Biogeographical land bridges of Bali-Nusa Penida-Lombok: A possible dispersal pathway for terrestrial fauna during the Pleistocene Glacial periods

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Abstract. Fossil records in the Lesser Sunda region provide evidence of colonization by prehistoric humans and terrestrial fauna, dating back to the Pleistocene glacial periods. We believe that Nusa Penida was once part of a dispersal pathway connecting a biogeographical land bridge between Bali and Lombok. Therefore, in this study, we aim to identify the presence of this land bridge using a bathymetric map and reconstruct it at different global sea levels corresponding to glacial conditions. The study also examined the Bouguer Gravity Anomaly to estimate its lithological characteristics. The results indicate that land bridges possibly existed on both the western and eastern sides of Nusa Penida during the Pleistocene glacial periods, at least since 800,000 years ago. These land bridges directly connected the southern part of Bali to the southern part of Lombok. As sea levels rose during interglacial periods, they gradually submerged. Particularly on the eastern side, the remnants of the land bridge are located approximately 225 meters below the modern sea level. This land bridge seemingly experienced intense abrasion due to the pre-modern Indonesian Throughflow (ITF); local tectonic events might also be responsible. This study provides insights into land-based biogeographical dispersal pathways across the Wallace Line.

1 Introduction

The Lesser Sunda Islands are an archipelagic region in the southeastern part of the Sunda Shelf. This geographical area extends from west to east and includes the islands of Bali, Lombok, Sumbawa, Flores, Sumba, Savu, Timor, Alor, and Tanimbar. Biogeographically, this region is part of the Wallace region, which serves as a transitional biogeographic zone between the Asian and Australian biogeographic regions [1]. The boundary between these zones is marked by Wallace’s Line, which runs through the Lombok Strait and separates the
islands of Bali and Lombok [1,2]. Paleontological studies have also revealed distinctive patterns between these zones based on terrestrial mammal fossil records found on almost every island in the Lesser Sunda. Some of these fossils have been identified as mammalian groups from the Asian region, such as Stegodon and Elephantidae [3]. Radiometric dating results indicate that these fossils belong to the Pleistocene fauna. Additionally, several archaeological records suggest the presence of a prehistoric human colonization period in the Lesser Sunda. However, further studies are needed to understand how these groups spread to the region.

The question arises: How could fauna such as Stegodon and Elephantidae be found in the Nusa Tenggara Islands, considering that this region primarily consists of islands separated by deep straits? Can these animals (sea)-cross to the islands with their entire herds, or is there a hidden land bridge connecting these islands when sea levels drop? If so, what was the paleogeography of the Nusa Tenggara Islands during global sea-level drops, particularly during the Pleistocene? In this study, we focused on tracing the land bridge between the Bali and Lombok Islands, which is most likely to cross the Lombok Strait. Based on bathymetric studies, it is highly probable that a land bridge exists in the southern part of the Lombok Strait, as this area tends to be shallower than the northern part (Figure 1).

![Fig. 1. Topography and bathymetry in the Western Lesser Sunda Island. The red box represents the area of interest (study area), which is located in the southern part of the Lombok Strait](image)

In this study, we conducted paleo-shoreline reconstruction based on modern bathymetric data, with sea-level changes referencing glacial conditions during the Pleistocene epoch. This reconstruction can be considered under the assumption that there have been no significant changes to the seafloor. Abrasion and past tectonic events may have caused deviations in these circumstances. At the very least, through this research, we can come closer to estimating the presence of landmasses and land bridges connecting Bali and Lombok Islands, which have been previously unexplored.
2 Methods

A systematic approach was employed to investigate the geological and bathymetric features of the Lesser Sunda Islands during the Pleistocene, particularly between Bali, Nusa Penida, and Lombok Island (the southern part of the Lombok Strait). Pleistocene global sea level change data were collected from Spratt and Lisiecki, in 2016 [4]. These data provided essential information about fluctuating sea levels during the specified timeframe from 800,000 years ago (Figure 2). The bathymetry data, referred to as high-resolution bathymetry data, were sourced from BATNAS by Badan Informasi Geospatial (BIG), Indonesia’s Geospatial Information Agency (https://tanahair.indonesia.go.id/demnas/#/batnas). This dataset serves as the foundation for comprehending the bathymetry of the study area.

![Fig. 2. Estimated Late Pleistocene sea level stack [4], dotted line represent scaled principal component](image)

The bathymetry reconstruction was conducted by interpreting the data from the bathymetry raster around the Nusa Penida region, supported by Pleistocene sea level stack data. This approach involves sequential adjustments that represent bathymetry corresponding to visualized sea levels. We reconstructed shorelines at various depths: -50 m, -75 m, -100 m, -125 m, -130 m, -150 m, and -225 m below the current sea level. Lithological estimation is based on regional geological maps of Bali and Lombok [5, 6], provided by the Indonesian Geological Agency (Figure 3). Additionally, we utilized Bouguer gravity anomaly data from the International Center for Global Earth Models (ICGEM). The Bouguer gravity anomaly map from ICGEM provides information on gravitational force distribution, considering variations in seawater density [7], thus allowing the representation of contours in offshore areas. Furthermore, we considered the complete Bouguer gravity map of Bali (Figure 4) published by the Geological Survey of Indonesia in 1972 as a local Bouguer gravity map (geologi.esdm.go.id/geomap). By overlaying bathymetry, geological, and Bouguer gravity maps, we enhance the interpretation of potential land bridge distributions and their lithological characteristics.

Geological Setting: Nusa Penida is an isolated karst island located in the southern part of the Badung Strait. This island primarily consists of reef limestone, marl, partly bedded, recrystallized, and fossiliferous rocks. The entire Nusa Penida Island is part of the Selatan Formation (Fm). This formation was formed during the late Miocene to early Pliocene. It extends east to west, from Nusa Penida Island to Nusa Dua, which is located in the southern part of Bali Island. On the island of Lombok, there is the Kawangan Formation, an Oligo-Miocene sedimentary rock consisting of alternating quartz sandstone, breccia, and claystone. This formation is located in the southern part of Lombok Island. Additionally, there is the Ekas Formation in Lombok, and Miocene limestone correlated with the Selatan Formation. Most of Bali Island consists of Quaternary volcanoclastic deposits from various volcanoes, such as the Buyan-Bratan, Jembaran, and Batur volcanoes. These volcanoclastics tend to
deposit southward. Furthermore, there are Oligo-Miocene volcanoclastic deposits that are part of the Ulakan Formation, consisting of volcanic breccias, lava, tuff, and calcareous sediment intercalations. This formation is one of the oldest formations in the Bali Region. In the Lombok Strait, there is a dextral strike-slip fault, known as the Lombok Strait strike-slip fault. It is located between the Bali and Lombok islands, oriented from north to south. This fault extends northward and cuts through the Flores back-arc thrust in the north of Bali and Lombok Island. This thrust has been known to result in earthquakes with significant magnitudes, reaching up to 7.0 in July-August 2018.

Fig. 3. Geological map around the Nusa Penida region

3 Results and Discussion

The results show that several landmasses emerged when the sea level dropped to -125 meters in the southern part of the Lombok Strait. This area expanded significantly, directly connecting Bali and Lombok via Nusa Penida. Moreover, at a sea level drop of -225 meters (as shown in Figure 5), Nusa Penida, Lembongan, and Ceningan were connected, forming an even larger island. The bedrock in this region primarily consists of limestone from the Selatan Formation. Also, the northern part of the island features thick fluvial deposits that mix with shallow marine sediments, potentially creating a broader mangrove landscape.
While the sea level dropped to -100 meters, a small island emerged in the eastern part of Bali toward Nusa Penida. This island became more pronounced when the sea level dropped to -125 meters, resulting in expansive terrestrial areas and additional islands. Similar conditions occurred in the western region of Nusa Penida on Lombok Island, where at least two small islands are emerging. Subsequently, as the sea level continued to drop to -150 meters, the channel distance between Bali and Nusa Penida began to decrease. Thus, the distance between the islands is less than 1 km.
Fig. 5. Reconstruction of paleo-bathymetry (by this study) under various sea level conditions. The red arrow indicates the emerging landmass, including islands and land bridges.
Interestingly, a fully-connected land bridge emerged when the sea level dropped to -225 meters. These land bridges connect the southern part of Bali, Nusa Penida, and the western part of Lombok. Supposedly, the land bridge between Bali and Nusa Penida consists of fluvial deposits and parts of the Mio-Pliocene limestone formation. Meanwhile, the land bridge between Nusa Penida and Lombok comprises Oligo-Miocene sedimentary rock, which is part of the Kawangan Formation. This interpretation is based on geological map information and the overlay of referenced Bouguer gravity anomaly maps (Figure 6).

This study has revealed that several land masses emerge when the sea level drops to -125 meters, including the area between Nusa Dua and Nusa Penida, as well as in the southern part of the Lombok Strait. These land masses become more extensive and directly connect Bali and Lombok via Nusa Penida when the sea level drops to -225 meters. However, a land bridge is unlikely to emerge in the northern part of the Lombok Strait or on the eastern side of Karangasem, Bali. The bathymetry east of Karangasem is more than -1000 meters, which means this seafloor would not be exposed during glacial periods and would not form a sufficiently large landmass to serve as a bridge between Bali and Lombok. Therefore, the land bridge that possibly connects Bali and Lombok may be located on the eastern side of Nusa Penida, and the land bridge connecting Bali and Nusa Penida is located in the western part of Nusa Penida (Figure 7).

Apart from older rock formations, the landmass of the land bridge in the Lesser Sunda could have originated from the resedimentation of volcaniclastic material from nearby paleovolcanoes on the northern side. Some quaternary volcanoes include Batur, Rinjani,
Kelimutu, Sangeang, Lewotolo-Lewotobi, and even the Tambora volcano complex. These volcanoes are known to have intense volcanic activity [8–12], which continues to the present day. Most of the volcanoes in Lesser Sunda have large calderas, indicating their ability to release significant energy and volcanic mass. It has been confirmed by records of the Tambora eruption in 1815 (VEI-7), which produced massive pyroclastic material and had the potential to cause lowered global temperatures [13]. However, it appears that this volcanic mass is still insufficient to form a landmass in the far distance to the south. These volcanoes mainly occur in the northern part of the Lesser Sunda Islands. Perhaps some other parts of the island have merged due to this, such as between Lombok and Sumbawa. The bathymetry conditions between these two islands are relatively shallower due to the presence of two large nearby-volcanoes. However, in the Nusa Penida region, this volcanic mass cannot compensate for the rising sea level and the ongoing subsidence rate until the present day.

![Image of land bridges and volcanic pathways](image_url)

**Fig. 7.** Land bridges and possible dispersal pathway across Bali to Lombok via Nusa Penida, during sea-level drop at -225 m (below recent sea level)

At least two land bridges have been identified: the Bali-Nusa Penida Land Bridge and the Nusa Penida-Lombok Land Bridge. These land bridges become significantly visible when the sea level drops to -225 meters. It appears that significant abrasion has occurred on both land bridges, primarily due to the presence of the Indonesian Throughflow (ITF) shortly after the glacial period ended. During the late Pleistocene, there were at least eight glacial conditions that led to a maximum sea level drop of over 100 meters. After the glacial period, the sea level rose more rapidly before entering an interglacial phase, followed by a gradual decline as the subsequent glacial period returned. These conditions undoubtedly resulted in remarkable abrasion on older exposed sedimentary rock formations, such as the Miocene Selatan Formation and the Oligo-Miocene Kawangan Formation. Both of these formations directly faced the Indian Ocean during that period. The ocean currents from the Indian Ocean are known to intensively erode the coastline in the southern part of Sundaland, including the regions of Java, Bali, and Lombok. Additionally, the presence of active tectonic faults, such as strike-slip faults in the Lombok Strait and vertical faults in the Selatan Formation (as
identified in Djimbaran), could gradually lead to subsidence of the seafloor. Consequently, the remnants of the land bridge would submerge deeper than their original paleotopography.

Previous paleontological and archaeological records have indicated eastward distribution patterns throughout the Lesser Sunda Islands, extending to the Alor region [14]. Land bridges between Bali, Nusa Penida, and Lombok suggest a higher possibility for Pleistocene fauna and prehistoric humans to colonize Nusa Penida before dispersing eastward to the Lesser Sunda Islands [15–17]. They were less able to do sea crossings, which are more challenging to achieve, especially given the high-energy sea currents between Bali and Lombok (ITF). The Indonesian Throughflow (ITF) is an oceanic current significantly influenced by global climate. It transports warm water across low latitudes from the Pacific to the Indian Ocean [18]. In recent modern conditions, aside from passing through the Lombok Strait, this current also flows through the Savu Strait and the Timor Passage. The ITF also had significant turbulent kinetic energy [19], which can intensively erode shallow sea floors and near-coastline areas.

Currently, Nusa Penida is one of the karst environments in the Lesser Sunda region that is highly influenced by annual monsoonal conditions [20–22]. Water availability on this island is highly dependent on the annual rainfall. The island has been exposed to this climate even before the Pleistocene, and this climatic condition triggered karstification processes in various parts of the island. These processes have resulted in the formation of numerous karst valleys and caves along its cliffs. Interestingly, archaeological excavations indicate that prehistoric human-hunting activities have been taking place since the Pleistocene. Several Asian-type mammals are often found as their hunting targets [17,23,24]. Moreover, similar archaeological evidence has also been discovered in the eastern Lesser Sunda region, such as on Flores Island [25], where Homo floresiensis activity was identified.

Substantial paleontological and archaeological records on Nusa Penida indicate a high possibility that Nusa Penida was part of a migration route during the Pleistocene for terrestrial-based fauna, including prehistoric humans. They would have easily colonized the islands when the land bridges emerged during glacial periods. However, these routes were disconnected over time due to rising sea levels, intensive abrasion of the landmasses of the land bridges, and/or possibly due to local tectonic events.

Through this study, we desire a more comprehensive investigation in further research. It is essential to consider the subsidence rate of the seafloor in the Badung Strait, especially in the western part of Nusa Penida and the Lombok Strait. Understanding the subsidence rate will help calibrate the contours for more precise paleobathymetry and paleotopography reconstruction. Additionally, the sedimentation rate of the seafloor should be considered. Ocean drilling programs in this region should acquire data from seafloor lithology. These data would reveal and confirm the paleoenvironments, mainly the existence of terrestrial ecosystems that were recorded in the seafloor lithology around Nusa Penida Island.

4 Conclusion

There are two identified natural land bridges in the southern part of Bali: the Bali-Nusa Penida land bridge and the Nusa Penida-Lombok land bridge. These land bridges connect the mainland of Bali to the mainland of Lombok through Nusa Penida during the maximum sea-level drop in the Pleistocene glacial periods. The presence of these land bridges implies that Nusa Penida was one of the important dispersal routes for terrestrial fauna of Sundaland when they attempted to disperse eastward to the Lesser Sunda region. Unfortunately, these land bridges have gradually submerged deeper due to intensive surface erosion and abrasion from sea currents in the Lombok Strait, along with global sea level rise during interglacial periods. Local tectonic activity might also be responsible for the subsidence of these land bridges.
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