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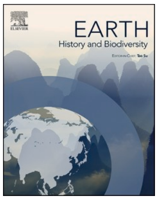

Stegodon SEA-crossing: Swim, shrink, and disperse

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ABSTRACT

Dispersal of terrestrial mammals into Wallacea requires the crossing of sea straits. Stegodons, an extinct family of proboscideans, managed to settle on roughly a dozen Wallacean islands during the Pleistocene. Their distribution pattern is, however, not well understood. It results from the interaction of two specific processes, namely respective swimming performances on the one hand, as well as island dwarfing on the other. Reduction of body mass has an impact on swimming performance, because smaller size leads to a slower swimming speed and lower deposits of available energy. In this study we conducted a series of experiments with the agent-based model SEAcross, designed to monitor swimming performances of terrestrial mammals across sea straits by measuring crossing success rates (CSR). We found that the dispersal pattern is in accordance with size-dependent swimming performances, geographic width as well as current speed and direction. Because currents change on a seasonal scale, bottlenecks decelerating or even preventing dispersal are rarely absolute, but should be considered as seasonal phenomena. Our results allow for an in-depth analysis of dispersal routes and success. Dispersal performances cannot, however, explain the lack of a fossil record of stegodons in the eastern part of Wallacea. With very few exceptions, routes should be manageable for terrestrial mammals with the size of a stegodon. Our results illustrate, however, the usefulness and applicability of agent-based models in order to further examine geographic dispersal barriers in conjunction with the dynamics of animal behavior.

1. Stegodon in insular Southeast Asia and beyond

The fossil record of islands worldwide shows that proboscideans are among the most successful island colonisers, thanks to their excellent swimming abilities and buoyancy. Fossil proboscideans have been described from about thirty islands worldwide, ranging from the Californian Channel Islands (*Mammuthus exilis*) in the West to Timor (*Stegodon timorensis*) in the East, occurring from the early Middle Miocene well into the Holocene, and represented by seven genera (van der Geer et al., 2021). The majority of insular populations known so far evolved body mass reductions in isolation in response to ecological release from predation and competition (Roth, 1992; Palombo, 2007; Herridge and Lister, 2012; Lomolino et al., 2013; van der Geer et al., 2016). In extreme cases, the decrease in body size reaches less than 10 % of the body mass of the precursors (Lomolino et al., 2013). Such body mass shifts are not unique to proboscideans, but follow the island rule, a graded trend among vertebrates that predicts that populations of large-sized species evolve dwarf forms and vice-versa in small-sized species (Benítez-López et al., 2021). The degree and direction of this trend of body size shifts can be explained by a suite of ecological and geographical variables (Lomolino, 1985; Lomolino et al., 2012).

Endemic stegodons (*Stegodon*), proboscideans with low-crowned molars with ridges and tightly spaced tusks, were common elements in insular Southeast and East Asia in the Pleistocene (van der Geer et al., 2021). They are known from the following islands, often represented by more than one species from subsequent geological periods: Java, Flores, Sangihe, Sumba, Timor, Sulawesi, Luzon, Mindanao, and Japan. These insular stegodons evolved body mass reductions, with remarkable dwarf

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species such as *Stegodon sondaari* (Flores) and *S. sumbaensis* (Sumba), the body mass of which were reduced down to 15 % and 8 % of the body masses of immigrating precursors, respectively. Some of these insular populations of *Stegodon* are likely the result of independent dispersal events by the same ancestral species, while others are likely part of a series of dispersals ('island hopping').

The Pleistocene fossil record of stegodons in insular Southeast Asia illustrates a distinctive pattern (Fig. 1). Stegodons from the Asian mainland crossed the islands of the Sunda Shelf, as illustrated by the fossil record in Java, and eventually reached the western part of Wallacea (van der Geer et al., 2016). Routes across this range of islands are, however, mainly reconstructed based on the spatio-temporal sequence of the known localities. Moreover, no fossil evidence for the presence of stegodons exists at present from islands east of Sulawesi and Timor. In order to examine that pattern with respect to potential barriers and routes we here simulate the dispersal of stegodons across insular Southeast Asia, Wallacea, into Meganesia with an agent-based modelling approach. We here apply the agent-based model (ABM) SEAcross (Hertler et al., 2022) to test the dispersal performances of stegodons of various body sizes. We then relate the results to the available data from the fossil record from the Southeast Asian islands to get insight in the likeliness of potential dispersal routes, the existence of bottlenecks or even barriers to stegodon dispersal.

2. The SEAcross model

The SEAcross ABM is designed to determine crossing success (CSR), to count the cases of disappearance (COD) by exhaustion, being washed off the map or leaving the map in either source or target area, and to count the number of aborted crossing attempts (Hertler et al., 2022). It is based on a more complex model, the HoWCrossing ABM, developed by Hölzchen (Hölzchen et al., 2021), which covers alternative ways for sea crossings, for instance drifting, hitchhiking, or rafting, and further parameters of the sea straits. Although the agents represent individuals, crossings only qualify as successful when a minimum number of individuals, representing a viable population, reaches the target shores.

Movement on land and into the water is driven by individual agents heading for attractive resource patches. Every land patch is assigned a random resource value between 0 and 1. The higher the resource score, the more attractive a patch is. In this version of the model agents perceive resources at the opposite shore irrespective of the distance. Because the SEAcross model is specifically designed to determine crossing success, it focusses on movement in water. Terrestrial movement is kept basic and only serves the purpose of entering the water.

When an individual enters the water, it decides on the basis of its hydrophobia score, whether it attempts to cross the sea strait by swimming or aborts the crossing attempt (Figs. S1–3). In the model, the physiological parameters, for instance optimum speed and/or costs of locomotion, correspond to quadrupedal paddling, a swimming style uniformly performed by terrestrial mammals (Fish, 1993; Fish and Baudinette, 1999; Meijaard, 2001). Species-specific parameters of the swimming performance are derived from body mass and head-body length of adult individuals and calculated by a physiological swimming model (Meijaard, 2001).

Relevant technical parameters of the model are summarized in supplement 1. A full technical report including ODD+D protocol (overview, design concepts, and details plus decision making following Grimm et al., 2010 and Müller et al. 2013), replication assessment, and sensitivity studies as well as the model itself are freely available at zenodo.org (Hertler et al., 2022). The ABM is designed with NetLogo (Wilensky, 1999; Wilensky and Rand, 2015).

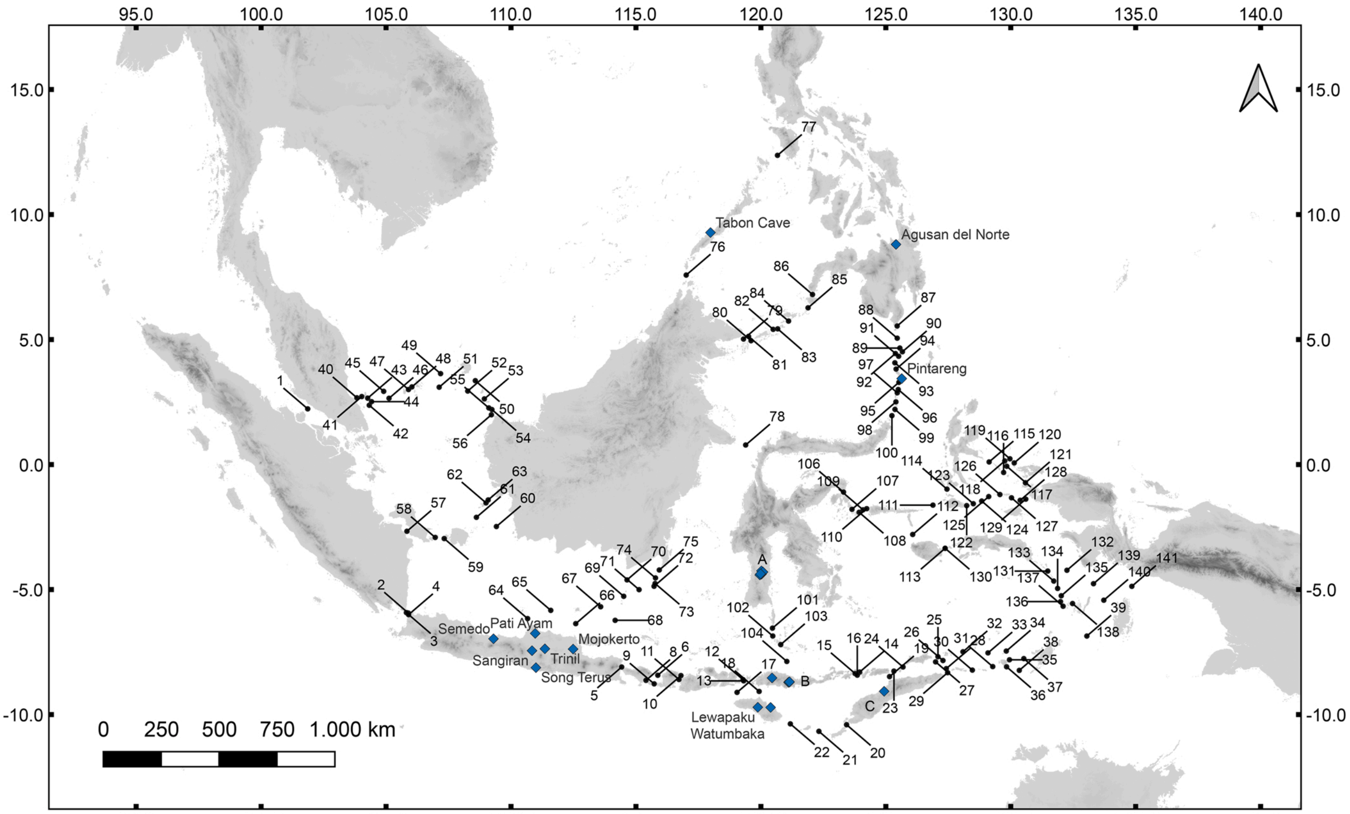

Fig. 1. Sea straits and fossil stegodon localities in Sundaland, Wallacea, and Meganesia; key to sea straits in supplement 2; A- fossil localities in Sulawesi: Talepu, Lonrong, Sompe, Lakibong, Bulu Cepo, and Tanrung; B- fossil localities in Flores: Liang Bua, Boa Leze, Wolo Sege, Mata Menge, Tangi Talo and Malahuma; C- Fossil locality in Timor: Atambua.

2.1. Environment

Each sea strait is characterized by width and features of the currents, particularly current speed and direction (complete list in table S2). These features were read out from maps depicting topography and currents in January and for a sub-set of sea straits additionally in August (Lellouche et al., 2021).

2.2. Agent features

Agents are characterized by hydrophobia score, body mass, head-body length, and population size. The hydrophobia score determines the probability with which a crossing attempt is started, when the agent enters the water. The hydrophobia score ranges in steps of 0.25 from 0.0 or semiaquatic to 0.75 or reluctant to get in contact with water. A hydrophobia score of 1.0 is theoretically possible, but would lead to the abortion of each crossing attempt irrespective of the features of the sea strait. It would prevent crossing attempts altogether and would result in crossing successes of 0.0. We assigned a hydrophobia score of 0.25 to the stegodon agents examined in this study (Table 1), assuming that they are equally ardent swimmers as Asian elephants are today (Johnson, 1980). Because Southeast Asian stegodons were more successful island colonisers than elephants (van den Bergh, 1999), a score of 0.25 represents a modest assumption.

Available energy deposits and costs of swimming by quadrupedal paddling are derived from head-body length and body mass of adult individuals. Body mass of mainland forms of adult stegodons is taken from the literature (Lomolino et al., 2013; van der Geer et al., 2016). In order to determine head-body length, we composed a reference sample for Asian elephants from the literature (Nowak, 1999; Francis, 2008; Smith and Xie, 2008) as well as from online databases (Animal Diversity Web, 2023, International Environment Library Consortium, 2023), and estimated head-body length for fossil stegodons by regression. The physiological swimming model then infers available energy deposits from body mass, and energetic costs of quadrupedal paddling from both, body mass and head-body length combined (Meijaard, 2001). In intermediate steps the model estimates costs of transportation, maximum and optimum swimming speeds, and results in maximum distance, which is in range before the energy deposits deplete (Table 1).

Table 1
Key variables for the swimming performance of stegodons of different sizes.

Stegodon sp.	Mainland size	-10 %	-25 %	-50 %	-75 %
Size:					
Body mass [kg]*	3680	3312	2760	1840	920
Head Body Length [m]**	6.0	5.9	5.7	5.4	4.8
Energy deposits***:					
Mobilizable energy [MJ]	2350.833	2122.671	1768.893	1.179,262	589,631
Quadrupedal paddling***:					
Costs of transportation [J per kg and m]	3.676	3.787	3.922	4.491	5.490
Optimum swimming speed [m per s]	0.505	0.501	0.492	0.479	0.452
Maximum distance [km]	174	169	161	143	117
Hydrophobia score	0.25	0.25	0.25	0.25	0.25
Population size	20	20	20	20	20

* source of the mainland data Lomolino et al. (2013);
** Head Body Length based on own regression;
*** energy deposits and data on quadrupedal paddling own calculations following Meijaard (2001).

The number of individuals determines when arrivals in the target area are considered as successful. We assume that the figure corresponds to the number of individuals in an average population. Because the stegodons in our model are assumed to be gregarious, based on trackways of Pliocene stegodons (Matsukawa and Shibata, 2015), we assume a group size of 20 adult individuals to be required for successful immigration (McKay, 1973). Although the figure has an impact on the absolute values, it does not affect CSR, because it constitutes a relative value.

2.3. The dwarfing model and swimming performance

Stegodons inhabiting islands with a small total surface area and/or offering a limited amount of food resources are predicted to undergo evolutionary body mass decrease, or island dwarfing (van der Geer et al., 2016). To accommodate dwarfing processes on islands, we determine CSRs for five categories of stegodons starting with a mainland size form (Table 1), as well as forms with body masses of 90 %, 75 %, 50 %, and 25 % of the mainland form. Stegodons with reduced body mass should differ in their energy deposits, optimum speed, and consequentially in their swimming performances (Table 1).

In our geographic model, the size of the mainland form is retained on the Malaysian peninsula and Sumatra. Java with a smaller total area and minimal isolation facilitates size reductions of −25 %. Although we do not consider that Borneo, the island with the largest surface area in our sample, initiates further size reduction, we selected the smallest candidate originating in Java to continue dispersal beyond this point. Mindanao and Sulawesi with higher degrees of isolation are expected to induce size reductions of around −50 %. These size reductions are in accordance with published reconstructions (van der Geer et al., 2016). On Flores, for example, fossil dwarf stegodons of the Early Pleistocene layer (*S. sondaari*) evolved body masses corresponding to at least −75 % of the mainland form. We assume similar degrees of size reduction for stegodons on Buru and Halmahera. In our model stegodons occurring east of Halmahera, Buru and Flores do not shrink any further. Small islands with uniform habitats are considered as mere stepping stones providing resting sites, but not supporting permanent habitation and thus not triggering evolutionary adaptations in body size.

2.4. Crossing success rates (CSR), effective distance (ED) and causes of disappearance (COD)

The CSRs are calculated by cumulative counts of agents arriving in the target area (Hölzchen et al., 2021). Crossing attempts are considered as successful, when a number of 20 stegodon agents arrive in the target area. A crossing attempt is registered as such as soon as an agent starts swimming. Because 25 % of the crossing attempts by stegodon agents are aborted due to their hydrophobia score, CSRs determined by SEAcross do not exceed 0.75. As a control for the total number of individual crossing attempts, the number of aborted attempts is monitored. The number of aborted attempts depends on the hydrophobia score, thus corresponding to 25 % of all crossing attempts in our experiments.

In order to further evaluate crossing performances, we integrated the features of the sea straits and optimum swimming speeds by calculating effective widths (EW), effective shifts (ES), and effective distances (ED) per sea strait and agent. Effective width calculates the direct distance which has to be covered by the agents taking into account their swimming speed and the impact of current speed and direction on the geographic width of the sea strait.

$$EW = W \bullet \frac{S_{opt}}{S_{opt} + (S_{cur} \bullet \cos\gamma)} \tag{1}$$

With W – width, S_{opt} – optimum speed of the agent, S_{cur} – current speed and γ – effective angle between swimming and current direction.

Supportive currents will reduce effective width to be covered by own force, currents directed against the swimming direction will expand effective width of the sea strait. Effective shift (ES), the horizontal component of the movement in water, is calculated as:

$$ES = \frac{W}{S_{opt}} \bullet (S_{cur} \bullet \sin\gamma) \quad (2)$$

With W – width, S_{opt} – optimum speed of the agent, S_{cur} – current speed, and γ – effective angle between swimming and current direction.

Effective distance to be covered is then derived as:

$$ED = \sqrt{EW^2 + ES^2} \quad (3)$$

With EW – effective width, and ES – effective shift. Dividing this value by optimum speed provides the total crossing time.

The map in SEAcross has open borders and permits the agents to be washed off by currents or to drown due to exhaustion. The agents can moreover randomly walk off the map in either source or target areas. Movement on land is a process with a constant speed and predominantly attracted by patches with high resource densities (Supplement 1). In order to prevent agents from getting stuck in resource maxima, we included a random component in the direction. Besides aborted crossing attempts, we counted the total number of individuals leaving the map by either one of these ways.

2.5. Initialization and experiments

In each of the 25 runs per experiment, the ABM ran for 2160 ticks corresponding to a period of three months (1 tick = 1 hour). We applied a uniform number of ticks to yield comparable results, and assuming that the environmental conditions would not decisively change in this time span. The map has a variable extension which is adapted to the width of the sea strait. Source and target areas possess a uniform size of 25 × 100 patches each. A patch corresponds to the size of 1 × 1 km.

Because of the stochastic elements in the ABM two consecutive model runs will not result in identical values in the target variables. In order to yield statistically robust results, an experiment requires 25 independent runs. The number of model runs required is determined in advance by carrying out a replication assessment as described by Hoad et al. (2010) and Lorig (2018), in which the CSR value resulting from a particular run is compared to the variance resulting from a cumulating number of individual runs until it does not deviate by more than 5 % (Hertler et al., 2022).

For each experiment we configured both, sea strait and agent features accordingly. We tested a total number of 139 sea straits for each one of the five agents (Fig. 1). We tested three of the sea straits twice, comparing configurations of the currents in January and August, respectively. Because relevant features of the sea straits, i.e. current speed and direction, are different, we assigned new numbers to them (i.e. sea straits #6 + #7, #91 + #283, and #104 + #105). We evaluated the crossing performances of agents in the five size categories with particular focus on those sea straits that appear to act as barriers and those where the agents display differential performances among the five agents. A total of 710 experiments were carried out. We then selected a particular combination for the dispersal model integrating the shrinking model (experiments marked by ‘x’ in supplement 2). We examined dispersal options between the islands in Sundaland, and along six routes across Wallacea.

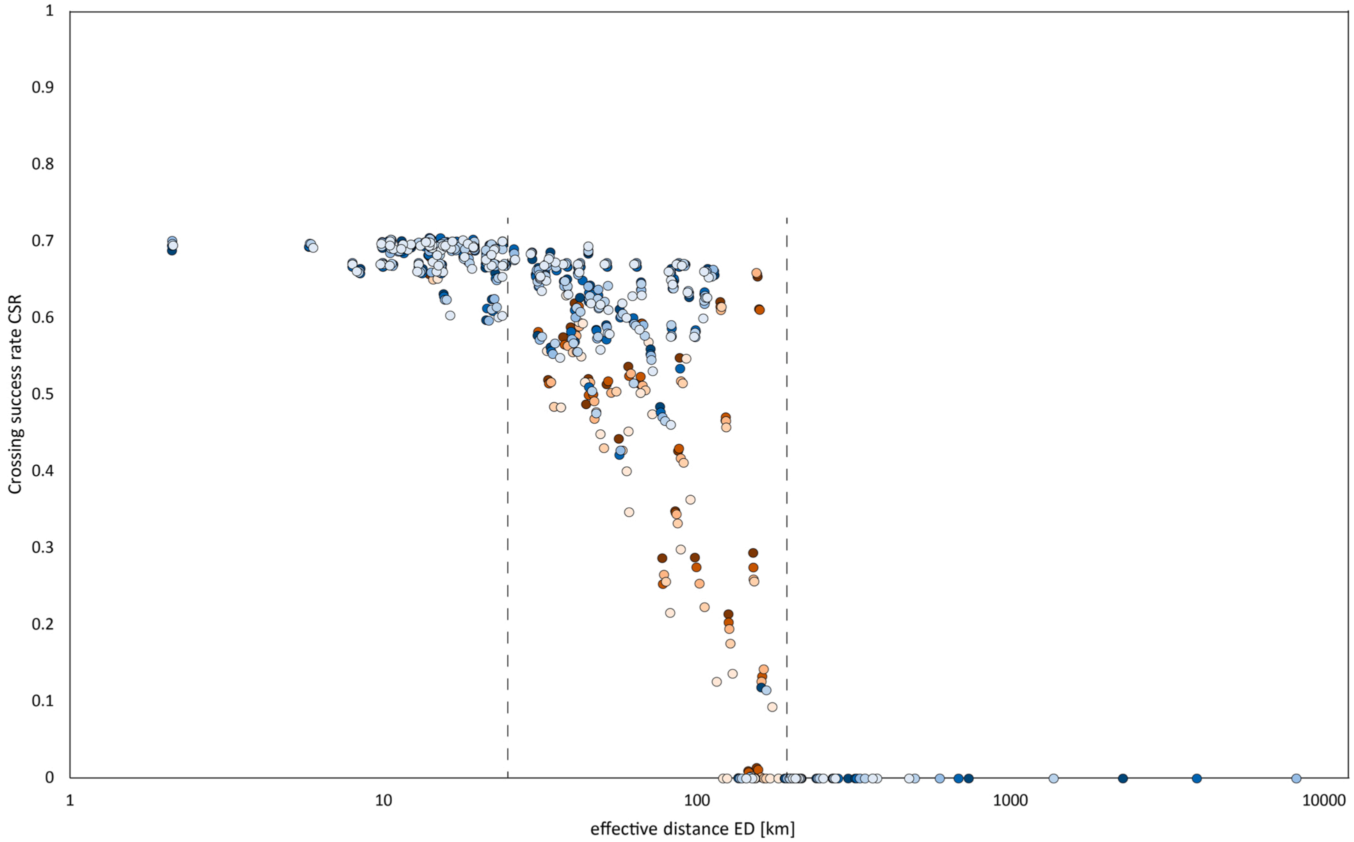

Fig. 2. Crossing success rates (CSR) for all experiments versus effective distances (ED); agents are distinguished by different shades from dark – mainland size stegodon to light– stegodon with a body mass reduction of −75 %; blue – no significant differences; red – significant differences occur; dashed lines indicate the range used for regressions. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3. Results

The majority of all 142 sea straits are crossed successfully by each of the five agents. Fig. 2 displays CSRs by effective distances of the sea straits for all 710 experiments. Sea straits with an effective distance beyond 170 km are not crossed successfully by any of the agents. This distance corresponds to the maximum ranges of both of the larger agents, thus constituting an absolute dispersal barrier. In order to rank descriptive features of the sea straits and CSRs we excluded the sea straits, which could not be crossed successfully and determined the Bonferroni corrected Pearson correlation coefficient for the remaining 648 experiments. The CSRs correlate with absolute width, current speed, effective width (EW), and effective shift (ES), but most robustly with effective distance (ED; $r = -0.68302$; $p < 0.05$). The correlation is negative, i.e. the larger the distance to be crossed, the lower crossing success. The correlation of CSR with ED is higher than with any of the other factors effective shift (ES) ($r = -0.62509$), effective width ($r = -0.56152$), current speed ($r = -0.48174$), and absolute width ($r = -0.39967$). In our sample, current direction does not correlate with crossing success ($r = 0.03731$). Effective distance is therefore the most reliable predictor for CSRs. We calculated linear regressions for each of the agents in order to supplement the dataset we used for route analyses.

The CSRs were further evaluated by comparing those rates resulting from 25 runs for each of the size categories of stegodons for all 139 sea straits in January plus three additional ones in August for statistical significance by pairwise Mann-Whitney-Tests with Bonferroni correction ($p = 0.05$). Results were assigned to either one of three cases: In case of ‘good’ sea straits crossing attempts by all size classes are successful and resulting CSRs do not differ significantly from one another. The majority of tested sea straits falls into this category ($n = 98$ or 69.0 %). In case of ‘bad’ sea straits all crossing attempts fail irrespective of the body size of the agent. 11 sea straits (7.7 %) in our sample fall into this category. Both categories of sea straits are further discussed in Section 3.1.

The last category, in which one or more pairs of agents perform significantly different, is the most interesting one because these cases may illustrate boundary conditions for dispersal. This affects 33 sea straits corresponding to 23.2 % of all cases, which are further introduced in Section 3.2.

3.1. *Sea straits without significant differences among the agents*

Fig. 2 displays the crossing performances of all agents in all sea straits. Straits where agents do not show significant differences in their crossing performances are shown in blue. Effective distances are lower than 111 km. Additionally, the uniformly successful performance of all size classes despite considerably deviating body masses is a consequence of the physiological swimming model. In the swimming model applied swimming speed is inferred from head-body length (HBL). Although body mass itself has an impact on energy deposits and costs of transportation, the influence of speed, exclusively derived from HBL, on the swimming performance is higher. A geometrical reduction of body mass is less reflected by linearly varying parameters like HBL (Table 1). When sea straits are smaller than 111 km and/or currents support crossing attempts, thus reducing effective distances, agents are capable of performing equally well irrespective of body mass and size.

In the ‘bad’ case, all crossing attempts are unsuccessful irrespective of the size of the agents (CSR = 0). Such sea straits constitute absolute dispersal barriers. This occurred in 11 cases, for which we examined the causes of disappearance (Fig. 3), in particular whether the agents were

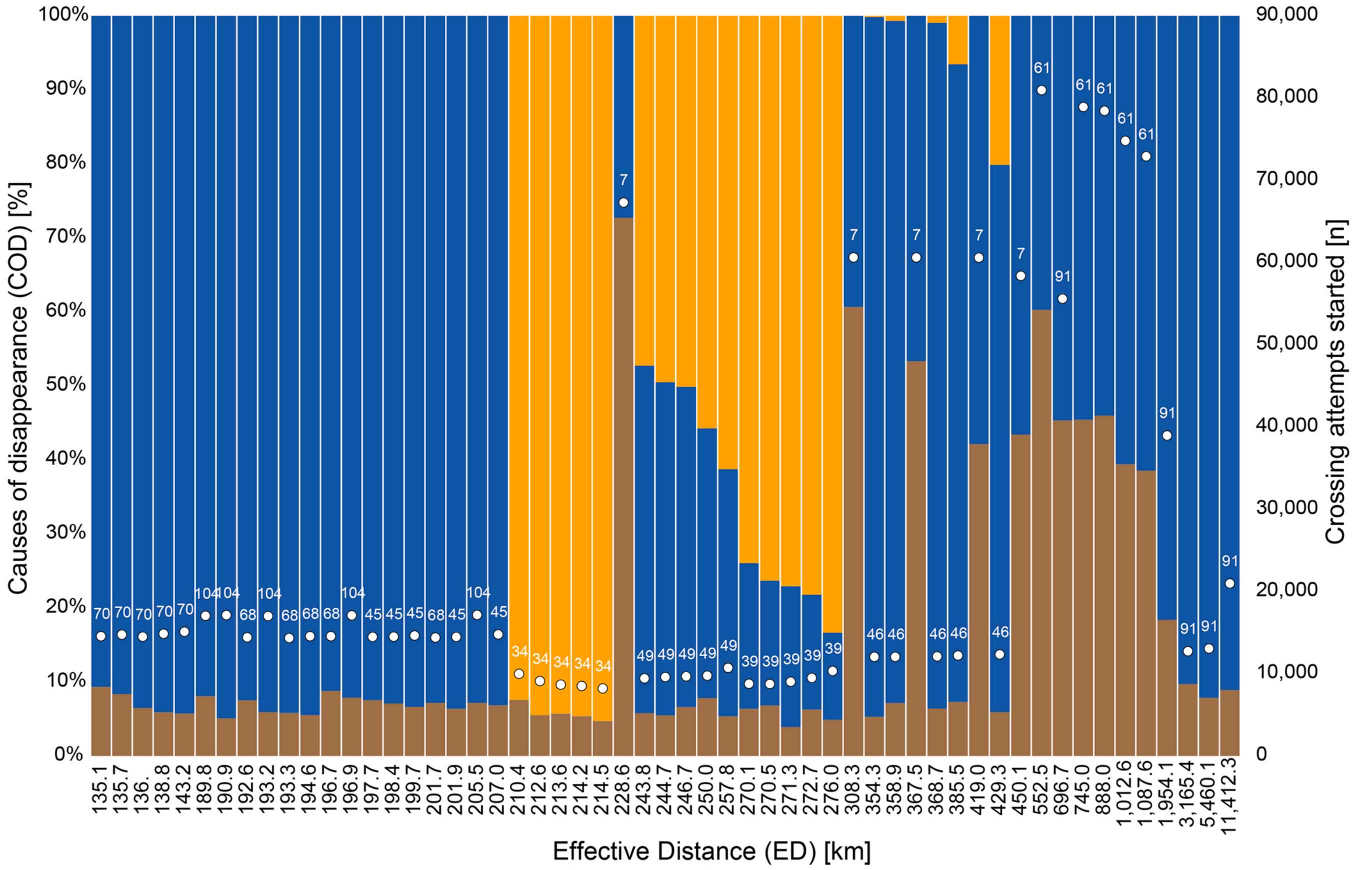

Fig. 3. Causes of disappearance (COD) vs. effective distances (ED) in sea straits which cannot be crossed successfully irrespective of the size; causes of disappearance (left axis): brown – leaving the map in the source area, blue – being washed off the map, orange – exhaustion; white dots - absolute numbers of crossing attempts started (right axis). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

washed off the map, died from exhaustion, or considerable numbers left the map in the source area. When arranged by effective distances, the set of sea straits allows to distinguish three cases. When effective distances are lower than 210 km, the majority of the agents is washed off the map, less than 10 % leave the map in the source area, and exhaustion does not play a role. With effective distances in a medium range, between 210 and 276 km, at least 50 % of the agents die of exhaustion. Sea strait #34 possesses an absolute width of 257 km. Despite favourable currents reducing effective distance, the absolute distance is simply out of reach for the agents. This result corroborates our decision to exclude wider passages from our dataset. Sea straits #39 and #49 are also comparatively wide measured by absolute distances, 230 km and 169 km, but sideward directed currents deflect the swimming movement and lead to higher ratios of agents being washed off the map. The larger the agent, the less pronounced is this effect, because smaller agents swim with a slower speed and possess lower maximum ranges. In the last set of sea straits with effective distances beyond 300 km, currents are directed against the swimming direction. They come with an angle and with speeds, compensating (sea strait #46) or exceeding swimming speeds (sea straits #7, #61, and #91). In the case of sea strait #46, currents have a sideward component, exerting a strong impact on net forward movement, but not preventing it altogether. As a result, the majority of the agents are washed off the map, but some agents swim sufficiently wide to exhaust. The smaller the agent, the higher effective distance and the higher the proportion of agents dying from exhaustion. In sea straits #7 and #61, current speed is twice has high as swimming speed preventing the agents from creating any forward thrust. Under these circumstances considerable numbers of the agents are washed ashore in the source area. In both cases the number of crossing attempts is unusually high. Because agents are replaced as soon as they leave the map, high total numbers of agents in the experiments indicate high replacement frequencies.

In sum, several constellations occur in our dataset in which agents are unable to cross sea straits successfully irrespective of their size. One sea strait in our sample is simply too wide and the agents exhaust. However, exhaustion only occurs in sea straits with a minimum effective distance between 200 and 300 km. In the majority of cases, a sideward directed component leads to high numbers of agents being washed off the map. When currents are directed opposite to the swimming direction and current speed exceeds swimming speed, elevated numbers of agents are washed ashore in the source area and leave the map there.

3.2. Size-dependent crossing success

In 33 sea straits corresponding to 23.2 % of our sample at least one of the agents of the different size categories performs significantly different from the others. Such cases occur in all three of the regions examined here: 16 in Sundaland, 15 in Wallacea, and 2 in Meganesia.

The distribution of the sea straits with significant differences in Fig. 2 illustrates that they contribute the cases located on the slope between high and low CSRs. For every sea strait we counted the number of instances, in which agents performed significantly different from others (Fig. 4) and tested pairwise correlations between the counts on one hand, and CSRs or effective distances on the other. The correlation with CSR is robust and negative (Pearson correlation = −0.42522, $p < 0.01$). When the specific features of the sea straits evoke a decrease in CSRs, then smaller agents are more immediately affected than larger ones and the number of pairs differing significantly are increasing. The correlation between counts and effective distance is even more robust (Pearson correlation = 0.50908, $p < 0.01$) and positive; the wider the effective distance, the higher the number of pairs.

The sea straits in which CSR is size dependent are listed in Table 2. In the majority of cases, pairs of agents performing significantly different are restricted to the larger and smaller agents in our dataset, for instance the mainland form performing significantly different than the −75 % agent, and the agents in between bridge both performances by differing insignificantly from their immediate neighbours.

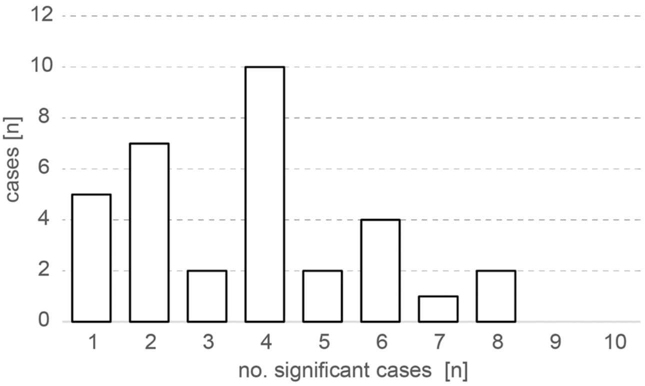

Fig. 4. Number of pairs differing significantly for every sea strait where the performance of agents depends on body size.

Three cases deserve a closer look, because neighbouring pairs differ significantly in 7 or 8 instances (Fig. 4). Sea strait #42 links the islands of Tinggi and Aur off the eastern coast of peninsular Malaysia *en route* to Borneo. This sea strait is moderately wide, but currents directed against the swimming direction and with a speed approaching swimming speeds almost triplicate effective distances. CSRs are generally low, between 0.1249 and 0.2853. A sideward directed component washes the majority of the agents off the map. Because of their slower pace and smaller energy deposits, smaller agents are additionally affected by exhaustion. Sea strait #62 is also located in Sundaland, but is part of the route connecting Sumatra with Borneo. It links the islands of Karimata and Buan in the last segment of the route before reaching the coast of Borneo. Although CSRs vary in a moderate range, between 0.3439 and 0.4952, a similar combination of factors leads to similar results: Current speed in January even exceeds swimming speed, but as the sea strait is only 14 km wide, all agents manage to cross with moderate success (Figs. S3–7). However, many are washed off the map, and the smaller the agents, the more they are prone to exhaustion.

Sea strait #22 is situated in Wallacea as part of route D linking Sumba with Sawu. This sea strait represents the interesting case that where both of the larger agents perform similarly well with CSRs of 0.6064 and 0.6053 respectively, the CSR of the −25 % agent already drops to 0.1253, and both of the smaller agents do not manage successful crossings at all (Figs. S3–3). The sea strait is 98 km wide, but currents in January oppose swimming direction with moderate speed. This combination of factors raises effective distances to 158 km for the larger agents, 160 km for the −25 % agent, and 163 km and 170 km for both of the smaller agents. While effective distances are still in reach of the larger agents, ED of the −25 % agent almost equals its maximum range of 161 km (Table 1), and ED exceeds maximum range for both of the smaller agents. Because movement in water is not deflected, smaller agents exhaust, while larger ones still manage successful crossings (S3–3). In other words: This sea strait represents a size-dependent filter, where agents with a particular body mass manage to pass, while agents with lower body masses exhaust and fail. The consequences of this selection process for dispersal are further explored in section 4.1.3.

4. Discussion

In order to test dispersal routes of stegodons across Sundaland and Wallacea and ultimately into Meganesia, we combined the dwarfing model for stegodons (Table 1) with the CSR measurements taken by the SEAcross ABM (Fig. 2; suppl. 2). This map (Fig. 5) provides an overview and allows for further route analyses for six different routes into and across Wallacea (Figs. 6–9). Irrespective of changing sea levels, the islands of Wallacea stretching between Bali, Borneo, and New Guinea always constituted a wide archipelago consisting of unconnected

Table 2
Sea straits depicting size-dependent crossing success.

Sea strait #	Route	Successful agents	Agents without success	Counts differences [n]	significant differences in performance of the agents
12	B	all	none	1	−10 % vs. −75 %
19	D	all	none	1	mainland size vs. −75 %
74	Sunda	all	none	1	mainland size vs. −75 %
114	F	all	none	1	mainland size vs. −75 %
119	F	all	none	1	−10 % vs −75 %
23	D	all	none	2	mainland size + −10 % vs. −75 %
27	E	all	none	2	mainland size + −10 % vs. −75 %
60	Sunda	all	none	2	−10 % + −25 % vs. −75 %
75	Sunda	all	none	2	−10 % vs. −25 % + −75 %
80	A	all	none	2	mainland size + −25 % vs. −75 %
100	A	all	none	2	mainland size + −25 % vs. −75 %
102	C	all	none	2	−10 % + −25 % vs. −75 %
79	A	all	none	3	mainland size, −10 % + −25 % vs. −75 %
87	A	all	none	3	−10 % vs. mainland size, −50 % + −75 %
29	E	all	none	4	mainland size, −10 %, −25 % + −50 % vs. −75 %
41	Sunda	all	none	4	mainland size, −10 %, −25 % + −50 % vs. −75 %
51	Sunda	mainland size, −10 %, −25 %, −50 %	−75 %	4	mainland size, −10 %, −25 % + −50 % vs. −75 %
52	Sunda	mainland size, −10 %, −25 %, −50 %	−75 %	4	mainland size, −10 %, −25 % + −50 % vs. −75 %
54	Sunda	all	none	4	mainland size vs. −25 % + −50 %; −25 % + −50 % vs. −75 %
63	Sunda	all	none	4	mainland size, −10 %, −25 % + −50 % vs. −75 %
71	Sunda	mainland size, −10 %, −25 %, −50 %	−75 %	4	−10 % vs. mainland size, −50 % + −75 %
76	Wallacea	all	none	4	mainland size, −10 %, −25 % + −50 % vs. −75 %
112	F	all	none	4	mainland size, −10 %, −25 % + −50 % vs. −75 %
139	F	mainland size, −10 %, −25 %, −50 %	−75 %	4	mainland size, −10 %, −25 % + −50 % vs. −75 %
64	Sunda	mainland size, −10 %, −25 %	−50 %, −75 %	5	mainland size vs. −25 %, −50 % + −75 %; −10 % vs. −50 % + −75 %
66	Sunda	all	none	5	mainland size vs. −50 % + −75 %; −10 %, −25 % + −50 % vs. −75 %
58	Sunda	all	none	6	mainland size, −10 % + −25 % vs. −50 % + −75 %
59	Sunda	all	none	6	mainland size, −10 % + −25 % vs. −50 % + −75 %
65	Sunda	mainland size, −10 %, −25 %	−50 %, −75 %	6	mainland size, −10 % + −25 % vs. −50 % + −75 %
81	A	all	none	6	mainland size vs. −10 %, −50 % + −75 %; −10 %, −25 % + −50 % vs. −75 %
42	Sunda	all	none	7	mainland size vs. −25 %, −50 % + −75 %; −10 % vs. −50 % + −75 %; −25 % + −50 % vs. −75 %
22	D	mainland size, −10 %, −25 %	−50 %, −75 %	8	mainland size + −10 % vs. −25 %, −50 % + −75 %; −25 % vs. −50 % + −75 %
62	Sunda	all	none	8	mainland size vs. −50 % + −75 %; −10 % vs. −25 %, −50 % + −75 %;

(continued on next page)

Table 2 (*continued*)

Sea strait #	Route	Successful agents	Agents without success	Counts differences [n]	significant differences in performance of the agents
					−25 % vs. −50 % + −75 %; −50 % vs. −75 %

islands. Even though the width of some sea straits may have changed, no major land bridges were exposed. In order to travel from one island to a neighbouring one, it was necessary to cross sea straits, either by drifting passively or by active swimming. The fossil record illustrates that stegodon, like other proboscideans, managed to disperse across the western part of Wallacea, while the eastern part lacks a fossil record. We apply CSRs and effective distances, EDs, to specifically examine routes into and across Wallacea and study six routes in further detail. Route options A link Sundaland with Sulawesi, either directly from Borneo, or via a northern route leading through Mindanao. The latter route includes at least six sea straits to Mindanao and a minimum of eleven between

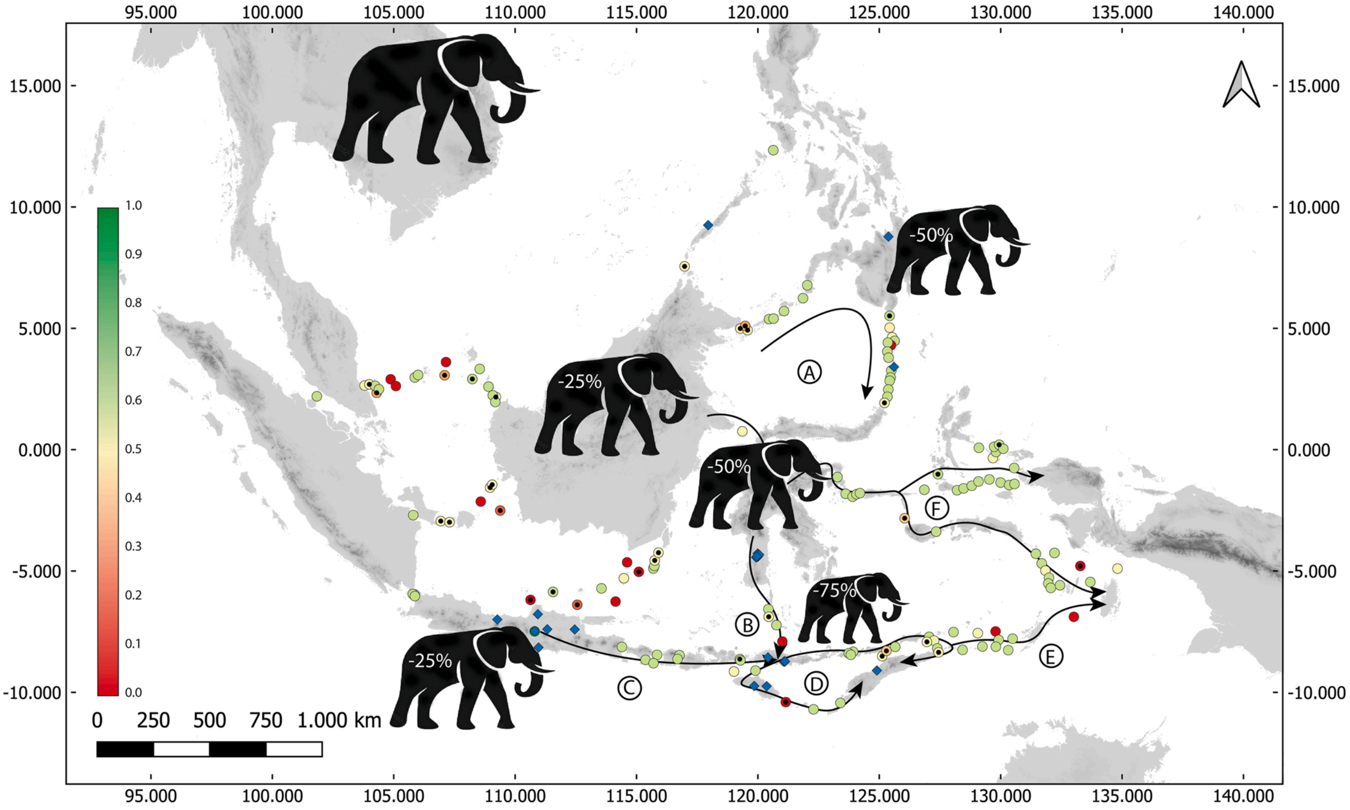

Fig. 5. Shrinking and dispersal model combined; coloured dots in the seastraits reflect the position on the CSR scale by a traffic light code; black dots – sea straits in which the agents display significant differences; blue diamonds – Pleistocene localities with Stegodon, names see Fig. 1. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

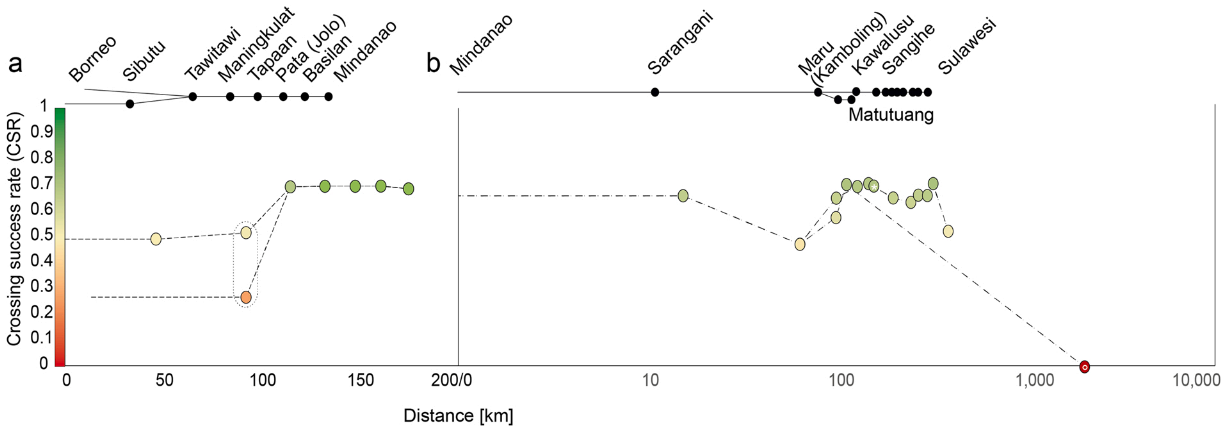

Fig. 6. Route analysis for route A leading from (a) Borneo to Mindanao for the −25 % stegodon, and (b) Mindanao to Sulawesi for the −50 % stegodon; circle – CSR in January, asterisk – CSR in August. Coloured plot displays effective distances (ED), while black line plots show absolute geographic distances. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

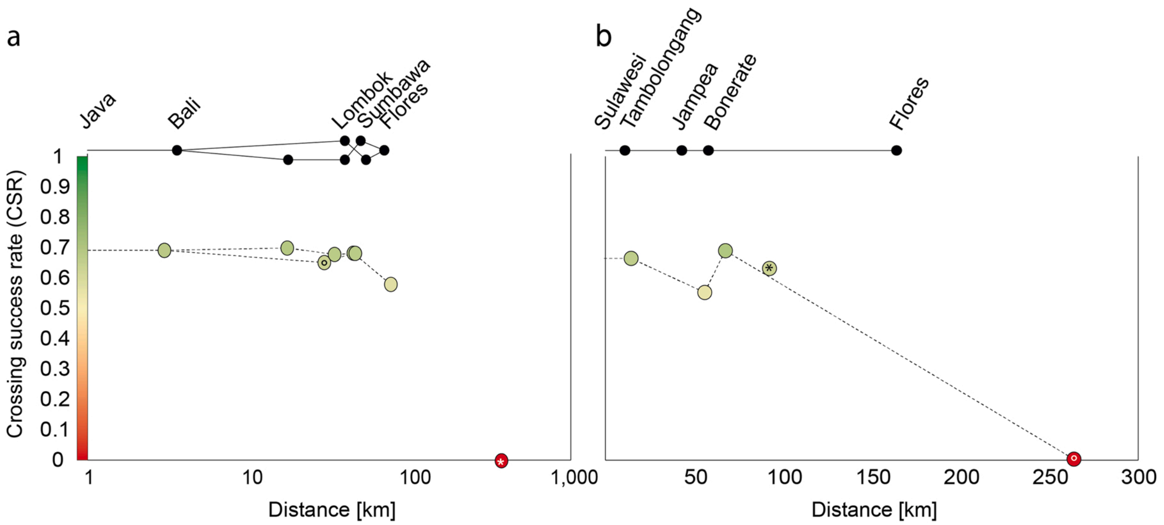

Fig. 7. Route analysis for (a) route B from Java to Flores for the −25 % stegodon and (b) route C from Sulawesi to Flores for the −50 % stegodon; circle – CSR in January, asterisk – CSR in August. Coloured plot displays effective distances (ED), while black line plots show absolute geographic distances. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

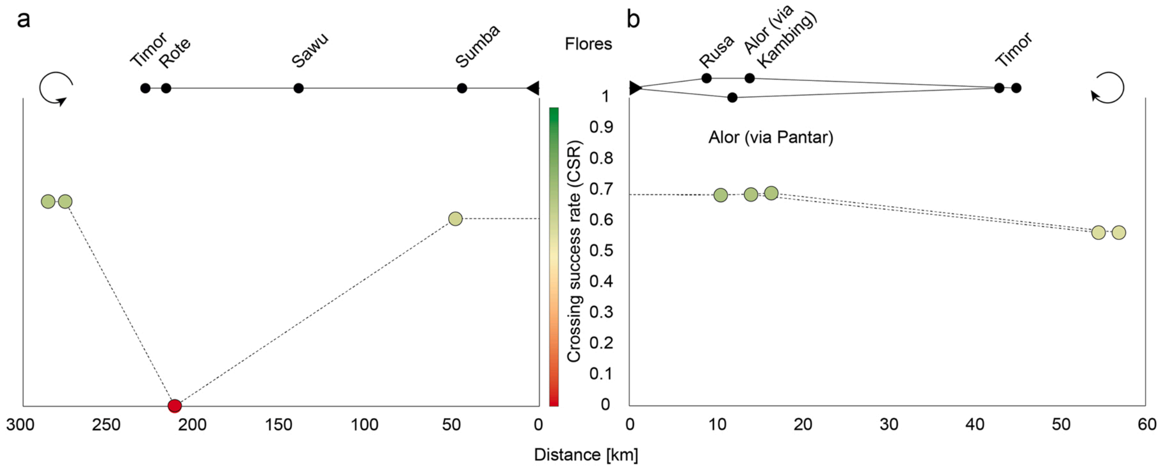

Fig. 8. Route analysis for routes D from Flores to Timor in (a) counterclockwise and (b) clockwise direction for the −75 % stegodon. Coloured plot displays effective distances (ED), while black line plots show absolute geographic distances. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Mindanao and Sulawesi. Routes B and C target Flores from either west or north, of which the sea passages along the northern route C are the longer ones. The four sea straits to be crossed add up to a geographic distance of 164 km, while the western route, passing through Lombok and Sumbawa, is required to cover total distances between 50 and 70 km depending on the option selected. The comparison of these alternatives reflects a long-standing discussion about preferential routes (Sondaar, 1989; van den Bergh, 1999). Route option D circles around the islands of East Nusa Tenggara representing a subsidiary archipelago either in a clockwise or counter clockwise direction. Routes E and F finally examine the potential range of stegodon dispersal along a southern or northern course across the islands of the Banda Arc. Unlike routes A to D, routes E and F lack a fossil record.

4.1. How to reach Sulawesi (route A)

Geographically, Sulawesi represents a veritable hub for the dispersal of mammals across Wallacea. However, the relatively high degree of endemism, in both in fossil and recent faunas alike provides evidence that it did not function as permanent crossroad between Sundaland and the southern and eastern part of Wallacea (Groves et al., 2001; Skeels et al., 2023; van den Bergh et al., 2001; Whitten et al., 2012). The fossil record of *Stegodon* from Sulawesi (mainly from the southwestern arm of the island) indicates several immigration events. The oldest Early Pleistocene fauna, the Walanae fauna, already features a dwarf stegodon, *Stegodon sompoensis*, with a body mass reduction of 68 %, which was replaced by a larger stegodon species (*Stegodon* sp. B) with a body mass reduction of 43 %, which arrived from the Sunda Shelf during the early Middle Pleistocene. This provides evidence that at least two mainland species successfully reached Sulawesi and established viable populations.

With our model, Sulawesi can be reached by swimming from Borneo along two separate routes, a wide detour leading from Borneo along a chain of islands to Mindanao and then south, towards the Minahasa Peninsula, and a direct one across the Makassar Strait. The coastlines of Borneo and Sulawesi are running in parallel for c. 500 km. The smallest distance to be crossed requires swimming across a distance of 100 km, in January reduced to an effective distance of 80 km by supportive currents for the stegodon with a body mass reduction of 25 %, the smallest size category arriving in Borneo from mainland Southeast Asia, Sumatra, or

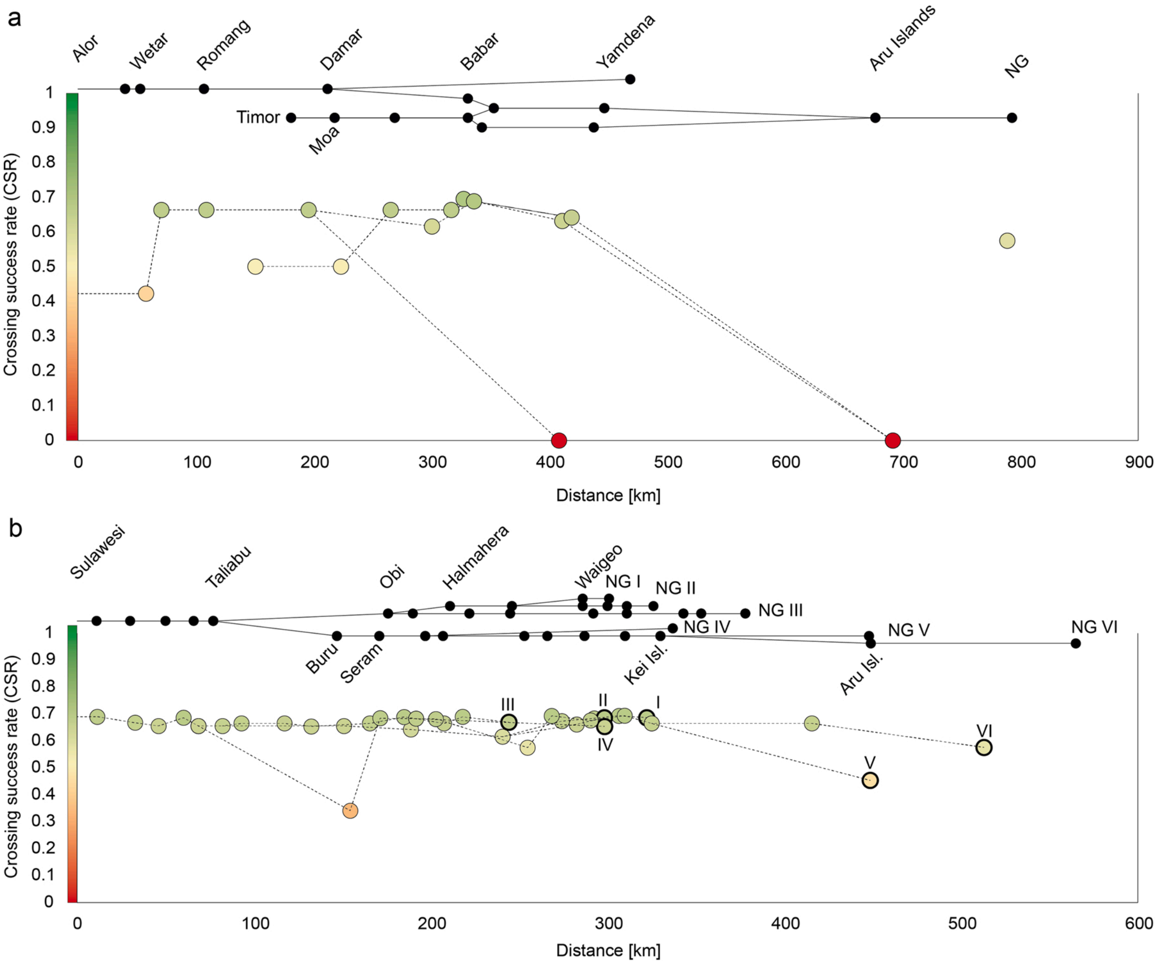

Fig. 9. Route analysis for (a) route E from Timor to New Guinea (NG) along the southern part of the Banda Arc and (b) route F from Sulawesi to PNG along the northern part of the Banda Arc for the −75 % stegodon; I-VI alternative routes to NG. Coloured plot displays effective distances (ED), while black line plots show absolute geographic distances. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Java (see Section 4.5). The direct route across the Makassar Strait is managed by stegodons of all size categories with CSRs ranging from 0.570 to 0.586. The agents do not perform significantly different. Although this route does not seem to be particularly challenging for stegodons, it implies crossing of the Wallace line, and is therefore selectively open for larger mammals.

The detour leading through Mindanao is definitively the more challenging one, but fossil stegodon attributed to *S. mindanensis* presumably from Agusan del Norte, a locality in Mindanao for which no precise location is given (de Vos and Bautista, 2003), and from the Pintareng Formation in Sangihe (*Stegodon* sp. B) illustrate that this route may have been taken. Both segments of the northern detour possess their own challenges. In both legs effective distances are larger than the cumulated geographic widths of the sea straits (Fig. 6). In the first leg linking Borneo with Mindanao, at least six sea straits with a geographic distance of 134 km, the entry is particularly challenging. This segment leads through Tawitawi, Jolo, and Basilan, as well as a set of stepping stone islands. While the crossings beyond Tawitawi are managed by all stegodon agents with CSRs between 0.667 and 0.698, the first steps from Borneo to Tawitawi are difficult. We examined two alternative routes, a direct one and an indirect one leading through Sibutu. With 55 km the direct one (#81) is not particularly wide, but effective distances rise to 78.4 km due to currents coming with an angle of 90°. Current speeds of 0.2 m/s approach swimming speed, so that many agents are washed off the map. Consequently, the CSR of the −25 % agent entering route A drops to 0.263. The agents attempting to reach Tawitawi through Sibutu face the same challenges. The absolute width of 65 km increases to an effective distance of 92.6 km by currents causing sideward deflections and washing the majority of agents off the map. With an intermediate stepping stone island, CSRs of both sea straits reach values of 0.487–0.511. Our knowledge of the fossil record in Mindanao is limited, and restricted to a single specimen thus far. The fossil, described from Agusan del Norte, belongs to a medium-sized representative of the genus (Beyer, 1947; de Vos and Bautista, 2003) of unknown geological age. Although the specimen was originally related to *Stegodon* species from Java (Naumann, 1887, 1890), additional fossil remains are moreover known from Luzon and the Visayas in the central part of the Philippines as well as Taiwan. These alternative origins are not tested in this study, but these routes also require to cross sea straits by swimming.

The second segment approaching Sulawesi from the North features the fossil locality Pintareng in Sangihe. This route is branching into a western and an eastern arm beyond the island of Maru (Fig. 6). Both branches rejoin in Kawaluso before passing to Sangihe. The passage to Maru is the most difficult one with a CSR of 0.4618 for a stegodon with a body-mass reduction of 50 %. The western branch requires the crossing of sea strait #92 from Kamboling to Kawaluso with an absolute width of 47 km; the eastern branch requires several shorter crossings until a passage from Matutuang to Kawaluso is reached. In January, stegodons encounter strong currents with a speed of 0.75 m/s, exceeding optimum swimming speed by around 0.25 m/s. The passive shift they experience in each swimming phase is therefore larger than the thrust they create towards the opposite shoreline. Furthermore, the currents come with an angle of 225°, opposite to their swimming direction thereby reducing swimming speed and multiplying effective width. Although the sea strait is only 45 km wide, effective distances rise to 1954 km (Fig. 6). Stegodons do not accomplish successful crossings here, because they cannot manage the currents. In August, however, no effective currents occur, the effective distance for all agents equals geographic distance and CSRs range from 0.678 to 0.687 (Figs. S3–1). Moreover, sea strait #92 also leads to Kawaluso, but approaches it from a northern rather than an eastern direction. The currents in this sea strait in January are less strong and come from an angle of 45°, i.e. they support swimming in a southern direction. Effective distances reduce absolute width from 47 km to 36 km. The CSR in January amounts to 0.634, it is hardly less favorable than the route from Matutuang in August. The passage from Mindanao to Sangihe is therefore open in every season, just not along all of the alternative routes. The route south of Sangihe towards the Minahasa Peninsula is generally open in January (Fig. 6). CSRs vary between 0.520 and 0.686.

The fossil stegodons that have been found in Sangihe and southern Sulawesi have the same size and are hence attributed to the same species (*Stegodon* sp. B), which implies a link between the two populations. The direction of the contact is however unknown: did the Sangihe stegodon originate from southern Sulawesi via the Minahasa Peninsula, an option which we did not test experimentally in our dataset, or the other way around, was Sulawesi colonised by stegodons from Sangihe? The accessibility of the route between Sangihe and Mindanao for all body size classes suggest a link between the medium-sized stegodons in the Philippines (Mindanao) and those in Sulawesi (Sangihe, southern Sulawesi). We used our dataset to predict CSR_{pred} from ED by regression, the latter being calculated directly from sea straits with inverted current direction. CSR_{pred} between Sulawesi and Sangihe varies between 0.612 and 0.641, indicating that Sangihe can be reached by a medium-sized stegodon from the South. The leg between Sangihe and Mindanao, however, seems to be blocked between Maru and the Sarangani Islands. Effective distances rise to 2996 km and CSRs drop to 0. Note, that the challenging sea strait between Kawaluso and Matutuang may be crossed with a CSR_{pred} of 0.595 in the opposite direction. It may be that these routes were taken in both directions seasonally for a longer period of geological time. This may then *inter alia* also have applied to hominins, whose Middle to Late Pleistocene lithic artefacts have been recovered from Luzon (Ingicco et al., 2018) as well as Sulawesi (van den Bergh et al., 2016). This segment of the route forms part of the hypothesis that overseas dispersal of hominins throughout Wallacea could have been primarily followed the major surface current flow patterns from Taiwan, Luzon, Sulawesi and ultimately Flores (Ingicco et al., 2018).

4.2. *Reaching Flores by swimming (routes B and C)*

The fossil record of *Stegodon* in Flores illustrates that stegodon populations reached the island at least twice. At the locality Tangi Talo, a dwarf *Stegodon* of −85 % body mass reduction, *S. sondaari*, occurs, dated to the Early Pleistocene (1.42–1.27 Ma; van den Bergh et al., 2022). A new immigration wave replaces this fauna approx. at 1 Ma (van den Bergh et al., 2022), and includes a larger stegodon species, with a body mass reduction of 49 % (*Stegodon florensis florensis*). In due time, this latter medium-sized stegodon progressively evolves further body mass reduction to −83 % at Liang Bua, where it is attributed to a separate subspecies (*S. florensis insularis*).

Two potential routes lead from Sundaland to Flores, a direct one approaching from Java in the West and a northern one from Sulawesi (Fig. 7). The western route leads from Java and Bali through Lombok, Sumbawa, and Komodo into Flores (Fig. 7a). In January, most of the sea straits are traversable for a stegodon with a body mass reduced by −25 % arriving from Java. CSRs range from 0.577 to 0.697, and the cumulated effective distance of 76 km is only 8.5 % larger than the total geographic width of the sea straits (70 km). The alternative route into Flores leads from the island of Selayar offshore Sulawesi through Tambolongang, Jampea, Kalao, and Bonerate to Flores (Fig. 7b). Particular the last and longest step from Bonerate to Flores (sea strait #104) cannot be managed by a stegodon with a body mass reduced by −50 %, albeit the effect is not size dependent and occurs in all stegodon agents. The distance to be covered is comparatively wide, 106 km. It rises to an effective distance of 197 km for a stegodon with half of the body mass of a mainland sized precursor arriving from Sulawesi, due to currents directed perpendicularly to the swimming direction. This maximizes deflection and therefore, effective distances almost double. The effective distances exceed maximum distances for all our size categories. The majority of agents is simply washed off the map (Figs. S3–2).

However, surface currents turn in August. The currents now are comparatively weak (0.1 m/s) and come from a supportive direction (315°) reducing effective distances to 93 km. Even stegodon agents with a body mass reduced by −50 % show a CSR of 0.629 (Fig. 7b). Now the majority leaves the map beyond the target shores. The opposite effect occurs along route B. In sea strait #7 linking Bali with Lombok, crossing success drops to 0 in August (Fig. 7a). The currents are quite strong in August and exceed the swimming speed of stegodon by factor 6. The actual width of 36 km increases to values beyond 367 km. Currents are so strong, that the majority of the agents are washed ashore in the source area and walks off the map. A smaller percentage is washed off the map while swimming. This effect is not size-dependent and occurs in all agents tested here (Figs. S3–2). In the set of experiments presented in this study, Flores can thus be reached along both of the routes, B and C, but successful crossings are a seasonal issue. While the western route B is open in January, the northern route C is traversable in August. According to our results, the debate of whether Flores was reached by stegodons from Java (Hooijer, 1957; based on geography) or from Sulawesi (van den Bergh, 1999; based on similar tooth morphology of *S. florensis* and *S.* spec. B) thus remains unsettled, but since two independent immigration events took place (*S. sondaari* and *S. florensis*), both routes may have been taken on different occasions and at different times. Medium-sized as well as dwarf stegodons could have reached Flores along both routes (either from Java or Sulawesi), albeit in different seasons.

4.3. *Around East Nusa Tenggara (routes D)*

The triangle spanned by the islands of Flores, Sumba, and Timor features a comparatively high number of fossil localities (Fig. 5). Together with the offshore islands of Lembata, Alor, and Wetar as well as smaller stepping stones, the islands form an archipelago, in which no major dispersal boundary existsThe fossil record of *Stegodon* in Flores spans the entire Pleistocene and is comparatively rich (van den Bergh, 1999), but isolated fossil finds of *Stegodon* are known from Sumba and Timor as well. The discoveries on Sumba date to the Early Pleistocene and probably also the Late Pleistocene (Turvey et al., 2017), while the discoveries from Timor date to the late Middle Pleistocene (Louys et al., 2016). The individuals from Sumba (*S. sumbaensis*) are extremely small, with a body mass of −92 %, but those from Timor (*S. timorensis*) also underwent a body mass reduction of −77 % (van der Geer et al., 2016). From Timor, a larger stegodon is known as well (*S. trigonocephalus* subspecies D) with the size of *S. florensis* (van den Bergh et al., 1992), either representing an intermediate stage during the dwarfing process on the island or an independent dispersal of a second species.

No dispersal barriers occur across the archipelago if the −75 % stegodon disperses in a clockwise direction (Fig. 8b). Absolute total distances sum up to 43 and 45 km, depending on whether the shorter route through Pantar or the longer option through Rusa and Kambing is taken. Effective distances rise to 56 and 58 km, respectively. This increase by 30 % is mainly caused by the passage to Timor, where CSRs drop to 0.551, the lowest value when dispersing in a clockwise direction. Interestingly, a bottleneck occurs when moving in a counterclockwise direction (Fig. 8a). Sea strait #22 is located between the islands of

Sumba and Sawu *en route* to Timor. In January, moderate currents with a speed of 0.2 m/s counter the movements directly opposing swimming direction (180°). The currents reduce swimming speed, and consequently have an impact on effective distance. The geographic width of 95 km is raised to an effective distance of 170 km exceeding maximum range of the −75 % stegodon. The majority of the crossing attempts is unsuccessful because the agents die of exhaustion (Figs. S3–3). However, stegodons differ significantly in their respective CSRs. Individuals with body masses reduced by −50 % or more, like *S. sondaari* from Flores or *S. sumbaensis* from Sumba, would not manage to swim across the sea strait. In contrast, taxa with no or only minor reductions in body mass, would manage crossings with CSRs of 0.606 and 0.605, due to their sufficient energy deposits and higher swimming speeds related to their higher body masses (Figs. S3–3). A stegodon with a body mass reduction of 25 % would, however, already experience severe difficulties (CSR=0.125). The minute dwarf stegodon known from the fossil record of Sumba would certainly not be able to swim across this sea strait in January. In this context, the fossil record from Timor is particularly interesting. According to our results, the ancestor of the dwarf stegodon on Timor should have entered the island via Lembata and Alor, if it had already evolved a body mass reduction of 25 % or more. If the reduction were lower, e.g. −10 %, it may have entered Timor via Sumba. This latter option is only feasible if the mainland ancestor dispersed all the way to Timor through intermediate islands in a relatively short time without noticeable reduction in body size, and size reductions as we observe them in the fossil record occurred only after. If the medium-sized Timor stegodon derived from the medium-sized Java stegodon (*S. trigonocephalus*) through Flores (*S. florensis florensis*), as first suggested by Hooijer (1972), then the route via Alor is the only option. The Sumba dwarf with a size reduction of −92 % then apparently stranded there, without descendants on other islands.

4.4. Towards Meganesia along the islands of Maluku and the Banda Arc (routes E and F)

We examined two routes east of Sulawesi and Timor along the islands of Maluku and the Banda Arc into Meganesia (Fig. 5). East of Flores, Buru, and Halmahera, these routes are taken by the −75 % stegodon in our model. Most of the sea straits along route E in the South and route F across northern Maluku are managed with CSRs > 0.6 (Fig. 9). There is, however, no fossil record for *Stegodon* in the islands of Maluku or in Meganesia. Evidence that routes E or F have been used as stepping stones in the dispersal process is absent.

Nevertheless, our results indicate an absolute dispersal barrier in route E along the southern islands of Maluku linking Timor with New Guinea (Fig. 9a). The islands east of Timor are generally reached by all −75 % stegodons, at least along alternative routes. The last step from Yamdena and Fordate to the Aru Islands with an absolute width of 230 km, however, is simply too wide. None of the agents manages when approaching along route D. This step constitutes an absolute dispersal barrier for stegodons irrespective of their body size (Figs. S3–4). Consequently, the Aru Islands and Meganesia cannot be reached through route E along the southern part of Maluku.

Our experiments show that the routes along the northern part of Maluku may be managed by all stegodons. We identified six alternative routes along the northern part of Maluku, which differ in total length, number of intermediate stepping stones, and location of arrival (Fig. 9b). Route I, passing through Obi, is the shortest one with absolute distances of 301 km. Interestingly, this route is hardly influenced by currents: effective distances equal absolute geographic distances. Route III, circumventing Halmahera and Waigeo, covers an absolute distance of 378 km which is reduced to an effective distance of 242 km. The routes through Buru and Seram are longer and arrive further south. Route VI approaches the Aru Islands from the North, which can be reached safely along this track.

Our findings raise the question of which factors prevented stegodons from expanding their range towards the eastern part of Wallacea and into Meganesia. The only fossil records known are Holocene in age (Flannery, 1995; Flannery et al., 1995; Gaffney et al., 2023) and are limited to small mammals and/or marsupials. Reasons may be sought in either the paleobiology of dwarf stegodons, or in coastal topography preventing successful landings. Mangroves and coral reefs may impose obstacles when entering an island, even though the sea strait itself may be generally passable. Mangroves dominate along route F across the islands of Maluku (Osland et al., 2017; Sarr et al., 2019). Low population densities and/or insufficient resource supply on some of the islands may also offer explanations. Most of the islands of Maluku cover areas of less than 10,000 square kilometres. Except for Halmahera and Seram, both covering > 15,000 square kilometres. Smaller islands may have offered resting sites, but long-term or even permanent establishment of a stegodon population may have been a challenge. The high degree of endemism in the region underlines that successful immigrations of mammals and/or marsupials are actually rare events here, promoting the evolution of endemic taxa (Natus, 2005).

The reasons for the absence of *Stegodon* along the islands of Maluku and the Outer Banda Arc deserve to be studied further. Our experiments show that crossing sea straits by swimming would have been a possible way for dispersal. Therefore, if stegodons did not occupy the islands of Maluku, swimming performances alone do not offer an explanation. Taphonomy and ecology may thus offer alternative explanations, apart from hampered landing due to coastal features (see above): small islands often lack suitable sedimentary basins for fossil preservation, and the dietary ecology of potential colonizing species from Indonesia indicates mostly grazing diet (Puspaningrum, 2016), which is not suited to colonise and survive in the mangroves and rainforests of the Meganesian islands.

4.5. Routes across Sundaland

Although we focus on dispersal in Wallacea in this study, the islands in Southeast Asia represent important entry points for terrestrial mammals from Asia. We therefore directed our attention additionally to dispersal across insular Southeast Asia. During interglacials the Sunda Shelf is submerged, but large landmasses, represented by the islands of Borneo, Sumatra, and Java, are exposed in glacial periods. Two of these islands, Java and Borneo, serve as potential entry points into Wallacea. Java, located on the southern arc, also provides us with the most extensive fossil record in the region (see Section 4.5.1), while we only possess anecdotal and undated evidence for the presence of stegodons in Borneo (Earl of Cranbrook et al., 2000). However, Borneo (see Section 4.5.2) provides a northern hub for routes towards the Philippines and into Sulawesi.

In our dataset 41 out of 142 sea straits examined are located in Sundaland. Six of them are entirely impassable in January, another two are only passable with success rates of < 1 % (Fig. 5). While the southern arc of islands leading from mainland Malaysia through Sumatra into Java and Bali is passable in January, the routes leading into Borneo are blocked. Adverse currents prevent stegodons from entering Borneo. The currents however change on a seasonal scale (Lellouche et al., 2021), leaving episodes in which crossings are possible. Under glacial conditions terrestrial land bridges are exposed by lowering sea levels (Voris, 2000) and, following reconstructions combining geomorphology and the distribution of coral reefs (Sarr et al., 2019), Sundaland was permanently exposed prior to 400 ka. This allows for dispersal independent from swimming performance (Salles et al., 2021). The critical intermittent bottlenecks developing after 400 ka may account for the unique character of the Pleistocene fauna in Borneo compared to Sumatra and Java (Louys et al., 2007; Lohman, et al., 2011; de Bruyn et al., 2014).

4.5.1. The route along the southwestern part of the Sunda Arc

Following our route analysis (Figs. S3–5) there is no major barrier for mainland size stegodons along the Sunda Arc in January. Even without terrestrial connection, this route may have been managed by swimming stegodons and they can freely disperse along this corridor. With an interglacial land-sea distribution, the water barriers along this route sum up to 61or 66 km depending on stepping stone islands between Sumatra and Java. Effective distances are however reduced to 51 or 57 km resp., by supportive currents in particular in the Strait of Malacca. The last step from Java to Bali is taken by the −25 % stegodon corresponding to the average body masses of *S. trigonocephalus* in Java (van der Geer et al., 2021), but it does not lead to a significantly reduced swimming performance.

The fossil record of stegodon in the area stems exclusively from the island of Java, where it is known to occur from the late Early Pleistocene in Sangiran and Trinil until the end of the Middle Pleistocene in Ngandong (van den Bergh, 1999; Puspaningrum et al., 2020; van der Geer et al., 2021). Most of the specimens are attributed to the endemic species *S. trigonocephalus*, which is smaller than associated mainland forms. The only discovery of stegodon from Malayan Peninsula representing a potential mainland precursor was reported from a cave in Gopeng, Perak (Muhammad et al., 2020). The find is undated, however, this corridor has most likely been taken by stegodons from the South and Southeast Asian mainland, i.e., *S. elephantoides* in the Early Pleistocene and *S. ganesha* in the Middle Pleistocene (van den Bergh, 1999). The high connectivity among the islands of the Sunda Arc during the Middle Pleistocene may also account for the fact that stegodons in Java, from which the fossil record exclusively originates, only experienced moderate size reductions of up to −35 %.

Nevertheless, size reductions were extensive, ranging from −75 % to −85 % in the Early Pleistocene, when Java likely consisted of separate islands and isolation was thus higher than tested here. This may be confirmed by the presence during the early Early Pleistocene in east Java of a −85 % pygmy stegodon from a region that probably constituted a separate island between central Java and what is now Bali (van den Bergh, 1999). On these grounds, Puspaningrum et al. (2020) proposed at least two independent immigration events for stegodon, a larger form leading to *S. trigonocephalus* and a true pygmy form possessing a patchy fossil record. Sumatra and Bali do not possess a fossil record of *Stegodon* (Louys et al., 2007, 2024).

4.5.2. *Routes into Borneo*

We examine three routes leading from the Sunda Arc to Borneo, linking Borneo with peninsular Malaysia, Sumatra, and Java, respectively (Figs. S3–6). According to the dwarfing model applied here, the routes starting in peninsular Malaysia and Sumatra are taken by a mainland sized stegodon, while the route starting in Java is taken by the stegodon with a body mass reduced by −25 %. Each of the three routes include severe bottlenecks in January. In the routes starting from peninsular Malaysia and Java, these bottlenecks prevent stegodons from crossing successfully altogether. They are therefore omitted from the discussion here (but see suppl. 3). The route starting in Sumatra permits crossings, but the agents need to pass a sea strait with a very low success rate.

The route from Sumatra into Borneo passes Bangka and Belitung. Although the absolute distance from Belitung to either the next stepping stone, Karimata, or directly into Borneo, can be generally covered by mainland size stegodons, adverse currents in January with comparatively high current speeds impede crossings by swimming (Figs. S3–6b). The CSRs for the direct route are very low (CSR=0.118). The alternative route through Karimata represents a barrier for mainland size stegodons, because the currents are directed against the swimming direction. This increases effective distance dramatically to > 1000 km.

In sum, stegodons are unlikely to reach Borneo by swimming in January, and this is mainly a result of adverse currents. The fact, that Borneo is only accessible by swimming restricted to episodes of low and/or inverse currents, may contribute to explain the rarity of stegodon finds in Borneo.

4.6. *Limitations of the SEAcross setup*

As a model the SEAcross ABM (Hertler et al., 2022) makes a number of simplifying assumptions on both the features of the sea straits as well as the behaviour of the agents, which may lead to an overestimation of CSRs. First of all, coastal geometries have an impact on crossing success. The model represents a sea strait with constant width over a distance of 100 km and start and target areas with uniform size and shape. This does not correspond to the topography of the sea straits tested with our model. The impact of this can be tested by replacing the standardized maps in the model by topographic maps and running the set of experiments a second time. The same applies to the currents, which we averaged and assumed to be homogenous across the sea straits. Also, the simple version of the SEAcross ABM (v. 1.0) does not take water temperature into account. Low water temperatures may, naturally, lead to hypothermia when the gradient between body temperature and temperature of the surrounding medium becomes too steep. This is especially the case when the body is submerged and surrounded by water. The danger of hypothermia severely reduces the time which an individual can spend in water, even in tropical waters where water temperature never drops below 18°C. In order to account for this gradient, the model contains a counter, which is disabled in version 1.0 (Hertler et al., 2022). To account for the gradient, surface temperature of the water in the respective sea strait needs to be included in the sea strait features.

The swimming model we applied to calculate swimming performances of the five different agents represents an estimation at best. Meijaard (2001) tried to validate the results of his model by comparing estimated distances with observations, but in some cases, there were large deviations between observed and estimated values which remained unexplained. The model assumes, that the agents are all capable of viewing (or scenting) across the sea strait to spot resources on the opposite shore, although either width and/or weather conditions may prevent this. It is possible to restrict sensing distance in the model version 1.0, but we did not make use of this function for this set of experiments.

These limitations and assumptions lead to an overestimation of swimming performance of stegodons. The experiments affecting critical passages should be repeated with respective settings, when absolute CSR values are requested. Nevertheless, the results allow to compare sea straits among each other and the experiments we introduced here demonstrate the usefulness of the contributions by the SEAcross ABM.

5. Conclusions

In this paper we examine dispersal options of *Stegodon* across Sundaland and Wallacea by swimming by means of a series of simulations and we examined potential routes for stegodons with different body masses. Our results show that ardent swimmers in the size of stegodons generally manage dispersal by swimming across insular Southeast Asia and Wallacea, although we discovered some remarkable bottlenecks, for instance in Sundaland from the Malayan Peninsula and/or Sumatra into Borneo in January, or *en route* to Flores between Bali and Lombok in August and Bonerate and Flores in January. The counter-clockwise movement around the archipelago in the eastern part of Nusa Tenggara can only be accomplished by stegodons with no or minimal body mass reduction. Our results contribute to the interpretation of the fossil record by suggesting particular routes and dispersal events.

The SEAcross ABM can be used to test dispersal performances of diverse taxa, including primates, deer, and/or marsupials, and to explore routes from Meganesia into Wallacea as well.

CRediT authorship contribution statement

Hertler Christine: Writing – review & editing, Writing – original draft, Visualization, Formal analysis, Conceptualization. **van der Geer**

Alexandra: Writing – review & editing, Writing – original draft, Conceptualization. **Puspaningrum Mika Rizki:** Writing – review & editing, Writing – original draft, Conceptualization. **Reschke Jan-Olaf:** Validation, Software, Data curation. **Anwar Iwan Pramesti:** Resources, Data curation. **van der Geer Alexandra:Hölzchen Ericson:** Software, Methodology.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.hisbio.2025.100026.

Data availability

The model with the standardized sea strait including documentation is available for download from Zenodo with open access (http://doi.org/10.5281/zenodo.6833780; Hertler et al., 2022). Data sets discussed in this paper are included in the supplements (suppl. 2). This study has been conducted using E.U. Copernicus Marine Service Information; http://doi.org/10.48670/moi-00021.

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