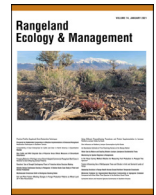




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## Original Research

Comparing the Predictive Capacity of Allometric Models in Estimating Grass Biomass in a Desert Grassland<sup>☆</sup>Adam T. Naito<sup>1,\*,#</sup>, Steven R. Archer<sup>1</sup>, Philip Heilman<sup>2</sup><sup>1</sup>School of Natural Resources and the Environment, University of Arizona, Tucson, AZ, 85721, USA<sup>2</sup>Southwest Watershed Research Center, United States Department of Agriculture, Agricultural Research Service, Tucson, AZ, 85719, USA

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## ABSTRACT

Allometric models provide a rapid, nondestructive means for estimating aboveground biomass (AGB) of perennial grass species. In the absence of site-specific models, allometric relationships developed at other sites at other times are often used. This implicitly assumes that size-biomass relationships are highly robust. In this study, we assess the comparability of allometric relationships developed at two points in time (2005 and 2015) on different soils on a Sonoran Desert savanna in southern Arizona. We used peak growing season field measurements to develop single-species and multispecies regression models using basal diameter and height to predict the current year's AGB for seven perennial grass species. Basal diameter exhibited the strongest relationship with AGB among single-species (adjusted  $R^2 = 0.54$  to  $0.87$ ) and multispecies models (adjusted  $R^2 = 0.73$ ). Inclusion of height did little to improve biomass predictions. Our models generally underestimated observed 2015 AGB on the loamy site, whereas models developed in 2005 on a sandier site overestimated the 2015 AGB. Results suggest site-specific allometric models should be used when possible. However, in lieu of such models, relationships developed at other sites or at other times may be appropriate depending on the level of precision needed to address a specific research question.

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## Introduction

Quantitative estimates of aboveground biomass (AGB) and net primary productivity (Scurlock et al. 2002) of perennial grasses are germane to rangeland conservation and management issues related to grazing, woody plant invasion, and other disturbances. However, direct site-specific estimates of AGB and its spatiotemporal variation requires time-intensive destructive plant harvesting and processing procedures (Sala et al. 2000) that may influence root growth (Derner et al. 2006) and competitive interactions (Holthuizen and Veblen 2016). Nondestructive assessments of AGB using dimensional analytic techniques (Niklas 1994) and allometric relationships circumvent these problems. Morphologic variables such as basal diameter, height, canopy diameter, and volume have

been used to estimate biomass of diverse plant functional types (Etienne 1989; Lambert et al. 2005).

Species-specific and multispecies allometric models provide a means for estimating AGB. When site- or species-specific models are not available, generalized allometric relationships may be used under the assumption they are reasonably robust (e.g., Pastor et al. 1984). However, these models may underperform if climate (Rudgers et al. 2019), disturbance (Johnson et al. 1988; Harrington and Fownes 1993) and topographic factors alter plant biomass allocation and architecture (e.g., Koerper and Richardson 1980). Our objective here was to determine the extent to which allometric relationships developed for grasses at one Sonoran Desert grassland site in 2005–2006 would be compatible with those developed in conjunction with a 2015 study on a different ecological site. In addition, we sought to determine whether there was a difference in size-biomass relationships between plants under and away from mesquite canopies.

## Methods

## Study site

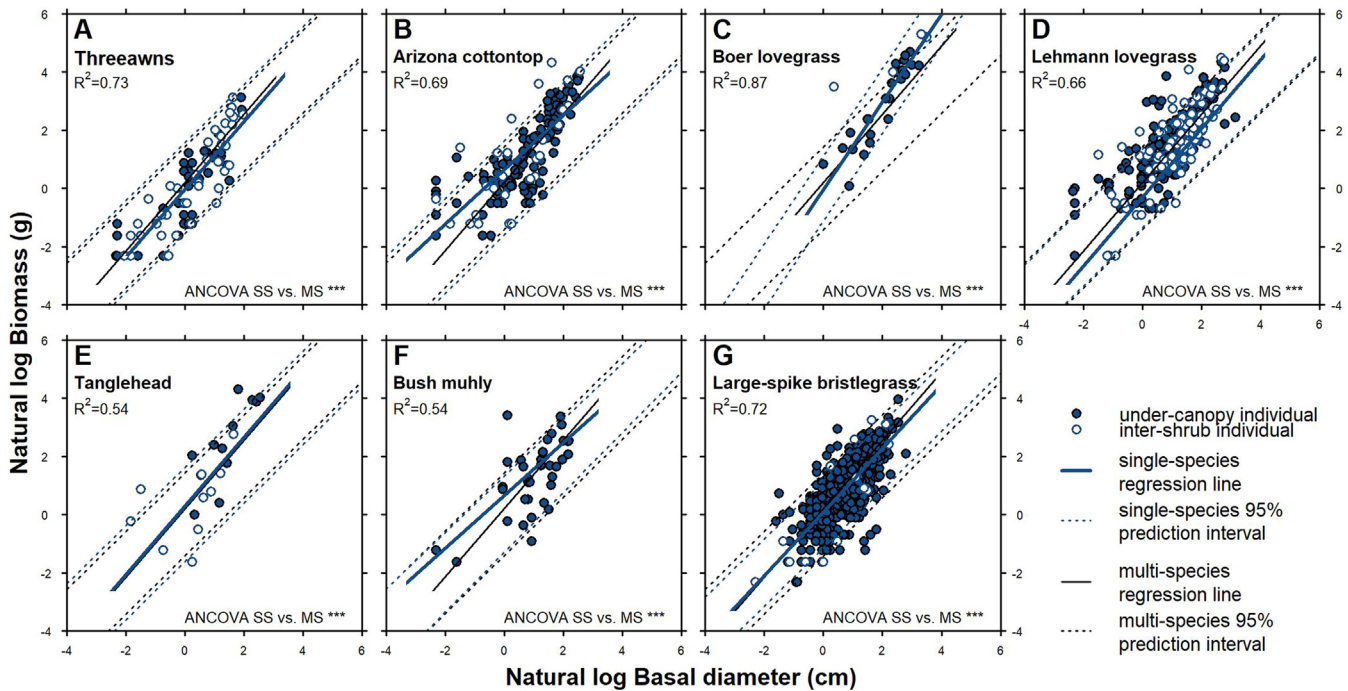
The 210 km<sup>2</sup> Santa Rita Experimental Range (SRER) is on the west side of the Santa Rita Mountains 45 km south of Tucson,

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**Figure 1.** Relationship (and adjusted  $R^2$ ) between aboveground plant biomass (g) and basal diameter (cm) in 2015 for seven grass species growing in the vicinity of velvet mesquite canopies. Diameter-only multispecies model detransforms to  $\text{biomass (g)} = e^{0.2044} \cdot \text{diameter (cm)}^{1.1736}$ . “ANCOVA SS vs. MS \*\*\*” denotes significant ( $\alpha < 0.001$ ) differences in slopes on single-species and multispecies regression lines.

Arizona. Elevation ranges from 900 to 1 400 m; climate is subtropical semiarid with precipitation (PPT) dominated by the North American Monsoon (Adams and Comrie 1997). Mean annual PPT and temperature ranges from 330 mm/18.9°C at lower elevations (978 m) to 430 mm/17.2°C at higher (1 293 m) elevations (Wheeler et al. 2007). Our study was conducted on instrumented, rotationally grazed watersheds (Polyakov et al. 2010) in the 990–1 200-m elevation zone, where vegetation is dominated by velvet mesquite (*Prosopis velutina* Woot.) and a ground layer of lovegrass (*Eragrostis lehmanniana* Nees.). Soils were sandy clay/sandy clay-loams in the Sasabe-Baboquivari soil complex (Breckenfield and Robinett 2003). Long-term (1987–2015) mean annual PPT and monsoon (July–September) PPT on the watersheds is 398 mm and 229 mm, respectively (ARS Rain Gauge 8) (Fig. S1, available online at ...). We conducted field measurements from 1 September through 10 October 2015 during the period of peak herbaceous AGB (Cable 1975) and preceding seasonal grazing. The cattle stocking rate of our site in 2014 before harvest (0.02 animals  $\text{ha}^{-1} \text{yr}^{-1}$ ) was comparable with that of the Nafus et al. (2009) site (0.03 animals  $\text{ha}^{-1} \text{yr}^{-1}$ ) (Mashiri et al. 2008; Nafus et al. 2009). The methodology described in the next sections follows that of Nafus et al. (2009), the only study providing allometric models for perennial grasses in southern Arizona of which we are aware.

#### Dimensional measurements and harvesting

We assessed perennial grass species under and away from  $n = 56$  mesquite canopies. At each mesquite individual, we placed a 1-m<sup>2</sup> PVC frame under its canopy and next to its stems and harvested all perennial grasses within the frame. We repeated this process by placing the frame along a randomly selected bearing at least 1 m away from the canopy dripline in the intershrub zone. Species and the range of basal diameters (BDs) encountered in our sampling included threeawn (*Aristida* spp.), 0.10–8.36 cm; Arizona cottontop (*Digitaria californica* [Benth.] Henr.), 0.11–13.20 cm; Boer lovegrass (*Eragrostis curvula* [Schrad.] Nees), 1.05–34.09 cm;

Lehmann lovegrass (*Eragrostis lehmanniana* Nees.), 0.33–16.88 cm; tanglehead (*Heteropogon contortus* [L.] Beauv. ex Roem. & Schult.), 0.17–13.37 cm; bush muhly (*Muhlenbergia porteri* [Scribn. ex Beal]), 0.11–9.26 cm; and large-spike bristlegrass (*Setaria macrostachya* [Kunth.]), 0.27–13.20 cm.

We measured basal diameter using cloth tapes (0.1-cm increments) on plants  $> 0.3$  cm BD and digital calipers (0.1-mm increments) on plants  $\leq 0.3$  cm BD. Regarding the latter, we recorded the average of two orthogonal measurements. Plant height (0.1-cm increments) was measured from the soil surface to the uppermost leaf collar. The height of bush muhly, with its spherical architecture, was based on an average peak height of tillers. After measurements, we clipped plants 1 cm above the soil surface, bagged them, and transported them to the laboratory to dry at 60°C for 48 h. Previous years' AGB was removed, and samples were weighed to the nearest 0.1 g.

#### Allometric models

We used natural log (ln) transformations of AGB and size metrics to model relationships between grass size and AGB to ensure comparability with models defined by Nafus et al. (2009). Our equations are of the form  $\ln y = a + b (\ln x)$ , which detransform to  $y = e^a x^b$  (e.g., Andariese and Covington 1986; Northup et al. 2005). Explanatory size variables included basal diameter (BD, ln [cm]) and height (H, ln [cm]). Models were not corrected for logarithmic bias (Baskerville 1972) to avoid confounding comparisons with Nafus et al. (2009). We used linear regression to predict AGB for each species separately (single species model) and all species combined (multispecies model) using R v. 3.6.3 (R Core Team 2020). We used the resulting equations to compare our modeled AGB estimates to 1) observed (measured) AGB and 2) AGB values generated by the Nafus et al. (2009) models.

The Nafus et al. (2009) models were based on field measurements obtained in September 2005 and 2006 during peak AGB at the SRER “Rodent Station” location  $\sim 3.3$  km southwest of our

**Table 1**  
Models of plant size-biomass relationships for grasses based on 2015 data. Size variables include basal diameter (BD, cm) and height (H, cm). Column headers include sample size (number of plants), regression intercepts, coefficients, adjusted  $R^2$ , standard error of the estimate (SEE), correction factor, and root mean square errors (RMSE) of natural log-transformed plant BD ( $X_{BD}$ ) and height ( $X_H$ ) for single-species and multispecies models to solve for the natural log of the current year's biomass. Rows show results for unique combinations of explanatory variables. The BD-only multispecies model detransforms to biomass (g) =  $e^{0.20} \bullet$  diameter (cm)<sup>1.17</sup>.

Species	No.	Variable	Intercept	XBD	XH	Adj. $R^2$	SEE	RMSE
Threewawns	86	BD	-0.03	1.16	—	0.73	0.78	0.77
		H	-6.43	—	1.89	0.45	1.12	1.10
		BD + H	-3.41	0.36	2.68	0.31	0.67	0.65
Arizona cottontop	85	BD	0.51	1.05	—	0.69	0.80	0.79
		H	-6.75	—	2.02	0.32	1.19	1.18
		BD + H	-3.05	0.91	0.92	0.74	0.73	0.72
Boer lovegrass	29	BD	-0.03	1.51	—	0.87	0.51	0.49
		H	-11.81	—	3.57	0.37	1.12	1.08
		BD + H	-4.98	1.33	1.26	0.90	0.44	0.41
Lehmann lovegrass	203	BD	0.30	1.18	—	0.66	0.68	0.68
		H	-5.79	—	1.83	0.35	0.94	0.94
		BD + H	-3.25	0.99	0.92	0.73	0.61	0.60
Tanglehead	22	BD	0.65	1.13	—	0.54	1.15	1.09
		H	-8.26	—	2.55	0.60	1.07	1.02
		BD + H	-5.38	0.61	1.67	0.68	0.96	0.89
Bush muhly	31	BD	0.65	0.91	—	0.71	0.60	0.58
		H	-1.29	—	0.82	0.06	1.08	1.04
		BD + H	-2.21	0.91	0.81	0.79	0.51	0.48
Large-spike bristlegrass	234	BD	0.09	1.09	—	0.72	0.58	0.58
		H	-5.73	—	1.83	0.41	0.85	0.84
		BD + H	-3.02	0.91	0.88	0.79	0.50	0.50
Multispecies	690	BD	0.20	1.17	—	0.73	0.72	0.72
		H	-6.28	—	1.97	0.42	1.06	1.06
		BD + H	-2.97	0.97	0.87	0.79	0.64	0.64

study site. Soils on the two sites are described in Table S1 (available online at [doi:10.1016/j.rama.2024.01.004]). The grass species assessed in our study overlapped with those in Nafus et al. (2009), with two exceptions: 1) Ours included large-spike bristlegrass, whereas theirs included plains bristlegrass (*S. leucopila*); and 2) black grama (*Bouteloua eriopoda* [Torr.] Torr.) was assessed in theirs but did not occur with sufficient frequency to warrant inclusion at ours.

## Results

Annual and monsoon PPT the year preceding our study (2014) was 378 mm and 237 mm, respectively, and was 415 mm and 201 mm, respectively, the year of our study (2015). The allometric relationships reported by Nafus et al. (2009) were derived from plants receiving annual PPT of 240 mm, 294 mm, and 317 mm, respectively (McClaran et al. 2002), and monsoon PPT of 163 mm, 204 mm, and 283 mm in 2004, 2005, and 2006, respectively (Nafus et al. 2009). The long-term annual and monsoon PPT for their site was 353 mm and 207 mm, respectively. Precipitation data are presented in Fig. S1 (available online at [doi:10.1016/j.rama.2024.01.004]).

Using Wilcoxon rank sum tests, we determined that size-biomass relationships of grasses under velvet mesquite canopies were comparable with those obtained for those away from canopies ( $P > 0.05$ ; Fig. 1). Our allometric models therefore reflect data pooled from plants under and away from mesquite canopies. Among our single-species models, BD alone accounted for 54%–87% of the variation in AGB (see Fig. 1); height alone accounted for 6%–45% of the variance (Table 1). Including height along with diameter did little to improve biomass predictions ( $R^2$  increases of 0.04 to 0.14). Pooled across species, BD and height accounted for 73% and 42% of the variance in AGB, respectively, with the two variables combined explaining 79% of the variance. In comparison, Nafus et al. (2009) accounted for 80%–91% of variation in AGB in their single-species models. With the exception of Boer lovegrass, our single-species models, like theirs, were within the 95% prediction interval of the multispecies models. Regression

line slopes of our single-species and multispecies models differed significantly (analysis of covariance [ANCOVA],  $P < 0.001$ ).

Our models underestimated observed AGB for plants with larger BDs (see Fig. 1), whereas those of Nafus et al. (2009) overestimated AGB (Fig. 2). Boer lovegrass was an exception, where equations from both studies predicted AGB well. ANCOVA revealed that differences between our single-species models and those of Nafus et al. (2009) were significant ( $P < 0.001$ ).

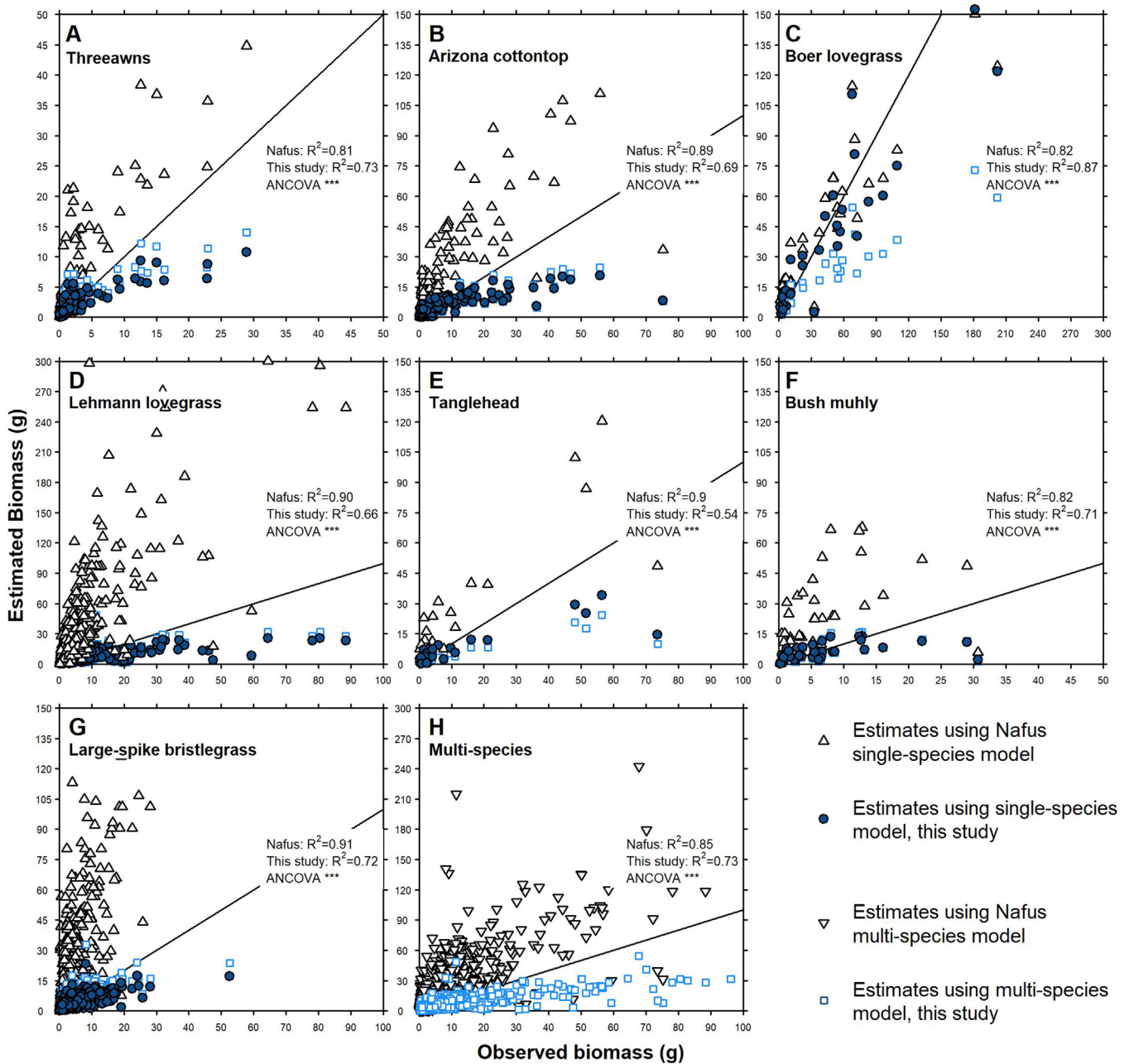
## Discussion

Our results are consistent with previous work on grass size-biomass relationships (e.g., Andariese and Covington 1986; Guevara et al. 2002) in that inclusion of height did little to improve the predictive capacity of either single-species or multispecies allometric models. The additional time investment associated with recording and processing height data may therefore not be justified (Nafus et al. 2009). Smith et al. (2021) noted that while effectiveness of multispecies allometric models varies depending on the species used for model development, such models may be useful in areas with mixtures of species. Our multispecies models performed similarly to our single-species models.

We observed different results using models developed for the same species at different points in time and applied to individuals occurring 3 km apart. This reinforces findings by Rudgers and colleagues (2019), who determined that spatiotemporal changes in precipitation, temperature, and drought influence allometric relationships between AGB and plant morphometrics. Plants at our site had a greater maximum BD than those at the Nafus et al. (2009) site. This reflects, in part, the higher annual and monsoon PPT at our site the year of and preceding our AGB measurements (e.g., Adar et al. 2022) (see Fig. S1). Models for Boer lovegrass may be more robust given they performed well in both studies.

Given that woody plants enhance soil nutrient pools and alter microclimate underneath their canopies (e.g., Throop and Archer 2007), grass size-mass relationships might be expected to differ between individuals growing under and away from velvet mesquite





**Figure 2.** Grass biomass–basal diameter relationships for seven grass species on a Combate soil in 2005 (Nafus et al. 2009) and those developed in 2015 (this study) for the same species on nearby Sasabe-Baboquivari soil. Line represents a 1:1 relationship. Note different x- and y-axis scales. “ANOVA\*\*\*” denotes significant ( $\alpha < 0.001$ ) differences in single-species regression line slopes for Nafus et al. 2009 and this study.

canopies. As this was not observed here, grass allometric relationships in this system may be robust. This is consistent with Gower et al. (1993), who found that fertilization did not influence plant allometry. Accordingly, differences in intershrub zone sampling schemes or microclimate do not likely explain differences in allometric relationships between our site and that of Nafus et al. (2009). The soil complex characterizing our site is finer textured than the soil at the Nafus et al. (2009) site (Table S1; available online at [doi:10.1016/j.rama.2024.01.004]). However, while this may account for the differences in plant size at the two sites, it does not explain why their multispecies and single-species models overestimated AGB at our site. Additional information would be required to characterize the spatiotemporal differences in environmental characteristics on the two sites.

Our results and those of Buech and Rugg (1989) suggest site-specific models should be used when possible. Reliability and robustness of future allometric models could ostensibly be improved by incorporating variables relating to precipitation, soil properties, and disturbance histories (e.g., stocking rates). In lieu of site-specific models, relationships developed at other sites or at other times may be appropriate, depending on the level of precision that may be needed for a specific research question. For example, plant- and small plot-scale experiments may require relatively precise information and one suite of dimension metrics (Williamson et al. 1987), whereas a different suite of dimensional metrics may suffice for accurately assessing biomass at broader scales using terrestrial lidar scanning (e.g., Wachendorf et al. 2017; Anderson et al. 2018) and uncrewed aerial vehicles (Zhang et al. 2022).

## 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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## Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.rama.2024.01.004.

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