

# Association of Community-level Traits with Soil Properties in a Tropical Coastal Sand Dune

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## ABSTRACT

There is limited information regarding plant functional traits for plant communities in tropical coastal sand dunes. This study investigated differences in species trait compositions and the relationship between community-weighted mean (CWM) traits and soil properties on the windward and leeward sides of the Bang Boet coastal sand dunes in southern Thailand. Ten sampling plots were randomly selected from each side of the dune. All woody plant species were collected and their functional traits were assessed. Soil samples were also collected. A redundancy analysis (RDA) was used to examine the relationship between CWM traits and soil properties. The results showed that species trait compositions and the CWMs of specific leaf area, leaf thickness, and leaf toughness were significantly different between windward and leeward sides. The RDA showed significant correlation between CWM traits and soil properties, particularly for specific leaf area, a functional trait that plays an important role in nutrient turnover on the leeward side. These results indicate that soil properties are predictable based on CWM traits and that leeward sand dune sides can support greater soil formation than windward sides. Hence, functional traits, as well as species, should be considered in coastal sand dune restoration and conservation programs.

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## 1. INTRODUCTION

Recent natural disasters have focused global attention on societal responses to environmental hazards and the potential of natural systems to moderate disturbance effects, especially for coastal areas (Stanturf et al., 2007). Plant communities in coastal areas play an important role in protecting the coastline during major disturbance events, including tsunamis (Cochard et al., 2008). During the 2004 Indian Ocean tsunami event, ocean waters inundated beaches and flowed over adjacent aeolian sand dunes in Thailand (Choowong et al., 2007). After such events, plant recovery processes in coastal sand dunes are dependent on individual beach structure and the degree of anthropogenic disturbance, including trampling pressure and beach development. Plant functional traits are effective tools for assessing

coastal sand dune status after disasters (Hayasaka et al., 2012). Although information concerning plant recovery after disasters in coastal ecosystems is relatively abundant, less research has focused upon plant functional traits in natural coastal sand dunes.

Plant functional traits are morphological, physiological, and phenological features that represent ecological strategies, determine how plants respond to crucial environmental factors and affect other trophic levels, and influence ecosystem properties (Kattge et al., 2011; Pérez-Harguindeguy et al., 2013). Functional traits allow for classifying species into functional types, providing insight into fundamental patterns and the effect of changing species composition on ecosystem functions. Assessing the community-weighted mean (CWM) of trait values is an approach used in plant ecology to

describe ecosystem properties (Lavorel et al., 2008), especially during succession (Eichenberg et al., 2015; Pinho et al., 2017). According to Maun (2009), the landward zonation of coastal sand dunes is a special case of primary succession due to the greater influence of several abiotic factors including soil properties, wind velocities, and salt spray. In particular, soil properties developed by dune vegetation establishment are a major factor. Soil properties control plant growth and species composition in coastal sand dune systems (Kachi and Hirose, 1983), which are recovered via native species in sand dunes (Zhang et al., 2013). Additionally, topography, specifically windward and leeward sides of dunes, is instrumental in determining vegetation establishment (Moreno-Casasola, 1986; Maun, 2009). Soil variability in sites probably results from redistribution of litter by gravity and would be rather side-dependent (Wardenaar and Sevink, 1992). As sand dunes are a special case of primary succession, it is assumed that the initial soil properties are totally the same between the windward and the leeward sides (Walker and Moral, 2003; Maun, 2009). Therefore, evaluating species and plant communities via functional traits may be effective in assessing differences in soil properties on the windward and leeward sides of coastal sand dunes.

Coastal sand dunes are very common in temperate zones, but found less frequently in subtropical and tropical zones (Hesp, 2004; Cochard et al., 2008; Maun, 2009). In the tropical zone, Bang Boet is one of the largest dunes, located on the inner gulf of Thailand. Bang Boet has varied topography and habitats, including coastal grassland and coastal scrub, which is composed of woody plants (Laongpol et al., 2009). However, woody plant species covering in the natural areas are considered to be the final-stage in the successional process (Walker and Moral, 2003). Therefore, this study investigated the difference in woody plant community functional traits and the soil properties underlying these differences on the windward and leeward sides of coastal sand dunes in the Bang Boet. Two research objectives were addressed in this study, first, determining how species trait compositions, CWM traits and soil properties vary between leeward and windward sides, and second, identifying the relationship between CWM

traits and soil properties. Although this study reflects sand dunes in the tropical zone, it is possible to generalise these results over broad geographic areas and diverse conditions for natural resource management after natural and anthropogenic disturbances (e.g., tsunami, flooding and mining).

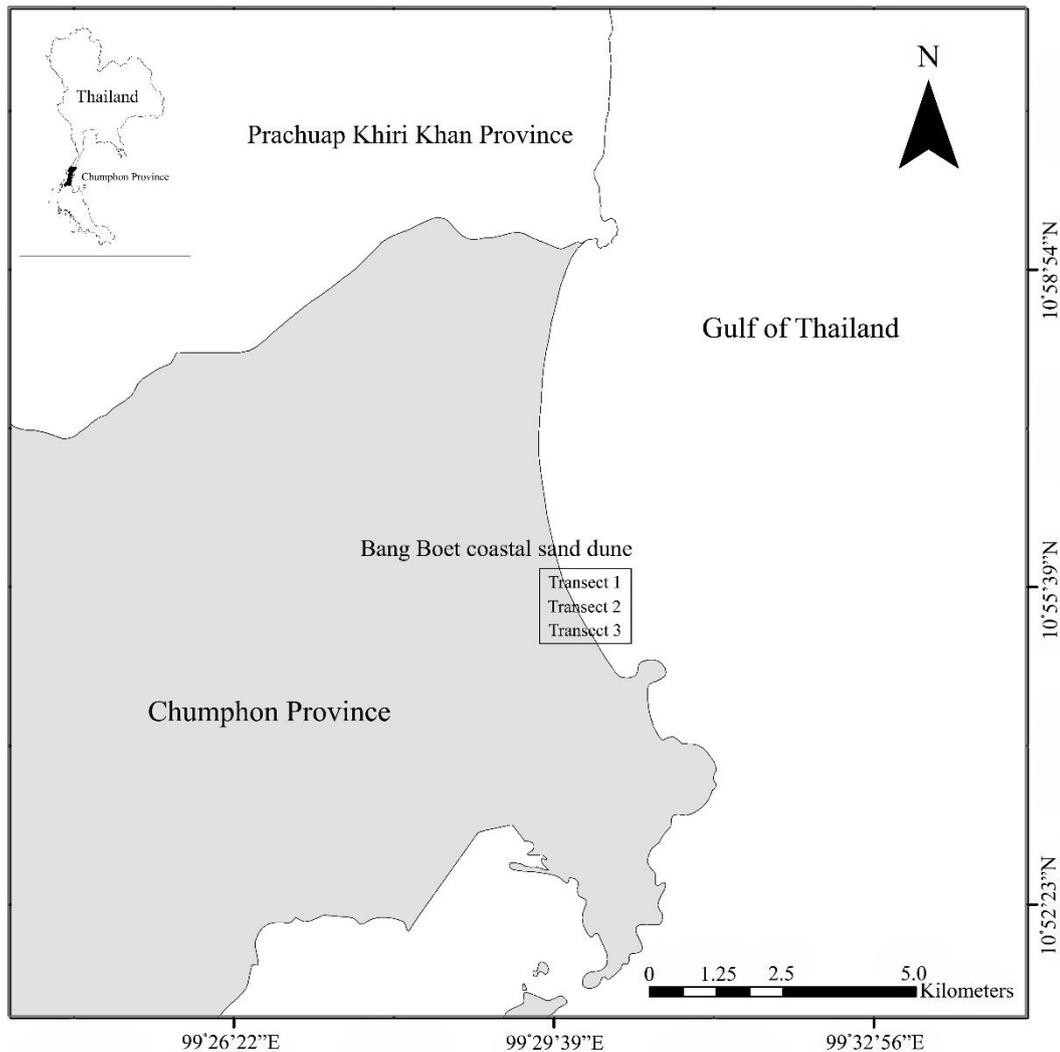
## 2. METHODOLOGY

### 2.1 Study site

The study was conducted on the Bang Boet coastal sand dune (10°55'22"-10°56'6"N, 99°29'25"-99°29'49"E), Pak Klong sub-district, Pathio district, Chumphon Province, Southern Thailand (Figure 1), 425 km south of Bangkok. The highest elevation in the dune is approximately 20 m above mean sea level (Choowong, 2011). Bang Boet coastal sand dune experiences a tropical monsoon climate with three main seasons: rainy, winter, and dry seasons. The rainy season occurs from May to October and is influenced by the southwest monsoon. The winter season occurs from November to January, followed by a dry season from February to April. The mean annual rainfall between 1990 and 2017 was 1,730.52 mm, with a minimum of 1,148.10 mm in 1994 and a maximum of 2,656.50 mm in 1996. The mean monthly temperature over this period was 24.83 °C, with a minimum of 19.12 °C in April and a maximum of 30.54 °C in December, recorded by Saithong Silvicultural Research Station. The soil is sandy (99.55%) and rather acidic (pH 4.20-6.30), and has a low water-holding capacity and a low nutrient content.

### 2.2 Data collection

In early August 2016, ten sampling plots (10 m × 10 m) were randomly selected from three permanent transect plots (10 m × 100 m) established in 2012, on the windward and leeward sides of a dune, for a total of 20 sampling plots. Within each sampling plot, all woody plants with a diameter at breast height (DBH) ≥ 1 cm were measured and identified to the species level. Species nomenclature was based on Smitinand (2014). Woody plants consisted of a total of 36 species representing 11 species in the windward and 32 species in leeward sides, with seven species present on both sides. In addition, ecological structures are explained in Table 1.



**Figure 1.** Study site in Bang Boet coastal sand dune on the inner gulf of Thailand.

**Table 1.** Ecological structure (mean±standard error) of all woody plants on the windward and leeward sides in the Bang Boet coastal sand dune.

Sides	Density (stem/0.01 ha)	Diameter (cm)	Height (m)
Windward	16±7	6.21±0.86	2.30±0.12
Leeward	111±13	3.75±0.31	3.45±0.25

Six plant functional traits were assessed, including leaf area (LA), leaf thickness (Lth), leaf toughness (LT), specific leaf area (SLA), leaf dry matter content (LDMC), and wood density (WD), using material collected from each species in accordance with Pérez-Harguindeguy et al. (2013). Each trait was quantified by measuring nine replicate samples from three different individuals randomly selected in each species from both the windward and the leeward sides. Mature sun-leaf samples from mature trees were collected to determine representative mean leaf trait values for each species. Fresh leaf weights were obtained before leaves were

scanned. LA (mm<sup>2</sup>) was estimated as the area of the fresh leaf, analysed using image analysis software (LIA for Win32, <https://www.agr.nagoya-u.ac.jp/~shinkan/LIA32/index-e.html>); Lth (mm) was estimated as the mean of a fresh leaf's thickness, measured in the middle of the leaf with a digital thickness gauge (model 547-401, MITUTOYO); LT (N/mm) was estimated as the mean of three punch tests per unit fracture length, performed with a digital penetrometer (2.0 mm diameter, model D2S, IMADA). SLA (mm<sup>2</sup>/mg) was calculated using fresh leaf area divided by leaf dry weight (oven dried at 70 °C for 72 h), and LDMC (mg/g) was calculated using

leaf dry mass divided by leaf fresh weight. WD ( $\text{mg}/\text{mm}^3$ ) was calculated using wood dry weight (oven dried at 105 °C for 72 h) divided by its fresh volume, which was collected at breast height from individual trees ( $\text{DBH} \geq 5$  cm) using 5.15-mm increment borers.

In addition, soil samples were collected from each sampling plot. Each soil sample was collected using a soil core sampler, from the topsoil layer, at a depth between 0 and 15 cm. For chemical property analysis, five soil samples of 100  $\text{cm}^3$  each were collected from the four corner and centre points of each plot, then combined into one sample. For physical property analysis, one soil sample was collected using a soil core sampler at the centre of the plot. Chemical and physical properties were determined based on standard methods (National Soil Survey Center, 1996). Seven chemical properties (organic matter, pH, salinity, available phosphorus, exchangeable potassium, exchangeable calcium, and exchangeable magnesium) and two physical properties (bulk density and saturated hydraulic conductivity) were analysed at the Laboratory of Soil Science, Faculty of Agriculture, Kasetsart University (Bangkok, Thailand).

### 2.3 Data analysis

Non-metric multidimensional scaling (NMDS) ordination was performed to visualise patterns among species for all six measured functional traits using the *metaMDS* function in the Vegan package (Oksanen et al., 2015). Next, species trait compositions and soil properties between the windward and the leeward sides were examined using the *adonis* function to perform permutational multivariate analysis of variance (PERMANOVA), performed with 9999 random permutations. The CWM traits in each plot were calculated using the *functcomp* function in the FD package (Laliberté et al., 2014). One-way analysis of variance was used to quantify the difference in CWM traits and soil properties between dune sides. Finally, a redundancy analysis (RDA) was used to examine the relationship between CWM traits and soil properties using the *rda* function in the Vegan package. All analyses were performed using the data analysis software R (R Core Team, 2016).

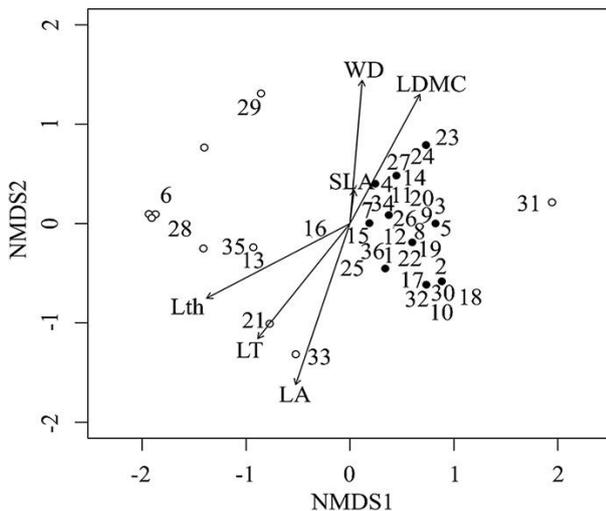
## 3. RESULTS AND DISCUSSION

### 3.1 Species trait compositions

The results of the NMDS analysis of species trait compositions indicated a low stress value (0.08), suggesting reasonable performance. Two groups were

created based on species trait compositions (Figure 2). The first group, representing a species trait community of LA, LT, and Lth, influenced the establishment of windward species, for example, *Casuarina equisetifolia* (6), *Hibiscus tiliaceus* (13), *Pandanus odorifer* (21), *Scaevola taccada* (28), *Syzygium grande* (33), and *Terminalia catappa* (35). The second group, representing a species trait community of WD, LDMC, and SLA, influenced the establishment of leeward species, including *Aporosa planchoniana* (1), *Chaetocarpus castanocarpus* (8), *Mischocarpus sundaicus* (19), *Ochna integerrima* (20), and *Planchonella obovata* (23). These results could be explained by heterogeneity in species trait compositions and differences in the availability of various environmental factors between the windward and leeward sites, suggesting that species occupying different dune sides do not share the same adaptive strategy. Maun (2009) and Santoro et al. (2012) previously demonstrated patterns of segregated coastal sand dune vegetation under stressful conditions. Soil property analysis showed that this sandy substrate is acidic, fine-grained, with a low water-holding capacity and low nutrient content; these properties represent stressful conditions for vegetation. Further, results from a PERMANOVA indicated that species trait compositions were strongly dissimilar and differed significantly between dune sides ( $F_{1,41}=3.44$ ,  $R^2=0.08$ ,  $P<0.05$ ). Five of the six functional traits (LA, LT, Lth, LDMC, and WD) showed a significant correlation with the first two NMDS axes ( $P<0.01$ ), excluding SLA ( $P=0.79$ ) (Figure 2). WD and SLA are considered to be key functional traits explaining plant growth rates globally (Kunstler et al., 2016). A high WD, associated with a slow potential growth rate, indicates high tolerance to competition and a strong competitive effect, while a low SLA is generally associated with slow-growing plant species (Kunstler et al., 2016) and may be low as a consequence of low nutrient availability (Ordoñez et al., 2009), indicating that woody plant species in this coastal sand dune are slow growing. Furthermore, some species demonstrated adaptation strategy, and species trait compositions on the windward side showed high values of Lth, LT, and LA. Generally, a higher Lth values are considered an indicator of a plant's adaptations to highly sunlit, dry, less-fertile habitat (Onoda et al., 2011), influencing photosynthetic pigments and chlorophyll which are vital components to the uptake of  $\text{CO}_2$ , indicating that a thicker leaf

would contain more photosynthetic apparatus per unit area (Onoda et al., 2008). Higher LT relates to leaf life span, prolonging the longevity (Kitajima and Poorter, 2010). LA is related to drought stress, nutrient stress and high-radiation stress, all of which tend to select for relatively small leaves (Pérez-Harguindeguy et al., 2013), while in contrast, this area showed high LA. The results showed that woody plant species on the windward side showed high values of Lth, LT, and LA, those species adapted under environmental or nutrient stresses (Pérez-Harguindeguy et al., 2013). Interestingly, those species had a high LT and LA which has been attributed to longer palisade cells or an extra number of cell layers that can increase the capacity for area-based photosynthesis, and have high relative growth rates (Lambers et al., 1998). Collectively, these traits suggest adaptation strategy; therefore, it was concluded that those traits would represent the adaptation to stressful conditions in this tropical coastal sand dune that has a high mean annual rainfall, but low water-holding capacity and low nutrient content.



**Figure 2.** Non-metric multidimensional scaling (NMDS) plots showing trait dissimilarity occurring in 36 woody plant species. Open and solid circles represent plots from windward and leeward side of the sampled dune, respectively. LA, leaf area; SLA, specific leaf area; Lth, leaf thickness; LDMC, leaf dry matter content; LT, leaf toughness; WD, woody density. The numbers indicate species: 1=*Aporosa planchoniana*; 2=*Atalantia monophylla*; 3=*Breynia glauca*; 4=*Calophyllum calaba*; 5=*Carallia brachiata*; 6=*Casuarina equisetifolia*; 7=*Catunaregam tomentosa*; 8=*Chaetocarpus castanocarpus*; 9=*Champerea manillana*; 10=*Clausena excavata*; 11=*Diospyros vera*; 12=*Eurycoma longifolia*; 13=*Hibiscus tiliaceus*; 14=*Ixora cibdela*; 15=*Ixora javanica*; 16=*Lanea coromandelica*; 17=*Lepisanthes rubiginosa*; 18=*Microcos tomentosa*; 19=*Mischocarpus sundaicus*; 20=*Ochna integerrima*; 21=*Pandanus odorifer*; 22=*Pavetta indica*; 23=*Planchonella obovata*; 24=*Pleurostyliya opposita*;

25=*Prismatomeris tetrandra*; 26=*Rhodamnia cinerea*; 27=*Rhodomyrtus tomentosa*; 28=*Scaevola taccada*; 29=*Sindora siamensis*; 30=*Suregada multiflora*; 31=*Syzygium antisepticum*; 32=*Syzygium claviflorum*; 33=*Syzygium grande*; 34=*Syzygium lineatum*; 35=*Terminalia catappa*; 36=*Vitex pinnata*.

### 3.2 Community-weighted mean (CWM) traits

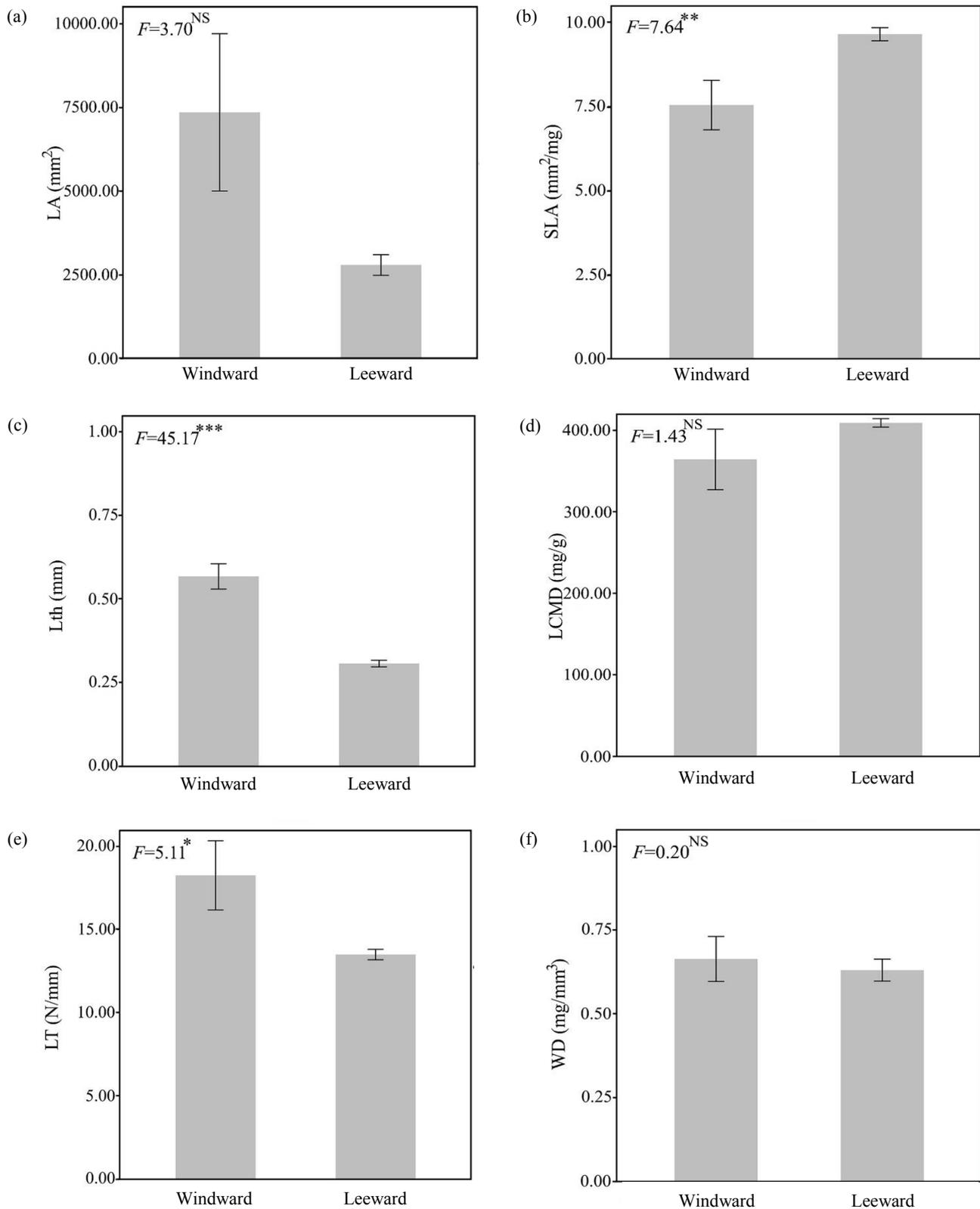
The CWM traits differed between the windward and leeward sides (Figure 3). Of the five leaf morphology traits, the CWMs were significantly different between dune sides for all except LA and LDMC (Figure 3(a)-(e)). The CWM for SLA was significantly lower on the windward side, contrasting with Lth and LT, which were lower on the leeward side. The CWM for WD was slightly higher for the windward side, but this difference was not significant (Figure 3(f)). Overall, CWM traits suggested that the functional structure of communities may be determined by differential environmental conditions (Garnier et al., 2004; Lavorel et al., 2008). The windward side showed a higher CWM of Lth and LT values than the leeward side, suggesting that Lth patterns are dominated by pioneer species in younger successional plant communities (Pinho et al., 2017), while LT patterns are often affected by disturbance intensity (Avila et al., 2018). Interestingly, woody plant communities on the leeward side (9.65 mm<sup>2</sup>/mg) showed a higher CWM of SLA than those on the windward side (7.54 mm<sup>2</sup>/mg) but lower standardised effect sizes (9.89 mm<sup>2</sup>/mg) (Bruehlheide et al., 2018), suggesting that these communities are dominated by slow-growing species (Garnier et al., 2004; Kunstler et al., 2016).

### 3.3 Soil properties

Several soil properties differed considerably between the windward and leeward sides (Table 2). PERMANOVA indicated that soil properties were significantly different between dune sides ( $F_{1,18}=18.94$ ,  $R^2=0.51$ ,  $P<0.001$ ). Soil properties presented low values in the windward and relatively high in the leeward side, except pH and bulk density. In the topsoil layer, plants leave a legacy in partially decomposed plant material, decomposing plant litters have an important role for fertility of soil properties (Adl, 2003). Although communities composed of slow-growing species tend to have low rates of litter accumulation, it is not yet known how litter production and decomposition could be estimated from litter input per unit of ground. The results from CWMs show that it differed between the windward and leeward sides. However, the CWMs of leaf traits

can reflect nutrient cycling and availability over forest succession (Eichenberg et al., 2015). Therefore, soil properties are likely to be predictable based on CWM

traits, particularly nutrients that are indicators of decomposition dynamics in the Bang Boet coastal sand dune.



**Figure 3.** Community-weighted means (mean±standard error) for each functional trait measured from windward and leeward dune sides: (a) leaf area (LA), (b) specific leaf area (SLA), (c) leaf thickness (Lth), (d) leaf dry matter content (LDMC), (e) leaf toughness (LT), and (f) woody density (WD). NS indicates non-significant, and asterisks (\*) represent significant differences at \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

**Table 2.** Soil properties (mean±standard error) in the Bang Boet coastal sand dune.

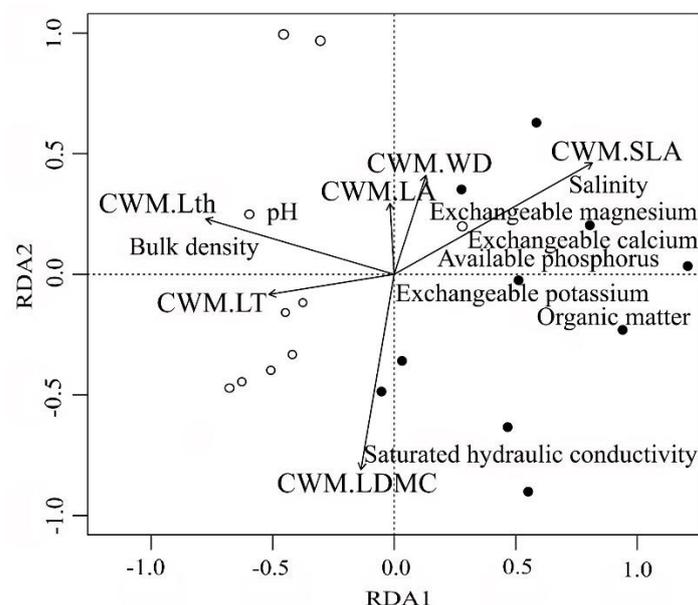
Soil properties	Windward	Leeward	$F_{(1,18)}$
Bulk density (g/cm <sup>3</sup> )	1.42±0.03	1.04±0.07	25.46***
Organic matter (%)	0.48±0.15	2.18±0.28	28.65***
pH (in H <sub>2</sub> O)	5.66±0.17	5.25±0.18	2.46 <sup>NS</sup>
Salinity (dS/m)	0.04±0.01	0.06±0.01	2.32 <sup>NS</sup>
Available phosphorus (mg/kg)	4.18±0.25	6.62±0.58	15.12**
Exchangeable potassium (mg/kg)	10.32±2.89	43.24±5.47	28.36***
Exchangeable calcium (mg/kg)	106.34±47.54	439.89±69.58	15.67***
Exchangeable magnesium (mg/kg)	31.28±16.58	89.99±10.89	8.71**
Saturated hydraulic conductivity (cm/s)	0.01±0.00	0.03±0.01	4.49*

NS indicates non-significant, and asterisks (\*) represent significant differences at \* $P<0.05$ , \*\* $P<0.01$ , \*\*\* $P<0.001$ .

### 3.4 Relationship between community-weighted mean (CWM) traits and soil properties

The RDA of soil properties explained 66% of total soil variation and included six CWM traits (Figure 4). The first and second axes of the model explained 53.64% and 10.87% of the variation, respectively. The first axis separated most of the assessed soil properties between windward and leeward sides, except for saturated hydraulic conductivity. The CWM for SLA (CWM.SLA), Lth (CWM.Lth), and LT (CWM.LT) contributed most to the first axis and explained 80.61%

of the fitted variation. The second axis separated the saturated hydraulic conductivity from dune sides, explaining within-side differences. The CWM for LDMC (CWM.LDMC), WD (CWM.WD), and LA (CWM.LA) contributed most to the second axis and explained 16.34% of the fitted variation. However, this study focused on between-side differences (RDA axis 1). Therefore, only two CWM traits (CWM.SLA and CWM.Lth) explaining soil properties were significantly correlated with the axis ( $P<0.001$  and  $P<0.01$ , respectively).



**Figure 4.** Redundancy analysis (RDA) of community-weighted mean (CWM) traits with soil properties. LA, leaf area; SLA, specific leaf area; Lth, leaf thickness; LDMC, leaf dry matter content; LT, leaf toughness; WD, woody density. Open and solid circles indicate plots from the windward and the leeward side, respectively.

The RDA results clearly indicate that the first axis separated most of the relationship between CWM traits and soil properties on both sand dune sides (Figure 4), which is a common approach in relating community-level trait responses to the environment (Kleyer et al.,

2012). CWM trait values are important for explaining soil properties, particularly because CWMs of leaf traits reflect nutrient cycling through decomposing plant material available for soil resources (Eichenberg et al., 2015). Typically, CWMs for SLA are shown to relate

to nutrient cycling and dynamics (Garnier et al., 2004; Eichenberg et al., 2015). These results clearly show that in habitats with abundant soil resources (i.e. the leeward dune side) the CWM of SLA is higher, whereas the CWMs of Lth and LT (Figure 3(b), (c), and (e)) are lower. Rapid nutrient cycling on the windward dune side reflects the 'fast-slow' plant economics spectrum (Reich, 2014). In addition, LT is a physical defence trait relating to litter decomposition rates, where high LT relates to decreased litter decomposition (Eichenberg et al., 2015). These responses reflect a fundamental trade-off (leaf economics spectrum) between traits related to nutrient conservation and traits related to nutrient acquisition and turnover (Wright et al., 2004). Therefore, these results suggest that soil properties are predictable based on CWM traits, and that nutrient turnover and conservation are greater on the leeward side of coastal sand dunes.

#### 4. CONCLUSION

Clear differences in functional trait composition between the windward and leeward sides indicate that the establishment of woody plant species on sand dunes reflects different successful adaptation strategies. The CWM of SLA was significantly greater on the leeward side, and SLA plays an important role in terms of soil turnover and nutrient conservation, particularly for these leeward sand dune sides. These results indicate that soil properties are predictable based on CWM traits and that leeward sand dune sides support nutrient turnover and conservation greater than windward sides. Therefore, to ensure success in restoration and conservation programs, management plans should focus on plant functional traits, specific conditions, and environmental factors.

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