Seed dispersal effectiveness: A comparison of four bird species feeding on seeds of invasive *Acacia cyclops* in South Africa

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A B S T R A C T

Seed dispersal effectiveness (SDE) for vertebrates is determined as a product of quantity (numbers of seeds dispersed) and quality (probability that a dispersed seed becomes a new adult plant) components. There is a limited understanding of seed dispersal effectiveness for different avian vectors in South Africa, yet birds are important for long-distance dispersal for native species, and are implicated in the dispersal of many invasive plant species such as *Acacia cyclops*. Consequently, SDE was investigated in four bird species that are common seed dispersers in South Africa, of which two are frugivorous species (the Knysna turaco *Tauraco corythaix* and the red-winged starling *Onychognathus morio*), and two are granivorous species (the red-eyed dove *Streptopelia semitorquata* and the laughing dove *Streptopelia senegalensis*). Individuals of these species were caged and fed mature seeds of *A. cyclops* to determine quality of seed treatment in the gut. SDE was computed as a product of germination rates of gut-passed seeds of *A. cyclops* (i.e. quality) and the average bird body mass (i.e. proxy for seed load as quantity component) for the four bird species. Results show that frugivorous birds had significantly greater SDE than the granivorous bird species. SDEs for respective bird species also showed notable differences: the Knysna turaco had highest SDE followed by the non-significantly different red-eyed dove and red-winged starling, while the laughing dove had the lowest SDE of all bird species. However, it is likely that the two ubiquitous dove species, and both the colonial and nomadic red-winged starling, might have higher SDEs associated with large home ranges than the Knysna turaco with its more restricted geographic range. The results highlight the previously overlooked importance of doves and the other birds in mediating the invasion of *A. cyclops*, and the dispersal processes for the seeds of other plants included in their diet.

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1. Introduction

Seed dispersal effectiveness (SDE) is defined as the contribution a disperser makes to the future reproduction of the plant (Schupp, 1993; Schupp et al., 2010). This is determined as a product of quantity (numbers of seeds dispersed) and quality (probability that dispersed seeds becomes a new adult plant) components (Schupp, 1993; Schupp et al., 2010; Traveset et al., 2001). Thus, net SDE for a particular plant species should be a composite value of the quality components of the multiple vector species (i.e. polychory) interacting with the seed crop, as well as the quantity component (Dennis and Westcott, 2006; Nathan, 2007; Schurr et al., 2009), yet it has been difficult to obtain data for both components in avian vectors and involved plant species. In fact, many studies suggest that there is a stronger correlation between the quality component and SDE than the quantity component

(see a review, Schupp, 1993), thereby explaining imbalances in data availability in the literature.

Quantity of SDE entails the number of seeds that are removed from the plant crop by a vector (Schupp, 1993; Schupp et al., 2010). This is a function of the vector's body size and frequency of the vector's visitation to the seed/fruit source (Jordano, 2000; Vazquez et al., 2005; Mokotjomela, 2012). It has been shown that large vectors are likely to transport more seeds than small vectors (Jordano, 2000; Schurr et al., 2009), and thus vector body mass can be used as a surrogate variable for quantity of dispersal (Schupp et al., 2010). Body mass data for different vertebrates are more readily available than seed load data for different bird species. Dispersal of large numbers of seeds over long distances from maternal plants reduces intra- and inter-species competition (Higgins et al., 2003; Schurr et al., 2009), and provides essential genetic links between disconnected plant communities (Nathan et al., 2008; Schupp et al., 2010). Long-distance dispersal also increases the chances for recruitment in the presence of seed predators by maximising access to safe microsites by seeds (Howe, 1986). Indeed, high vector visitation has been demonstrated to improve the quantity

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of seeds removed and dispersed by small birds in the South African Mediterranean-climate region (Mokotjomela et al., 2013).

The quality of endozoochorous dispersal can be determined by experimentally passing seeds through the gut of a vector (Schupp, 1993; Traveset et al., 2001). It has been suggested that seed mortality and dispersal distances are influenced by gut transit time in birds in a vector-specific manner (Jordano and Schupp, 2000; Nathan, 2007; Traveset et al., 2007; Schurr et al., 2009; Tsoar et al., 2011; Mokotjomela et al., 2013), but very little is known about transit times in relation to seed germination rates. Seed germination rates could either be improved, remain unchanged, or suppressed after passage through a bird's gut (Traveset, 1998; Mokotjomela, 2012; Mokotjomela et al., 2015). Out of four caged bird species that ingested seeds of *Acacia cyclops*, only three bird species improved germination rates (Mokotjomela et al., 2015). Conversely, germination rates of fleshy fruits of alien plant species consumed by generalist birds did not change in the tropical areas of South Africa (Jordaan et al., 2011). Similarly, Chama et al. (2013) reported no change in the germination rates of seeds of fleshy fruits of 16 plant species to four generalist bird species. Neither of the studies accounted for the dispersal distance, yet it has a substantial influence on the quality component of seed dispersal effectiveness (Schupp, 1993).

In spite of the recognised importance of seed dispersal in the conservation of plant communities under climate change, vertebrates' seed dispersal is subject to several threats including increased habitat fragmentation and extinction dispersal vectors (Opdam and Wascher, 2004; Muller-Landau and Hardesty, 2005), competition for seed dispersal services posed by increasing presence of alien flora (Trakhtenbrot et al., 2005; Richardson and Rejmánek, 2011; Mokotjomela et al., 2013), and climate changes (Mokany et al., 2014). Mitigation of these threats to biodiversity requires the development of adaptive conservation management strategies that are resilient to climate change (Travis et al., 2013), and this requires an understanding of ecological process essential for restoration of particular habitats. In cases where fleshy-fruited plant species are of conservation concern, high seed dispersal effectiveness may be critical for a habitat to attain stable state (Payton et al., 2002; de Visser et al., 2012). In view of this wider context, the aim of this study was to investigate SDE in the four bird species that are common seed dispersers in South Africa, which are two frugivorous species (Knysna turaco *Tauraco corythaix* and the red-winged starling *Onychognathus morio*), considered to be legitimate dispersers (Jordano and Schupp, 2000; Thabethe et al., 2015), and two granivorous species (red-eyed dove *Streptopelia semitorquata* and laughing dove *S. senegalensis*) considered to be seed predators (Hockey et al., 2005; Schaefer and Ruxton, 2011). We predicted that frugivorous bird species, which are considered to be legitimate dispersers, would have higher SDEs than the two dove species that are generally seed predators.

2. Materials and methods

2.1. Bird-ingested seed germination quality

The procedure followed to determine the quality of seed dispersal is described in Mokotjomela et al. (2015). Bird species were obtained either by live-trapping in walk-in traps baited with fruits and millet seeds, or using captive birds kept in aviaries at the School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg. The four native bird species included in the feeding trials were the frugivorous Knysna turaco ($n = 4$) and red-winged starling ($n = 4$); and the granivorous red-eyed dove ($n = 5$) and laughing dove ($n = 8$). The frugivorous bird species represented legitimate dispersers while the granivorous bird species represented seed predators (Jordano and Schupp, 2000; Schaefer and Ruxton, 2011; Thabethe et al., 2015). The natural ranges of these four bird species overlapped with *A. cyclops*, and these bird species are well-known seed consumers and potential dispersers (Hockey et al., 2005; Mokotjomela et al., 2013; Rogers and Chown, 2013).

The birds were kept overnight for at least 12 h for acclimation to experimental conditions before feeding trials started (Conour et al., 2006). At least 10–30 arilate seeds were presented to the different bird species in Petri dishes at the beginning of the experimental day (0600 h) when the photophase began. The birds were then observed for 4 h to determine how they processed and ingested the seeds, after which any remaining seeds were removed and the commercial maintenance diet provided. Egested seeds were collected on newspaper-lined plastic trays placed beneath the aviaries. Seed egestion was monitored until the end of the experimental photoperiod at 1800 h. For frugivores, the egested seeds were collected during each 30 min interval through the day and recorded. For granivores, the number of defecated seeds and the length of gut passage times were recorded. The gut transit time was estimated as the interval between first ingestion of seeds and the time at which the excreta were voided with seeds was observed, assuming that the seeds that were ingested first would be either regurgitated or defecated first. For two frugivorous bird species, gut transit time estimation stopped after 4 h while the two granivorous species were monitored until the end of the day.

Feeding trials with each species were repeated until at least 50 gut-passed seeds were gathered for subsequent germination trials. The total number of all egested seeds was recorded, and the batches of seeds were kept in dry paper bags for germination rate tests in a greenhouse at the Department of Biological Science, University of Cape Town. Intact seeds were extracted from the birds' faecal samples and regurgitated pellets. Batches ($n = 50$) of ingested and un-ingested seeds were sown separately into labelled 195×60 mm germination trays which were 60 mm deep. Each tray contained sterilised beach sand into which 10 seeds were buried in two rows of five seeds each. The 40 germination trays were irrigated each morning (at 0900 h) by an automated irrigation system from the date of commencement (18 September 2013) to the date of termination of the experiment (15 January 2014). The numbers of seedlings that emerged in each germination tray were recorded at weekly intervals over the 16-week monitoring period, and expressed as percentages of the numbers of seeds initially sown (Mokotjomela et al., 2015).

2.2. Seed dispersal effectiveness

Seed dispersal effectiveness was derived as a product of the quality and quantity components. To quantify the quality component, mean germination rates (%) for the gut-passed seeds of *A. cyclops* (Mokotjomela et al., 2015) were used, while the average adult body mass of each bird species was used as a proxy for potential seed load, which represents the quantity component for each bird species (Schupp et al., 2010; Schurr et al., 2009). The germination rates were multiplied by average adult body mass (kg) of each bird species obtained from Hockey et al. (2005).

Records of geographic distribution and approximate abundance of the studied bird species were obtained from the Southern African Bird Atlas database at Avian Demography Unit, University of Cape Town. These records were used to infer the potential effectiveness of each bird species in providing seed dispersal services, as the abundance of birds is positively correlated with seed removal (Carlo et al., 2007).

2.3. Statistical analyses

Differences in the impact of seed treatment by different bird species and their categories (i.e. legitimate dispersers and seed predators) on seed germination rates were analysed using a General Linear Model ANOVA (SPSS version 22) with germination rates fitted as dependent variable, while the bird species (i.e. treatments) and their categories were fixed factors. All treatments were compared with the experimental control and among each other. GLM-ANOVA was also applied to compare seed dispersal effectiveness of different bird species. All bird species were equally represented and data sets were normally distributed. Dunnett's

post hoc test was applied to distinguish between significantly different means of germination rates between the gut-passed seeds and the untreated seeds of *A. cyclops* in the experimental control while Duncan's *post hoc* distinguished significant differences between the SDEs generated for each bird species. The geographic distribution and abundance of the four studied bird species were plotted to relate the occurrence of each species to its potential importance in providing seed dispersal services in the future.

3. Results

Non-significant differences were observed in the quality of seed treatment in the gut between the frugivorous and the granivorous groups of birds studied ($F_{(1, 488)} = 0.03$; $p = 0.859$). However, the individual bird species were significantly different in terms of the quality of seed treatment in the gut ($F_{(4, 555)} = 4.04$; $p = 0.003$; Fig. 1). Dunnett's *post hoc* test demonstrated that the red-eyed dove, red-winged starling and Knysna turaco had the highest seed treatment quality with respective decreasing order, with the large Knysna turaco, however, being significantly lower than the red-eyed dove but equivalent to the red-winged starling (Fig. 1). The laughing dove had the lowest seed treatment quality, which was non-significantly different from the experimental control ($F_{(1, 138)} = 0.31$; $p = 0.567$; Fig. 1).

Overall seed dispersal effectiveness for the frugivorous bird species (legitimate dispersers) was significantly greater than for the granivorous species ($F_{(1, 488)} = 10.7$; $p = 0.001$). SDE values generated for the four different bird species were also significantly different ($F_{(3, 486)} = 21.6$; $p < 0.001$; Fig. 2). Duncan's *post hoc* test demonstrated that the larger Knysna turaco had the highest SDE (7.9 ± 0.7) followed by the equivalent red-eyed dove (5.2 ± 0.5) and red-winged starling (4.0 ± 0.6), while the laughing dove had the lowest SDE (2.1 ± 0.3; Fig. 2).

Unlike the Knysna turaco with its narrow geographic distributions (Fig. 3a), the geographic distributional records suggested that the two ubiquitous dove species and the red-winged starling, are likely to provide important seed dispersal services for seeds of plants included in their diet in future since they can tolerate more diverse habitat conditions (Fig. 3b, c, d).

4. Discussion

The aim of the study was to investigate seed dispersal effectiveness (SDE) for four bird species that are important dispersal vectors in South Africa, using seeds of *A. cyclops* as a model plant species. Consistent with the study prediction, frugivorous birds collectively had significantly greater SDE than the granivorous bird species, which

may be associated with their ability to release intact seeds with improved germination ability (Jordano, 2000; Traveset et al., 2001; Thabethe et al., 2015). The apparent relationship of the SDEs with the quality of treatment and the bird body mass suggested a higher consistency in seed treatment in guts of frugivores than in granivores (Jordano, 2000; Schaefer and Ruxton, 2011; Thabethe et al., 2015). Indeed, the red-eyed dove reflected the highest quality while the laughing dove had the lowest quality of all the examined bird species (Mokotjomela et al., 2015), which might be associated with the varying ability of each species to process ingested food material such as the seeds of *A. cyclops*, which are naturally difficult to break (Tame, 1992). It was expected that body mass would be more positively correlated to SDE, as studies have shown that larger birds are likely to remove and retain larger numbers of seeds for longer times in the gut than smaller ones (Jordano, 2000; Nathan, 2007; Nathan et al., 2008; Schurr et al., 2009). The large Knysna turaco would, by that argument, have higher seed dispersal quality than other bird species. However, it is possible that even though the red-eyed dove had the highest dispersal quality component, the quantity component might be suppressed by the body size and the bird's ability to grind ingested seeds, thereby reducing its SDE to be equivalent with that of the red-winged starling. This is, however, combined with a relatively lower quality component reported in Mokotjomela et al. (2015). This was supported by the observation of a fewer numbers of seeds (e.g. 20%) that survived gut transit in doves during feeding trials (Mokotjomela et al., 2015).

Generally, birds provide important long-distance seed dispersal services, which increase the quality component of their SDE (Schupp, 1993; Schurr et al., 2009; Tsoar et al., 2011). Therefore, a low SDE associated with poor seed treatment quality in the gut of the laughing dove suggested that other bird species may transport seeds without any treatment in the gut (Traveset et al., 2001; Mokotjomela et al., 2015). However, these seeds might benefit long-distance-related quality of dispersal (Schupp, 1993); since doves tend to have large home ranges (Bucher and Bocco, 2009; Hockey et al., 2005). Thus, the poor quality of seed treatment in the gut of the laughing dove may also be offset by its ubiquitous occurrence, which may facilitate the transport of larger numbers of seeds, supported by the positive correlation between the vector abundance and the number of seeds removed (Carlo et al., 2007). Similarly, the colonial and nomadic behaviour of the red-winged starling in South Africa (Hockey et al., 2005) may improve its SDE to be better than that of the Knysna turaco. Indeed, these bird species are likely to provide important long-distance dispersal services for many plant species threatened by future climate change because their current conservation status is "*less concern*" in the IUCN database (Chen et al., 2011; Travis et al., 2013; IUCN, n.d). Effective species'
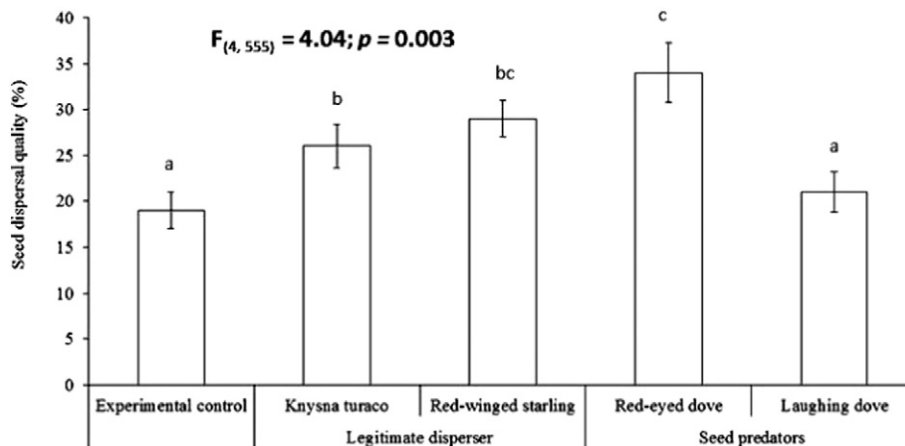

Fig. 1. Seed dispersal quality (i.e. mean germination rates % ± SE) for untreated (experimental control) and gut-passed *Acacia cyclops* seeds through different bird species: the frugivorous Knysna turaco *Tauraco corythaix*, and the red-winged starling *Onychognathus morio*, the granivorous red-eyed dove *Streptopelia semitorquata*, and the laughing dove *S. senegalensis*. Different letters above the bars show statistically significant difference. Error bars show standard error of mean.
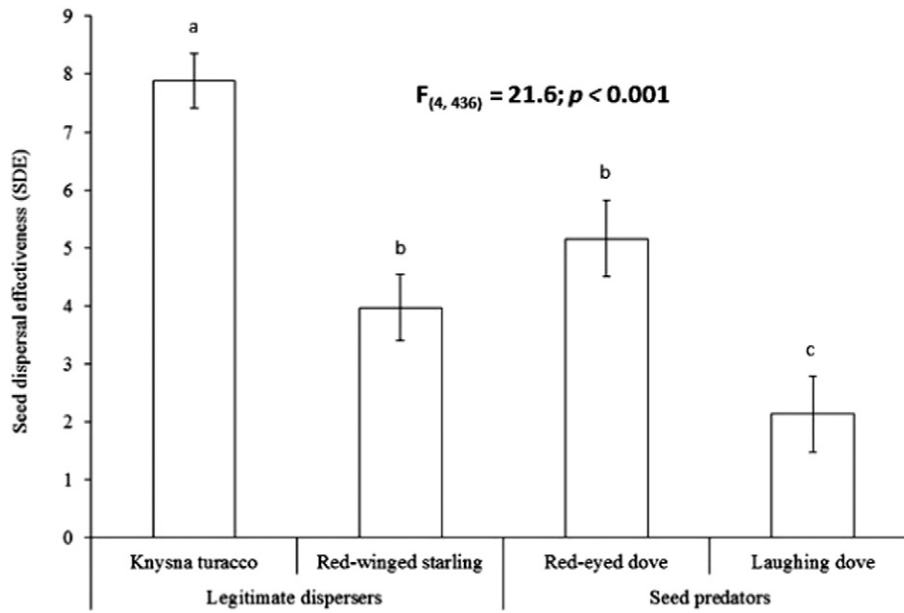
Fig. 2. Seed dispersal effectiveness (i.e. a product of germination rates (quality) and average adult body mass as proxy for seed load (quantity) for different bird species that ingested seeds of *Acacia cyclops*: the frugivorous Knysna turaco *Tauraco corythaix*, and the red-winged starling *Onychognathus morio*, the granivorous red-eyed dove *Streptopelia semitorquata*, and the laughing dove *S. senegalensis*. Different letters above the bars show statistically significant difference. Error bars show standard error of mean.
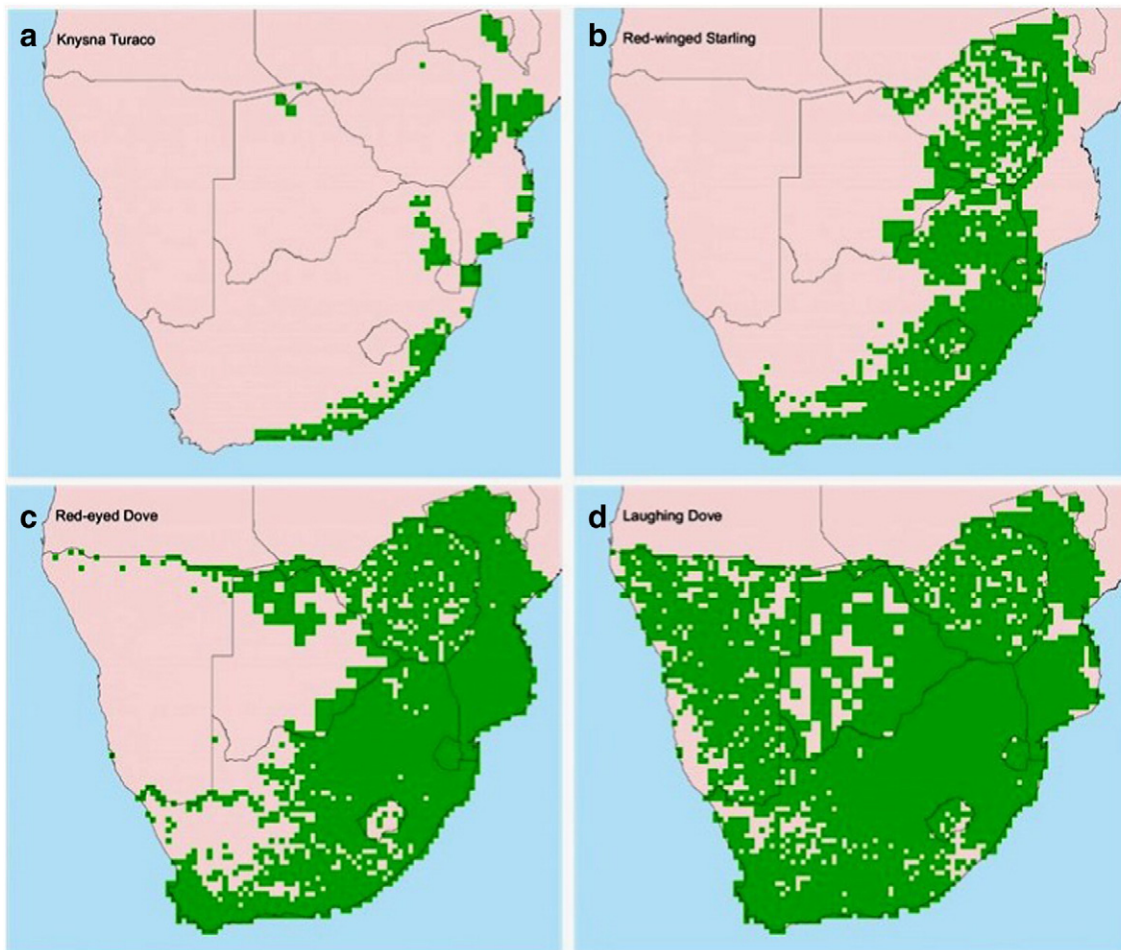
Fig. 3. Geographic distribution (i.e. green colour) of the studied bird species in Southern Africa, namely, the frugivorous (a) Knysna turaco *Tauraco corythaix*, and (b) the red-winged starling *Onychognathus morio*, (c) the granivorous red-eyed dove *Streptopelia semitorquata*, and (d) the laughing dove *S. senegalensis* (SABAP 2 http://www.adu.org.za/ accessed 23 June 2015).

dispersal ability has been recommended as a strategy for increasing the plant species' resilience to extinctions related to habitat fragmentation and declining vertebrate dispersal services (Muller-Landau and Hardesty, 2005; Schurr et al., 2007; Nathan et al., 2008; Mokany et al., 2014).

5. Conclusions

This study reports for the first time in South Africa that SDE as a product of quality and quantity may vary between the four studied bird species for the invasive *A. cyclops*. The results explain the role of birds in the spread of many invasive plants including *A. cyclops* in South Africa, with particular new findings regarding doves, which are generally understood to be seed predators. Since doves show a broad habitat tolerance (Baptista et al., 2009), and are ubiquitous in South Africa (Hockey et al., 2005; IUCN, n.d), we suggest that they are likely to provide important seed dispersal services for the seeds of plant species included in their diet in future especially for plant species with the dispersal agents threatened by climate change. Although our study did not use actual seed load for the quantity component of SDE, the results are reliable as the allometric relationships between body size of birds and seed dispersal distances have been confirmed (Schurr et al., 2009; Tsoar et al., 2011). Moreover, seed loads measured in the field are likely to be biased by the preference of different birds for particular fruits/seeds, and the degree of availability to the forging birds. As the seeds of different plant species have different attributes, such as hardness and absolute number of seeds produced per individual plant, more studies are required to conduct further tests using a variety of vectors and plant species to discern trends in bird-mediated seed dispersal effectiveness.

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