorded until 1-year survival. Seedling survival could not be estimated for *Canarina canariensis*, *Scilla haemorrhoidalis* and *Tamus edulis*, since they are geophytes that spend the dry season underground and afterwards emerge. Thus, it was difficult or even impossible to distinguish young seedlings from older plants and to track individuals throughout the year. In all cases, they made up less than 1% of the fruits available per month. See Table S1 for a summary of variables involved in model parameterization.

2.4 | Benchmark model and validation

Recruitment was simulated for 100 replicates. Then, to validate our model, for each frugivore type we compared the patterns of fruit choice and microhabitat of deposition. In the case of fruit

choice, we regressed relative abundances of plant species in the observed seed rain (on a monthly basis) against those predicted by our model (averaged across replicates). To evaluate the microhabitat use for each frugivore type, we estimated upper and lower quantiles ($q_{0.05}$, $q_{0.95}$) of the proportion of seeds deposited in open microhabitats. Then, we compared the quantiles of observed and simulated data. We used these simulations, where all frugivorous types and behaviours were functioning, to obtain benchmark values of Shannon diversity (diversity, hereafter), richness and Pielou's evenness in the community of early-emerged and 1-year-old seedlings.

2.5 | Simulation experiments to quantify complementarity effects

Complementarity effects can arise at two scales. At the finest scale, they can respond to differences in a specific behaviour (i.e., size-driven foraging choices, attraction to certain areas, 'behaviour effects'). At a broader scale, the joint effect of all behaviours can result in complementary community-scale dispersal services ('frugivore-type effects'). In this study, we performed three simulation experiments to evaluate both types of complementarity.

In a first experiment, the contribution to diversity of each of the behaviours displayed by each frugivore type was quantified. For this, we performed simulations where we 'switched off' one behaviour of one frugivore type at a time. That is, we maintained the same structure as the benchmark model, but the effects of one of the behaviours driving fruit choice or microhabitat use were cancelled out for either lizards or birds (α or β equal to 0). The difference between diversity in the seedling community of these simulations and the benchmark model was considered as a proxy of the contribution of behaviours to diversity in the community of recruits (early-emerged and 1-year-old).

In a second experiment, we quantified the effects of behavioural complementarity on diversity of the seedling community. Behavioural complementarity was quantified as $Q_b = |\bar{\beta}_{b_b} - \bar{\beta}_{b_l}| \times \omega$. Complementarity of the b -th behaviour (Q_b) depended on the absolute difference between mean values of the posterior distributions for birds ($\bar{\beta}_{b_b}$) and lizards ($\bar{\beta}_{b_l}$) and the term ω , which weighted these differences. If the sign of mean posterior distributions differed, ω was 1. If their sign was equal, ω was 0.5. In this way, complementarity was higher in foraging behaviours where birds and lizards displayed opposite responses. Since we were interested in complementarity between frugivore types, we simultaneously cancelled out each of the behaviours in both types of frugivores (i.e., size-driven fruit choice in birds and lizards). Then, we plotted changes in diversity of the community of seedlings as a function of behavioural complementarity. In this experiment, we wanted to evaluate the overall effects of complementarity, and hence, we quantified changes in diversity throughout the whole recruitment (1-year-old seedlings).

Finally, to assess whether each frugivore type provided complementary dispersal services we performed an extinction

experiment. For each frugivore type, we simulated scenarios of reduced abundance (L_s), from 10% of reduction to total extinction. To adjust for the effects of abundance on frugivore roles (Vázquez, Blüthgen, Cagnolo, & Chacoff, 2009) on a monthly basis, the number of events was reduced proportionally to the relative abundance of each frugivore type. $E_{sm} = E_m - [E_{dm} \times (1 - L_s)]$. The number of events in the m -th month in the s -th scenario (E_{sm}) is the number of events in the benchmark model in that month (E_m) minus the number of events driven by the frugivore type (E_{dm}) whose loss is simulated through the reduced abundances (L_s). In addition, before simulations and after frugivore loss we recalculated relative abundances of each frugivore type. This way, as the abundance of one frugivore decreased, the other became increasingly important. In the most extreme scenario (extinction), the seed-rain community relied solely on the remaining frugivore. Once all dispersal events were assigned to a certain frugivore type, dispersers foraged and deposited seeds according to the above-mentioned behavioural rules, and recruitment was simulated. Here, we were interested in evaluating the presence of complementary dispersal services. Thus, we tracked changes in richness and evenness in the seedling community because both metrics represent complementary aspects of diversity maintenance. The former ensures that all plant species are present in the community; the latter promotes a more even distribution of them. In these analyses, we restricted ourselves to the early-emerging community because we were interested in richness patterns, and the probability of 1-year survival could not be assessed for geophyte species. In all three experiments, each scenario was replicated 100 times.

3 | RESULTS

3.1 | Foraging patterns and model validation

At the seed traps, we found that lizards dispersed 11 plant species, whereas birds acted as seed disperser for eight plant species. Our model provided good predictions of both fruit consumption and microhabitat of deposition. For both types of frugivores, the regression between the observed and predicted seed-rain composition included an intercept of zero and a slope of one. Thus, we neither over- nor under-estimated resource use (lizards—intercept = 0.02 ± 0.03 , slope = 1.23 ± 0.25 , $R^2 = .72$; birds—intercept = 0.02 ± 0.03 , slope = 0.78 ± 0.23 , $R^2 = .56$). Furthermore, the model also accurately predicted the microhabitat of deposition. In the case of birds, the observed frequencies of deposition in open microhabitats laid between 0.05 and 0.50, and those predicted were between 0.06 and 0.40 ($Q_{0.05}$, $Q_{0.95}$). For lizards, they ranged between 0.76–1 and 0.77–0.95 ($Q_{0.05}$ – $Q_{0.95}$, observed and predicted, respectively).

As expected, birds and lizards displayed distinct choices of fruits and microhabitat use. Lizards were attracted towards large-fruited species—irrespective of their nutritional value—while birds mostly

consumed small sugar-rich fruits. In both cases, fruit abundance positively affected the probability of consumption. Regarding microhabitat use, birds preferentially used covered microhabitats, whereas lizards avoided them, especially in cool humid periods. Both frugivore types used covered areas more frequently when fruit availability was high (Figure 2, Table 1). The behaviours that showed the highest values of complementarity were size-driven fruit selection and cover effects (Table 1).

3.2 | Behavioural complementarity and community-level dispersal services

Size-driven fruit consumption always promoted diversity. By feeding on different sets of plants (small- vs. large-fruited), birds and lizards promoted Shannon diversity in the early-emerged and 1-year-old seedling community. In contrast, consumption of fruits according to their relative abundance or nutrient content had no effect (Figure 3, triangles). In the case of microhabitat use, the attraction of lizards towards open areas decreased diversity in the early-emerged community (Figure 3a), whereas it promoted it 1 year afterwards, at the stage of seedling survival (Figure 3b). The other microhabitat-use behaviours did not contribute to diversity, or had minor effects (<5%). Complementarity was the underlying cause of the positive effects of size-driven fruit choices and microhabitat use. Only those behaviours with high complementarity

contributed significantly to diversity in the seedling community (Figure 4).

Both frugivore types displayed distinct and complementary community-level dispersal services (Figure 5). Lizards were important for plant species richness, as their extinction implied that 27% of plant species were no longer present in the seedling community (Figure 5a). In contrast, bird loss did not affect richness but decreased evenness by 11%. Accordingly, when dispersal services solely relied on birds (due to lizard extinction), evenness in the community of seedlings increased (Figure 5b).

4 | DISCUSSION

Overall, our work shows that behavioural complementarity promotes enhanced community-level dispersal services. By feeding on different sets of plants, birds and lizards generated a rich seed-rain community; and by depositing seeds in contrasting microhabitats, all plant species could find optimal recruitment sites. This reinforces the idea that behavioural complementarity can play a pivotal role in diversity maintenance in the community of recruits (Schleuning et al., 2015). Hence, from a functional perspective, a comprehensive approach of plant community assembly needs to integrate the contribution of different types of dispersers (García & Martínez, 2012).

As expected, birds and lizards provided singular and complementary dispersal services. Lizards facilitated the presence of all plant

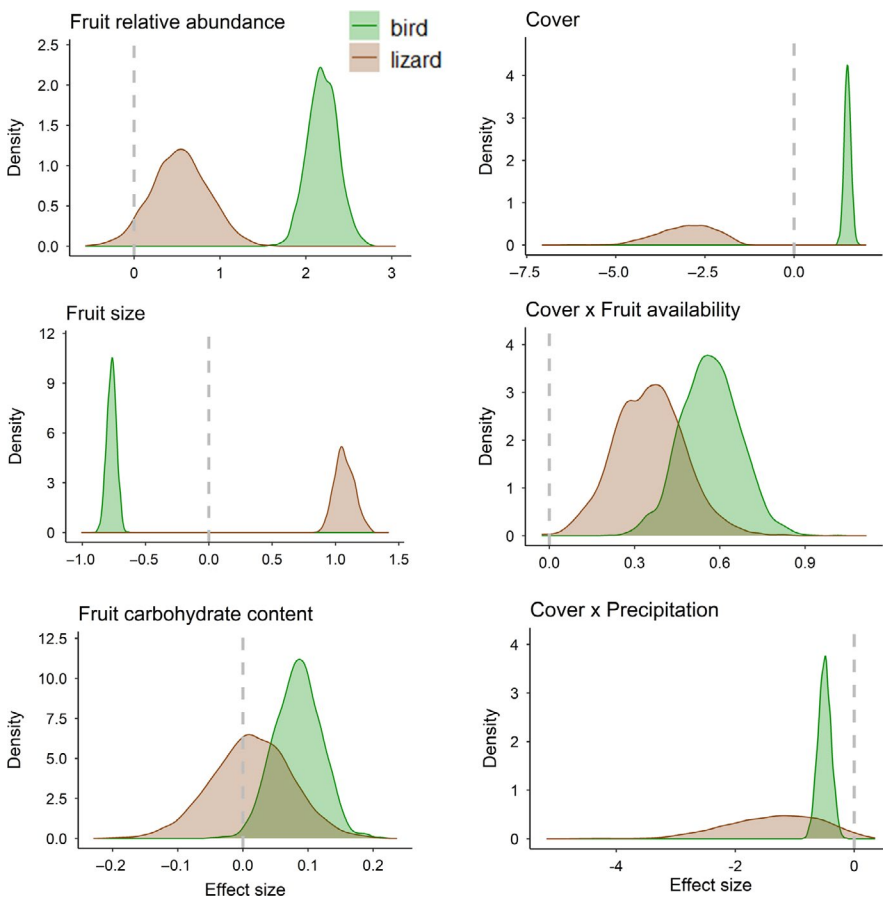


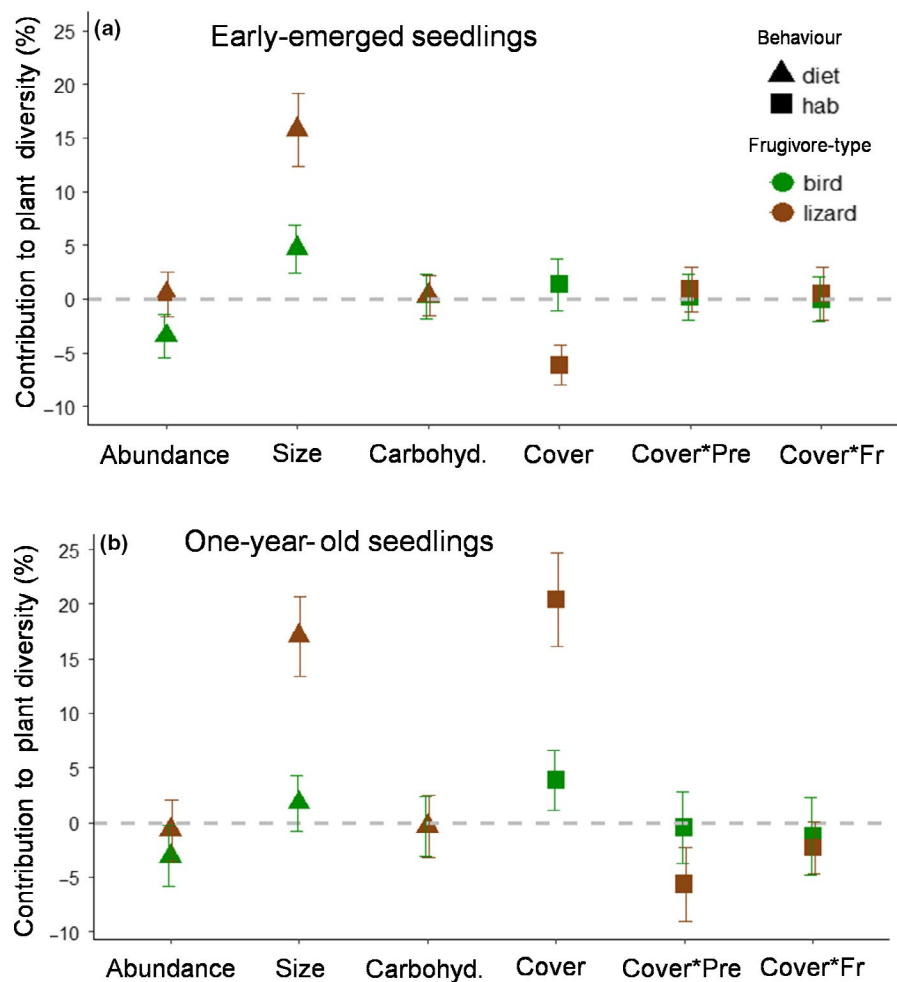
FIGURE 2 Left panels—posterior distributions of the effects of fruit relative abundance, size and carbohydrate content on fruit choice by birds (green) and lizards (brown). Right panels—posterior distribution of the effects of cover and its interaction with precipitation and fruit availability on microhabitat use by each type of disperser. Dashed vertical lines depict a 0 effect size (no effects)

TABLE 1 Summary of posterior distributions from Monte Carlo Markov Chain (MCMC) parameterization

Behaviour	Effects	Parameter	Guild	Mean	HPD	Comp.
Diet choice	Fruit abundance	β_{1d}	Bird	2.20	1.85, 2.52	0.83
			Lizard	0.53	-0.07, 1.21	
	Fruit size	β_{2d}	Bird	-0.77	-0.84, -0.69	1.84
			Lizard	1.07	0.93, 1.23	
	Carbohydrate content	β_{3d}	Bird	0.08	0.02, 0.15	0.04
			Lizard	0.01	-0.10, 0.14	
Habitat use	Cover	α_{1d}	Bird	1.50	1.33, 1.67	4.52
	Lizard	-3.15	-5.05, -1.31			
	Cover × Precipitation	α_{2d}	Bird	-0.50	-0.69, -0.29	0.43
			Lizard	-1.48	-3.30, 0.34	
	Cover × Fruit availability	α_{3d}	Bird	0.57	0.39, 0.78	0.11
			Lizard	0.36	0.12, 0.64	

Note: HPD depicts highest posterior density interval. Complementarity values of behaviours are also provided (Comp.)

FIGURE 3 Contribution of different behaviours of each frugivore type to Shannon diversity in the (a) early-emerged and (b) 1-year-old community of seedlings. In the case of fruit choice, only size-driven fruit choices contributed to diversity. In the case of microhabitat use, while frequent use of open areas by lizards negatively affected diversity of the early-emerged community, its effects turned positive in 1-year-old seedlings. Each point is the average (\pm SD) across 100 replicates. Abundance: relative abundance; Carbohyd: carbohydrate content; Fr: fruit availability; Pre.: precipitation



species in the community of recruits, while birds promoted a more even distribution of them. On islands, lizards tend to increase their abundance and expand their dietary breadth (Olesen & Valido, 2003). The former facilitates their encountering with all plant species in the community, including rare ones (Vázquez et al., 2009). The latter

results in a more frugivorous diet (Olesen & Valido, 2003). These factors, plus their ability to consume all types of fruits including large-fruited species, explain their key role in richness maintenance throughout recruitment. In accordance with previous work (Valido & Olesen, 2007), our results point to lizards as important dispersers

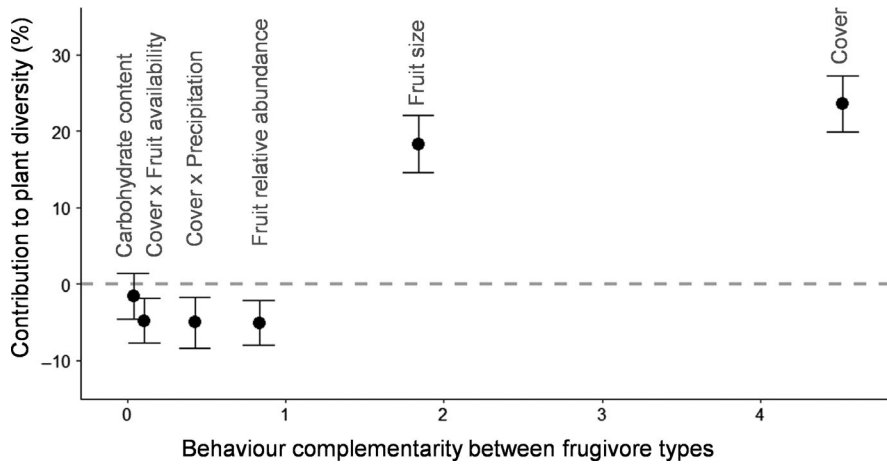


FIGURE 4 Relationship between behavioural complementarity and contribution to Shannon diversity in the community of seedlings (1-year-old). Only those behaviours with high complementarity (fruit size and cover effects) significantly contributed to diversity. Each point is the average (\pm SD) across 100 replicates of scenarios in which one behaviour was cancelled for both types of frugivores

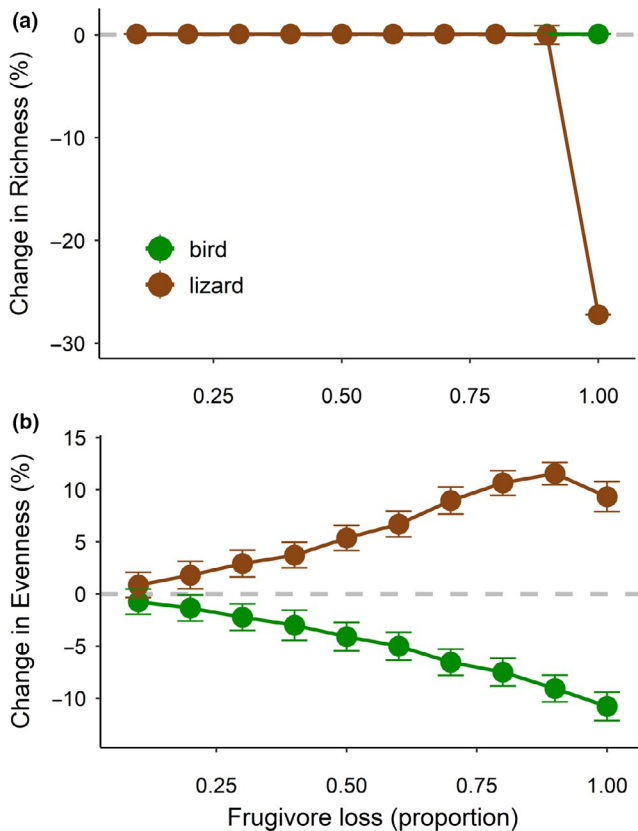


FIGURE 5 Effects of reduced abundance of birds or lizards in (a) richness and (b) evenness of the early-emerged seedling community. The extinction of lizards implied a richness loss of 27%, but plant species were more evenly distributed. In contrast, bird extinction did not affect richness but resulted in a less equitable community of seedlings. Abundance of frugivore types was reduced from 10% to 100% in decrement steps of 10%

in insular plant communities. In addition, they support the view that species that are abundant (Vázquez et al., 2009), or have no body size restrictions in their foraging choices (Vidal, Pires, & Guimarães, 2013), provide critical dispersal services to plant communities.

In contrast, birds did not affect richness but promoted evenness in the seedling community. At first glance, this pattern appears

counterintuitive because, contrary to our expectations, birds preferentially foraged for common fruits. However, the role of birds as promoters of evenness was mediated by size-driven fruit choices rather than by frequency-dependent fruit selection. In our community, the number of seeds per fruit largely varies across species (from 1 to >300). Consequently, multi-seeded species that are not dominant in the community of fruits can become very abundant among the seeds available. For instance, *Withania* only represented 5% of fruits but its relative abundance in the community of seeds was 26%. Small fruits usually show a lower number of seeds per fruit (Pearson correlation, .99 $p < .001$), and birds fed on them more frequently because they are easier to handle (González-Castro, Yang, et al., 2015). Therefore, by selecting small and mostly single-seeded species, they contributed to a more even composition of species in the seedling community. These patterns add to the growing evidence that fruit choice by birds can promote diversity maintenance in the community of recruits (Carlo & Morales, 2016; González-Castro et al., 2019; Morán-Lopez, Carlo, & Morales, 2017).

Trait-mediated abiotic filters in early recruitment can be an important driver of plant-community assembly, especially in areas with high environmental heterogeneity (Larson & Funk, 2016). Accordingly, beyond fruit choices, birds and lizards jointly contributed to diversity through their distinct microhabitat use. Although seed deposition in open microhabitats negatively affected diversity in the early-emerged community, 1 year later its effects shifted to positive. In Mediterranean areas, the mortality of early-emerged seedlings is higher in vegetation gaps than under cover, due to a more intense summer water scarcity (Granda, Escudero, & Valladares, 2014). Nonetheless, at later stages of growth, seedlings are more drought-resistant (Lloret, Penuelas, & Estiarte, 2005) and species-specific responses to environmental filters become accentuated (Poorter, 2007). In general, plants can either efficiently cope with water stress or exploit an impoverished light environment (Niinemets & Valladares, 2006). Thus, through mobilizing seeds towards microhabitats with contrasting light and water availability, birds and lizards ensured that heliophilous and ombrophilous species could find optimal recruitment sites. It is important to note, however, that our work is based on 1-year seed dispersal effectiveness,

while recruitment is a multi-year process (Schupp et al., 2010). For instance, under milder conditions differences between open and covered microhabitats are expected to narrow (Lloret et al., 2005), lowering the impacts of microhabitat use on the diversity of the recruited plants. Thus, although our results show that complementarity promotes diversity in the community of seedlings, the strength of its effects will most likely vary between years.

A low number of frugivorous species in an isolated community might cause the low redundancy between birds and lizards, as is observed in this study. Functional redundancy is more likely as species number increases (Walker, 1995). Therefore, richer communities tend to show a higher overlap in the dispersal services provided by frugivores (Loiselle, Blendinger, Blake, & Ryder, 2007), buffering the effects of disperser loss (Rumeu et al., 2017). However, functional redundancy can be decoupled from taxonomic richness (Zamora, 2000). Whether two dispersers perform redundant or complementary roles depends on how their morphological, physiological or behavioural traits affect fruit choice and seed deposition (functional niche sensu Rosenfeld, 2002). Therefore, irrespective of species richness, complementarity will occur whenever frugivores display unique behaviours (Jacomassa & Pizo, 2010; Stocker & Irvine, 1983; Wenny & Levey, 1998); especially when they imply the consumption of different sets of plant or the use of different microhabitats. Our results show that when this occurs, diversity in the community of seedlings is enhanced but also more vulnerable because community-level dispersal services rely on the presence of all 'functional types'. Hence, preserving a functionally diverse dispersal community should be a conservation target if we want to promote diversity maintenance in early-regenerating plant communities.

ACKNOWLEDGEMENTS

Authors are especially grateful to Airam Rodríguez, David Padilla, Beatriz Rumeu, Daniel González, Benito Pérez, Yurena Gavilán, Patricia Marrero, Elsa Bonnaud, Manuel Martín and Concepción Nieves, who helped at different stages of the field and greenhouse work. Frugivory data on Tenerife were collected by AG-C during his doctoral fellowship (JAE-PRE from the Spanish National Research Council, CSIC), and the fieldwork was financed by a project from the Spanish Ministry of Science and Education (CGL2007-61165/BOS), supported by FEDER funds from the European Union. The Cabildo de Tenerife provided permission (FYF 48/10) to perform the fieldwork. AG-C is currently funded by the Cabildo de Tenerife, under the identification mark Tenerife 2030 (Program TF INNOVA 2016-2021) with MEDI and FDCAN funds. TML was beneficiary of a CONICET postdoctoral grant.

AUTHORS' CONTRIBUTIONS

T.M.-L. conceived the aims of this work, designed model parameterization and analyses and drafted the first version of the manuscript. A.G.-C. conceived the idea of complementarity in the community-level dispersal services of birds and lizards, gathered field and greenhouse data and revised the manuscript. J.M.M. mentored T.M.-L., helped in designing and improving the concepts of the model and

revised the manuscript. M.N. designed the research project that provided data for model parameterization, revised the manuscript and provided guidance for this work. All authors approved the final version of the article.

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DATA AVAILABILITY STATEMENT

Data will be deposited in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.7wm37pvn5> (Morán-López, González-Castro, Morales, & Nogales, 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Morán-López T, González-Castro A, Morales JM, Nogales M. Behavioural complementarity among frugivorous birds and lizards can promote plant diversity in island ecosystems. *Funct Ecol*. 2020;34:182–193. <https://doi.org/10.1111/1365-2435.13476>