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Estimation of biomass from shape-specific length-mass equations for arboreal spiders in subtropical montane forest of Taiwan

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Abstract. Accurate estimation of invertebrate biomass is essential for studies of ecosystem structure and function. To estimate seasonal changes in spider biomass on canopies of two coniferous and three broadleaf tree species in plantation and native forests of subtropical Taiwan, 6,554 spiders were collected from February to August 2015. A part of the collection ($n = 887$) was weighed and measured to develop appropriate body size-mass equations for subtropical montane forest systems. By comparing different equations, we demonstrate that use of shape-specific equations and incorporation of body width measurements provide the most accurate biomass estimates. Generalized whole-fauna equations produced accurate estimates for the entire pooled sample but caused relatively higher biases than shape-specific equations when applied to spider assemblage subgroups. Applying coefficients derived from the best equations, we describe the seasonal variation in spider biomass on five dominant tree species. Compared to broadleaf trees, Taiwan cedar and Japanese cedar supported higher spider biomass and abundance. Spider biomass on the two conifers declined in early spring, then increased over time, and reached its highest in August. In contrast, spider biomass on caudate-leaved chinkapin and Mori oak formed bell-shaped curves with a high peak in late spring. Spider biomass on deciduous Formosan alder remained at a low level from February to June and increased in August. Moreover, phenological patterns of spider biomass differed from those of abundance on some tree species. We expect that regression parameters from our study are appropriate for biomass estimation of spider assemblage in subtropical montane forest systems.

Keywords: Body shape, conifer plantation, mixed-oak forest, spider phenology, tree canopy

Forest canopies have diverse substrates and microhabitats that support a wide variety of arthropod assemblages (Moran & Southwood 1982; Southwood et al. 1982; Stork 1991). Spiders (Arachnida: Araneae) are an important component of these arboreal arthropod communities. They are mostly generalist predators of insects (Nyffeler & Benz 1987; Nyffeler 2000) and are essential food resources for insectivorous birds (Gunnarsson 2007) and bats (Schulz 2000; Burles et al. 2008) among others, thus forming important links in the canopy food webs. Quantification of arboreal spider biomass can therefore be of great importance by providing basic information for ecological studies dealing with community structure, ecosystem processes, and food web dynamics (e.g., Schuldt & Staab 2015).

Spider distribution is affected by the structure of the substrate and thus the abundance and richness of spider species may differ between tree species (Halaj et al. 1998; Korenko et al. 2011; Oguri et al. 2014). Field and experimental studies have shown that complexity in physical structures of tree canopies, such as foliage and twigs (Uetz 1991; Halaj et al. 2000), provides microhabitats for spiders for hiding or web placement, and hence affects spider abundance. Old trees in primary forests possess structurally more complex crowns and support a higher abundance of arboreal spiders than the same tree species in managed forests (Floren et al. 2008). In addition, the structure of branches and foliage also affects the availability of prey for spiders (Halaj et al. 1998, 2000). For example, Japanese cedar (*Cryptomeria japonica* (Thunb. ex L.f.) D. Don) trees usually have a large amount of dead foliage attached to their trunks in the lower part of the canopy, resulting in high abundance of detritivorous microarthropods (Hijii 1989) and their predators - wandering spiders (Oguri et al. 2014). Despite several studies on interactions between spiders and tree microhabitats, relatively few have investigated spider assemblages of multiple tree species in the same landscape (but see Halaj et al. 1998; Korenko et al. 2011), and detected seasonal variation in spider biomass, which is potentially critical for food-web dynamics of the local community.

The most common practical method for estimating invertebrate biomass of bulk samples is the length-mass regression (Schoener 1980; Gowing & Recher 1984). While several length-mass equations have been developed for spiders and other invertebrates (Gowing & Recher 1984; Hódar 1996; Sabo et al. 2002; Brady & Noske 2006), two points should be considered when using such equations. First, geographic variation in species composition and body shape leads to the length-mass relationship being climatic region-specific (Brady & Noske 2006). The regression equations derived from species in one locality may not be universally applicable (Höfer & Ott 2009; Penell et al. 2018). Consequently, the fauna used to construct the length-mass regression should be sampled from locations as similar as possible in continental origin to the community being studied (Gowing & Recher 1985). Second, spider species vary in body shape from globular round to elongated cylindrical and broad flattish. There is debate concerning the necessity for constructing specific equations when dealing with bulk samples including many specimens of different taxa or shapes. Some authors (Schoener 1980; Hódar 1996; Wardhaugh 2013) have suggested that equations should be constructed based on taxon or body shape, whereas others (Henschel et al. 1996; Höfer & Ott 2009; Penell et al. 2018) have recommended that only single generalized equations derived from all individuals combined are appropriate for estimating the spider biomass of bulk samples. Moreover, generalized equations could be improved by adding a body-width measurement to the regression models (Sample et al. 1993). Therefore, development of appropriate equations from the same or similar environments, while also considering variation in body shape, is required for determining spider biomass accurately.

Our main objective was to derive appropriate biomass equations and apply them to estimate arboreal spider biomass on two coniferous species in a mixed plantation of Japanese cedar and Taiwan cedar (*Taiwania cryptomerioides* Hayata) and three broadleaf trees dominant in mixed-oak forest in subtropical Taiwan. Dominant tree species have a critical role in influencing the species composition of spider assemblages within multispecies forest ecosystems (Samu et al. 2014). Japanese cedar and Taiwan cedar plantations represent 13% of total plantations in Taiwan, whereas mixed-oak forest is the most representative indigenous vegetation of montane areas (Qiu et al. 2015). We sampled spiders on canopies of five tree species and weighed a part of the collection to construct body size-mass equations for subtropical montane ecosystems. We tested whether different equations were necessary for different body shapes and whether incorporating body width into regressions improved model fit. We then used the valid equations thus obtained to estimate the biomass of all samples. Finally, we compared spider biomass and abundance between tree species and their seasonal variation within each tree species.

METHODS

Study area.—Our study was conducted in a subtropical montane cloud forest at Guanwu (24°31′N, 121°06′E; 1,900–2,200 m elevation) in Shei-Pa National Park, north-central Taiwan. The mountainous landscape is a mosaic of conifer plantations and mixed-oak forest. The study area has a humid, subtropical climate with distinct annual cycles of temperature and rainfall. Weather data obtained from the nearest weather station (~2.4 km from study site, automatic weather station C0D550 of the Central Weather Bureau, 24°31′37″N, 121°06′58″E) shows that ambient temperature generally increased from January (monthly average temperature ± SD: 8.0 ± 1.2 °C) to July (18.4 ± 0.5 °C) and annual rainfall ranged from 1,905 mm to 3,840 mm (mean ± SD: 2,514 ± 575 mm) in 2009–2018.

Vegetation was surveyed in 2012 in 22 plots (10×10 m^2) in plantation forest and 21 plots in native forest. Relative dominance (RD) of each tree species was computed as the total basal area at breast height of the species relative to the sum of basal area of all species. The plantation forest, which was planted ca. 30–40 years ago, was dominated by Japanese cedar (RD: 54%), with a smaller number of Taiwan cedar (RD: 25%) and Chinese fir (*Cunninghamia lanceolata* (Lamb.) Hook.; RD: 13%). Dominant interior species in native forest were Mori oak (*Quercus morii* Hayata; RD: 19%) and caudate-leaved chinkapin (*Castanopsis cuspidata* (Thunb. ex Murray) Schottky var. *carlesii* (Hemsl.) Yamazaki; RD: 17%). Dominant edge species were pioneer colonizers following fires and landslides and included Formosan alder (*Alnus formosana* (Burkill) Makino; RD: 11%) and Taiwan red pine (*Pinus taiwanensis* Hayata; RD: 26%).

Fieldwork.—We sampled arboreal spiders from February 10 to August 24, 2015 using the tree-shaking method (Hsu 2010). We sampled six similar-sized trees each of six species in the study area: two conifers, Japanese cedar (mean ± SD of basal area at breast height, BA: 0.21 ± 0.06 m^2) and Taiwan cedar (BA: 0.31 ± 0.07 m^2); two evergreen oaks, Mori oak (BA: 0.18 ± 0.13 m^2) and caudate-leaved chinkapin (BA: 0.22 ± 0.17 m^2); and one broadleaf deciduous species, Formosan alder (BA: 0.11 ± 0.06 m^2), which leafs out rapidly in early April and loses all leaves in November to December. For seasonal replicates, we sampled spiders from one set of three trees per species, alternating by set at two-week intervals. We used a 10-m rod with a hook to reach three mid-story canopy branches of ca. 10 cm diameter and bearing many leaves. The branches were shaken vigorously, and spiders were collected on a 3×3 m^2 ground cloth. Spiders captured by shaking method constitute a minimal population in the sample foliage. This may somewhat underestimate total spider biomass in the canopy layers.

To construct valid equations, specimens collected during February and March (n = 887; first data set) were stored individually in vials during transport to the laboratory, killed by freezing and weighed to the nearest 0.1 mg with a microbalance (fresh mass). Their length (from the front end of the carapace to the hind end of the opisthosoma) and width (the widest part of the opisthosoma) were measured to the nearest 1 mm, using graph paper placed under the specimen and counting the number of grids covered by the specimens (similar to Brady & Noske 2006). We chose the widest part of the opisthosoma rather than carapace (see Penell et al. 2018) as representative of specimen width because the opisthosoma can reflect the nutritional status and development of the sexual organs and contributes most of the variation in size and mass within the species (Jakob et al. 1996). Chelicerae, spinnerets, and legs were excluded from the length and width measurements. Specimens collected during late-March to August (n = 5,667; second data set) were stored and measured in the same way, but not weighed.

Data analyses.—We used the body measurements of the first data set to determine the relationship between spider mass and body size, and grouped them into five different body-shape categories based on the ratio of body length to body width (≤1.5:1; 1.6–2.0:1; 2.1–3.0:1; 3.1–4.0:1; ≥4.1:1). The body shape distribution among tree species was compared by a chi-square test of independence. For post hoc comparisons, we calculated adjusted standardized residuals of each cell to examine the statistical significance (~Z distribution) in the contingency table (Agresti 2007). To control for multiple cell calculations (5×5 cells), a Bonferroni correction was applied (MacDonald & Gardner 2000) with $\alpha = 0.002$ (0.05 divided by 25), for a critical value $N(0,1)_{1-\alpha/2}$ of ± 3.09. An adjusted standardized residual that exceeded the critical value indicated that an individual cell had a greater discrepancy between observed and expected values than independence predicted.

Previous studies have found that body size-mass relationships are generally best described by the linear model, ln mass

Table 1.—The body shape distribution (categorized by the ratio of body length to width) of the first data set collected from five tree species. Asterisks represent values that significantly differed from the hypothesis of independence (adjusted standardized residual > 3.09, $P < 0.002$, see Methods). Bold letters indicate a significantly higher proportion, while italics indicate a significantly lower proportion.

	Taiwan cedar	Japanese cedar	Caudate-leaved chinkapin	Mori oak	Formosan alder
≤1.5:1	21	*25**	20	**40***	3
1.6–2.0:1	91	*93**	54	58	10
2.1–3.0:1	72	138	80	47	1
3.1–4.0:1	23	39	16	6	0
≥4.1:1	12	**36***	2	*0**	0
Total	219	331	172	151	14

$= a + b$ (ln length) or ln mass $= a + b$ (ln length × width) when incorporating body width measurements (Brady & Noske 2006; Penell et al. 2018), where the regression parameter a is the intercept, and the parameter b is the slope of the regression line. Therefore, we logarithmically transformed the first data set and applied the two models by linear regression (function *lm* in R). Regression equations were calculated for the group combining all spiders and for subgroups categorized based on body shape. Therefore, we developed four types of equations: length-mass regression equations for all spiders combined (equ. 1) and for each shape-ratio subgroup (equ. 2); length × width-mass regression equations for all spiders combined (equ. 3) and for each shape-ratio subgroup (equ. 4). We used these equations to estimate the biomass of the different groups and compared the estimated values to the measured biomass by *t*-tests. Bias was calculated as the relative error, i.e., the difference between the measured and estimated value divided by the measured value. The equation with the lowest estimated bias was regarded as the appropriate equation for our study system.

Coefficients from the best equations were applied to estimate the biomass of a total of seven monthly spider samples from each tree species. The estimated biomass was pooled per tree (i.e., three branches) in each survey trial and grouped by month. As we sampled the same tree repeatedly, to account for the lack of independence of the observations, we constructed a linear mixed-effects model with Gaussian error structure (LMM, function *lmer* in R package *lme4*) including data from all the trees for tree species comparison. Tree species was treated as an independent variable, while the estimated biomass per tree was treated as a response variable and tree identity as a random effect. To examine seasonal variation within each tree species, we implemented five LMMs for each tree species individually. The month was treated as an independent variable while the full model included spider biomass as the response variable and tree identity as the random effect. Tukey's post hoc test was used to detect significantly different group means. In addition, to clarify whether the variation in spider abundance between tree species and seasons was similar to that of variation in spider biomass, we used the number of individuals per tree (i.e., three branches) instead of spider biomass to carry out similar analyses. We constructed a generalized linear mixed-effects models with Poisson error structure (GLMM, function *glmer* in R package *lme4*) including data from all the trees for tree species comparison, and five GLMMs individually for season comparisons within each tree species. Global effects of parameters in GLMMs were tested by likelihood ratio test (LR test, function *drop1*). All values are presented as means ± standard error (SE), unless specified otherwise. The alpha threshold was set at 0.05. All statistical analyses were carried out using R version 3.5.1.

RESULTS

We collected 6,554 spiders in total from the five dominant tree species over the seven-month survey period. The first part of the collection ($n = 887$) was weighed and measured to construct body size-mass regressions. The body lengths of the spider assemblages ranged from 1 mm (one juvenile araneid spiders, three juvenile linyphiid spiders, and one juvenile and two adult mysmenid spiders) to 12 mm (one juvenile agelenid spider), with a median of 2.7 mm; and body mass ranged from 0.1 mg to 165.0 mg (same specimens), with a median of 2.1 mg. The body shape (length to width ratio) of spiders ranged from 1.0 to 7.5 (median $= 2.3$), and their distribution differed among tree species ($\chi_{28}{}^2 = 629.6$, $P < 0.001$, Table 1). Mori oak had relatively higher percentages of spiders with a globular round body (i.e., low body length to width ratio), while Japanese cedar had relatively higher percentages of spiders with a long, narrow body (i.e., high body length to width ratio). The group with an extreme shape (i.e., shape ratio ≥4.1:1 group) was composed of the genera *Rhomphaea* (Theridiidae; 42%), *Miagrammopes* (Uloboridae; 16%), and some species in the families Linyphiidae (38%, including *Turinyphia yunohamensis* (Bösenberg & Strand, 1906)), Salticidae (2%), and Segestriidae (2%).

Both the length-mass and the length × width-mass relationships were well described by linear models for all groups except for the group with shape ratio ≥4.1:1 (Table 2). Incorporation of body width into the predictor variable improved the model for all-spiders group and four out of the five shape-ratio subgroups. This was especially the case for the group with a high body length to width ratio (≥4.1:1). For the shape-ratio subgroup 2.1–3.0:1, body length alone was a better predictor of biomass ($r^2 = 0.913$), with incorporation of body width into the model resulting in only a small loss in explanatory power ($r^2 = 0.909$).

The generalized all-spiders equations (1 and 3; Table 3) provided accurate biomass estimates for the group combining all spiders sampled but caused biases in estimates for most of the shape-ratio subgroups, especially for the ≤1.5:1 and ≥4.1:1 subgroups. Biomass estimates derived from the shape-ratio equations 2 and 4 (Table 3) were close to the measured biomass of all groups. For individual estimates of the total spider biomass on each tree species, length × width-mass

Table 2.—Parameter estimates (*a* - intercept, *b* - slope) for length-mass and length × width-mass regression models, using equations based on mass = exp(*a* + *b* (ln body size)), for the combined spider (all spiders) group and subgroups categorized by the ratio of body length to width. Bold type signifies best model according to r^2.

	Length–mass model			Length × width–mass model		
	a ± SE	*b* ± SE	r^2	*a* ± SE	*b* ± SE	r^2
All spiders (*n* = 887)	-1.76 ± 0.04	2.54 ± 0.04	0.85	-0.95 ± 0.02	1.49 ± 0.02	**0.90**
Shape-ratio subgroups						
≤1.5:1 (*n* = 109)	-1.61 ± 0.08	2.93 ± 0.09	0.90	-1.14 ± 0.06	1.46 ± 0.04	**0.91**
1.6–2.0:1 (*n* = 306)	-2.04 ± 0.05	3.06 ± 0.06	0.89	-1.10 ± 0.03	1.51 ± 0.03	**0.90**
2.1–3.0:1 (*n* = 338)	-2.14 ± 0.05	2.82 ± 0.05	**0.91**	-0.81 ± 0.03	1.41 ± 0.02	0.91
3.1–4.0:1 (*n* = 84)	-2.42 ± 0.17	2.86 ± 0.12	0.87	-0.62 ± 0.09	1.43 ± 0.06	**0.88**
≥4.1:1 (*n* = 50)	-0.64 ± 0.37	1.38 ± 0.24	0.40	0.07 ± 0.14	0.98 ± 0.10	**0.68**

regression equations (equ. 3 and 4) could provide accurate biomass estimates that did not differ significantly from measured values (Table 3). Moreover, the shape-ratio equation constructed from length × width-mass regression (equ. 4) produced the most accurate biomass estimate with the lowest bias for all tree species.

We applied the coefficients derived from length × width-mass regression equations for each shape-ratio subgroup (i.e., equ. 4; Table 2) to estimate the biomass of a total of seven monthly samples. Taiwan cedar and Japanese cedar supported a generally higher spider biomass than did the broadleaf tree species (Fig. 1A; LMM, $F_{4,176} = 12.79$, $P < 0.001$). All Tukey comparisons between the two conifers and the broadleaf tree species were significant except for the comparison between Japanese cedar and Mori oak (Tukey's post hoc test: $q = 2.60$, $P = 0.067$; Fig. 1A). Spider abundance showed distribution patterns between tree species similar to those for biomass, and all post hoc tests between the coniferous and broadleaf trees were significant (Fig. 1B; GLMM, LR test: $\chi_4^2 = 54.3$, $P < 0.001$).

For seasonal variations within tree species, spider biomass on Taiwan cedar and Japanese cedar declined slightly in early spring, then increased steadily over time and reached its highest value in August (Fig. 2A, 2B; LMM, Taiwan cedar: $F_{6,30} = 2.62$, $P = 0.033$; Japanese cedar: $F_{6,30} = 3.42$, $P = 0.011$). Spider abundance on the two conifers also showed increasing trends over season (Fig. 2F, 2G; GLMM, LR test, Taiwan cedar: $\chi_6^2 = 448.0$, $P < 0.001$; Japanese cedar: $\chi_6^2 = 408.1$, $P < 0.001$). Arboreal spider biomass on the two evergreen oaks, caudate-leaved chinkapin and Mori oak, was lower in early spring and had a slight peak in June and May, respectively (Fig. 2C, 2D; LMM, caudate-leaved chinkapin: $F_{6,30} = 2.78$, $P = 0.029$; Mori oak: $F_{6,30} = 2.50$, $P = 0.044$). However, different trends were found in spider abundance on the two oaks. Spider abundance on caudate-leaved chinkapin fluctuated between March and August (Fig. 2H; GLMM, LR test: $\chi_6^2 = 81.1$, $P < 0.001$), while spider abundance on Mori oak increased over the season and peaked in July (Fig. 2I; GLMM, LR test: $\chi_6^2 = 124.6$, $P < 0.001$). Both spider biomass (Fig 2E; LMM, $F_{6,30} = 7.68$, $P < 0.001$) and abundance (Fig 2J;

Table 3.—Comparisons between measured and estimated spider biomass (mg) of the combined spider (all spiders) group and subgroups categorized based on the ratio of body length to width. Biomass was estimated using four equations for length-mass and length × width-mass regression models. See Table 2 for parameters used in each equation. Bias is the difference between the measured and estimated value as a percentage of the measured value. Values in bold indicate biomass estimates that differ significantly from measured values (*t*-test, $P < 0.05$).

		Length-mass model				Length × width-mass model			
		All-spiders equation (equ. 1)		Shape-ratio equation (equ. 2)		All-spiders equation (equ. 3)		Shape-ratio equation (equ. 4)	
Groups	Measured biomass	Estimated biomass	Bias	Estimated biomass	Bias	Estimated biomass	Bias	Estimated biomass	Bias
All spiders (*n* = 887)	3258.1	3093.2 ± 89.2	5.1	3274.9 ± 127.5	-0.5	3286.4 ± 111.7	-0.9	3258.3 ± 105.4	-0.0
Shape ratio subgroups									
≤1.5:1 (*n* = 109)	322.3	**185.6 ± 11.4**	42.4	330.2 ± 17.8	-2.4	**414.1 ± 22.2**	-28.5	329.0 ± 16.6	-2.1
1.6–2.0:1 (*n* = 306)	963.5	**643.6 ± 50.6**	33.2	1014.1 ± 117.7	-5.3	1060.3 ± 95.1	-10.0	976.6 ± 93.0	-1.4
2.1–3.0:1 (*n* = 338)	1296.0	1257.7 ± 49.3	3.0	1276.2 ± 40.7	1.5	1276.5 ± 48.4	1.5	1285.7 ± 42.9	0.8
3.1–4.0:1 (*n* = 84)	440.1	**515.8 ± 32.1**	-17.2	430.2 ± 16.1	2.2	**345.2 ± 20.0**	21.6	435.0 ± 15.6	1.2
≥4.1:1 (*n* = 50)	236.2	**490.5 ± 42.4**	-107.7	224.2 ± 12.8	5.1	**190.3 ± 13.8**	19.4	232.0 ± 10.1	1.8
Tree species									
Taiwan cedar (*n* = 219)	817.9	766.7 ± 40.0	6.3	**761.4 ± 28.2**	6.9	772.8 ± 30.3	5.5	772.9 ± 26.7	5.5
Japanese cedar (*n* = 331)	1253.9	**1403.6 ± 58.5**	-11.9	1249.8 ± 40.3	0.3	1194.1 ± 47.8	4.8	1247.6 ± 41.1	0.5
Caudate-leaved chinkapin (*n* = 172)	656.0	**543.3 ± 50.3**	17.2	750.8 ± 115.0	-14.5	728.9 ± 91.6	-11.1	710.4 ± 89.7	-8.3
Mori oak (*n* = 151)	489.1	**348.7 ± 19.0**	28.7	471.2 ± 23.8	3.7	539.9 ± 28.6	-10.4	482.3 ± 24.7	1.4
Formosan alder (*n* = 14)	41.2	30.9 ± 5.6	25.0	41.7 ± 6.3	-1.1	50.7 ± 7.7	-23.2	45.1 ± 6.6	-9.4

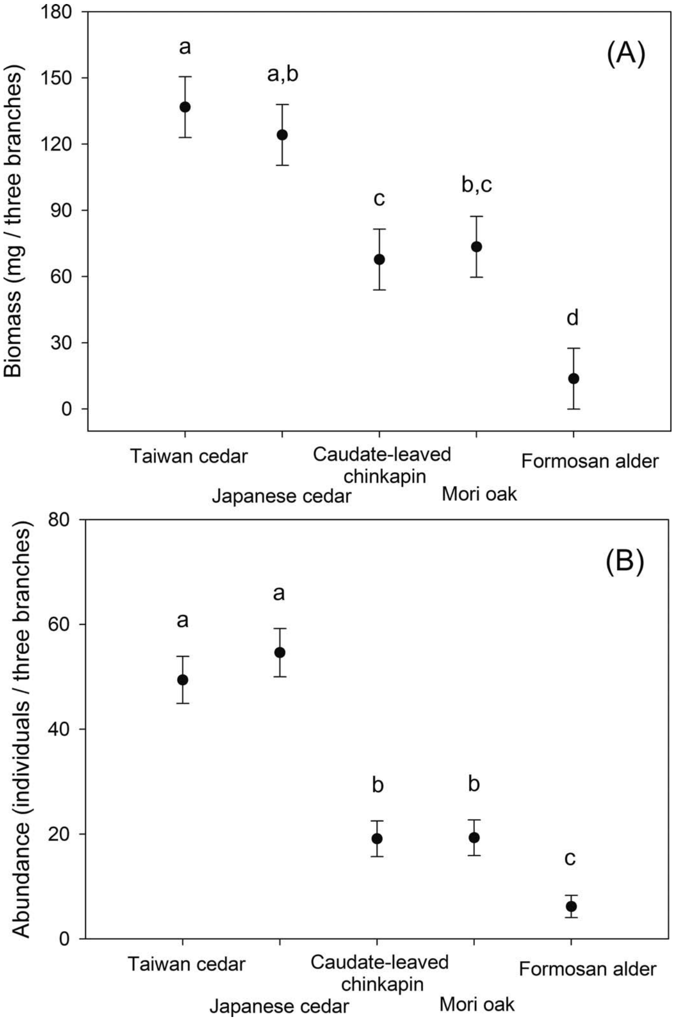

Figure 1.—Comparison of spider biomass (A) and abundance (B) on five dominant tree species in a mixed-oak forest and a conifer plantation. Different letters above the error bars represent statistically significant differences (Tukey's post hoc test, $P < 0.05$).

GLMM, LR test: $\chi_6^2 = 197.0$, $P < 0.001$) on Formosan alder remained at a low level from February to June and increased slightly in July and August.

DISCUSSION

We expect that our study presents shape-specific regression equations appropriate for spider assemblages in subtropical montane forest systems, though the applicability to areas outside Taiwan needs to be tested. Through comparison of different equations, we demonstrate that using shape-specific equations and incorporating body width into the regression model produce the most accurate estimates of spider biomass. This finding is consistent with previously published results for invertebrates (Wardhaugh 2013) that body size-mass relationships vary by body shape. Shape-specific equations have more structural flexibility and therefore provide greater accuracy for estimating biomass than whole-fauna equations, even for spider assemblages with relatively more similar body shapes compared to other invertebrate taxa.

In our study, generalized whole-fauna equations (i.e., all-spider equations) produced accurate estimates for spiders with the most common shape (Table 3; 2.1–3.0:1 subgroup), but caused serious biases for spiders with extreme body shapes. When applying generalized whole-fauna equations to estimate biomass of spider assemblages including different body shapes, the net bias from total biomass estimation is the sum of bias derived from each specimen. The net bias may be somewhat reduced during summing, resulting in relatively accurate estimates for the all-spiders group. This result is consistent with previous studies that found generalized whole-fauna equations were suitable for biomass estimation of whole assemblages (Henschel et al. 1996; Höfer & Ott 2009; Penell et al. 2018). However, for ecological comparisons, spider biomass is often calculated in subunits (e.g., tree species subgroups) rather than as whole assemblages. Our results showed that generalized whole-fauna equations generated relatively higher bias than shape-specific equations, when applied to spider assemblage subgroups with fewer specimens (see estimates from equ. 3 for Mori oak and Formosan alder subgroups in Table 3).

In contrast to the generalized whole-fauna equations, shape-specific equations performed well for all spider assemblage subgroups. Different body shapes imply that spiders have different body dimensions and may belong to different taxa. Although the r^2 values for the regression equation of the $\geq$4.1:1 subgroup were relatively low—perhaps due to various species with different body dimensions like elongated cylindrical *Miagrammopes* (Uloboridae), the long, slender opisthosoma of *Rhomphaea* (Theridiidae), and the relatively greater opisthosomal mass of *Turinyphia yunohamensis* (Linyphiidae)—our simple measurements of body size (length and width) could not fully cover their variations in physical appearance. The low biases between weighed and estimated biomass in all comparisons suggested that shape-specific equations are suitable for our study system. Taxon-specific equations are the most accurate for estimating biomass of invertebrates with different body shapes (Hódar 1996; Benke et al. 1999; Wardhaugh 2013; but see Penell et al. 2018); however, they can be superfluous and impractical (Henschel et al. 1996; Höfer & Ott 2009) or may be unavailable for taxa under study. Therefore, we recommend shape-specific equations as more accurate and less biased alternatives with wider applicability to different datasets, especially to datasets partly comprised assemblages with extreme body shapes.

Due to a cubic relationship between mass and body dimensions, the slope *b* is expected to be 3 for length-mass regression equations and 1.5 for length × width-mass regression equations if body shape and specific gravity remain constant across differently sized species within a given group (Benke et al. 1999; Wardhaugh 2013). However, for the $\geq$4:1 shape-ratio subgroup, *b* was lower than 2 in the length-mass equation and lower than 1 in the length × width-mass equation. This may indicate that either body shape becomes increasingly elongated and narrower with increasing body size (Schoener 1980; Benke et al. 1999) or specific gravity decreases with increasing body size, possibly due to a reduction in the proportion of heavy chitin in individuals with a long body (Smock 1980; Sabo et al. 2002). In addition, the regression slope *b* in the length-mass equation for the all-spiders group in

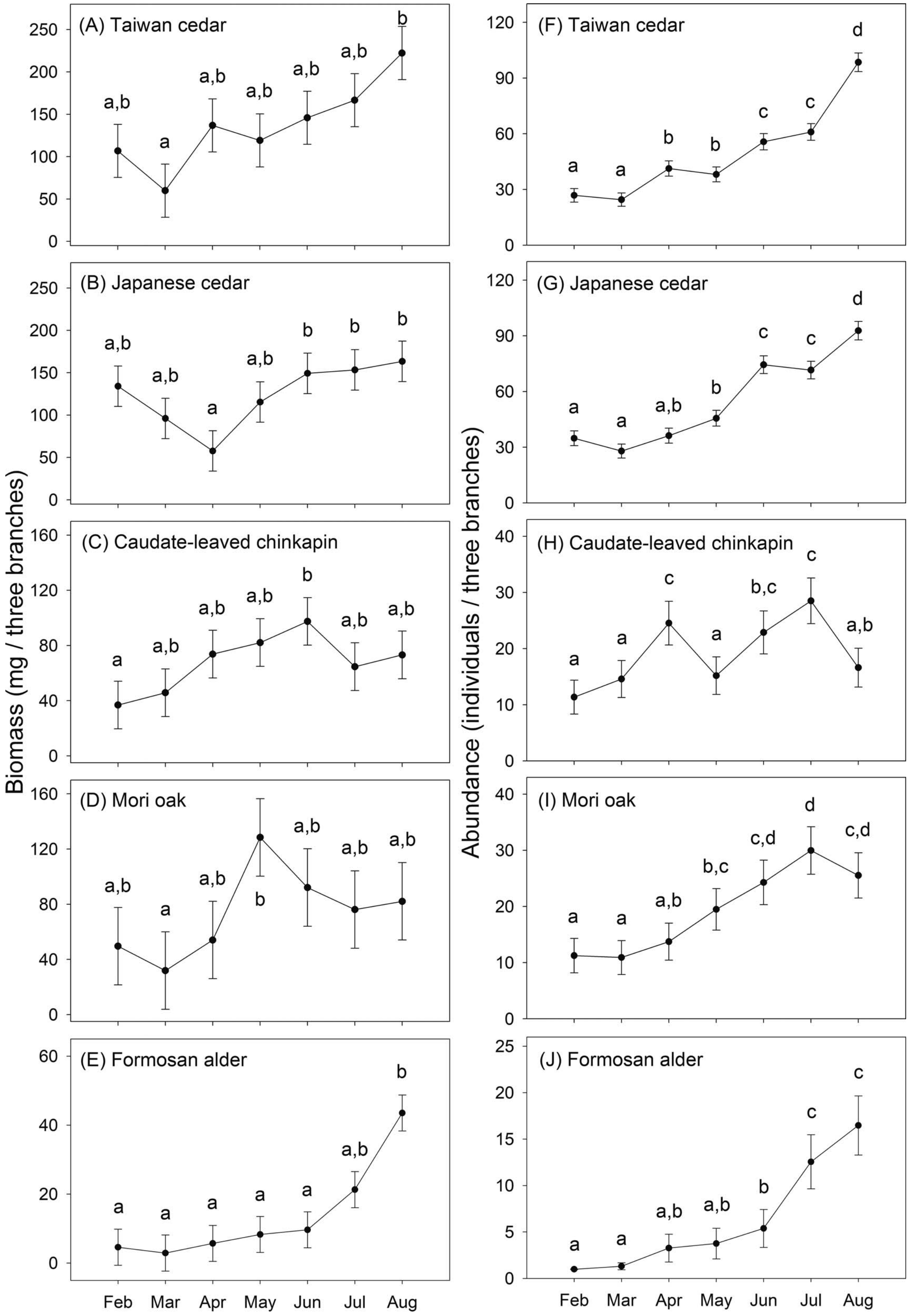

Figure 2.—Seasonal variation in spider biomass (A–E) and abundance (F–J) on five dominant tree species in a mixed-oak forest and a conifer plantation. Different biomass and abundance scales are used for each tree species. Different letters above the error bars represent statistically significant differences (Tukey's post hoc test, $P < 0.05$).

our study (2.54 ± 0.04) was similar to that of the monsoonal tropics of northern Australia (2.54 ± 0.08; Brady & Noske 2006), but different from that of temperate Europe (2.70 ± 0.04, Penell et al. 2018), temperate south-eastern Australia (2.91 ± 0.06; Gowing & Recher 1984), the tropics of central Amazonia (2.98 ± 0.02), and South America (2.87 ± 0.10; Höfer & Ott 2009). Differences in the regression slope between localities presumably reflect differences in body proportions. The lower *b*-value in our study may reflect a tendency for spiders to be relatively narrow bodied or the dominance of certain taxa representing this type in subtropical montane forests.

Our study is the first to characterize differences in spider biomass and abundance between dominant tree species from native forests and those from plantations in a subtropical montane ecosystem. Taiwan cedar and Japanese cedar supported generally higher spider biomass and abundance than broadleaf tree species, which may be explained by their needle-covered branches and high prey availability. Needles on coniferous trees appear to offer spiders high quality habitats, possibly by providing a wider selection of web-attachment sites for web-building spiders to support their webs (Halaj et al. 1998, 2000; Korenko et al. 2011), or a higher needle density, increasing protection against predatory birds (Askenmo et al. 1977) and parasitoids (Gingras et al. 2002). Moreover, dead foliage on the two conifers, usually still attached to the trunks in the lower part of the canopy, accommodates a high abundance of detritivorous micro-arthropods (Hijii 1989) and wandering spiders (Oguri et al. 2014) that prey on them. Higher spider abundance on coniferous trees than on deciduous trees was also observed in previous comparative studies (Halaj et al. 1998; Korenko et al. 2011, Kozlov et al. 2015). Moreover, our study found that spider biomass on the two conifer species declined slightly in early spring, then increased steadily over time, and reached its maximum in August. Similar seasonal increases were also found in spider abundance on the two conifers, consistent with previous findings (Hijii 1989; Oguri et al. 2014) for Japanese cedar, which showed a spider biomass peak from August to September.

Our results show that the phenological patterns of spider biomass may differ from those of spider abundance. Spider biomass on the two evergreen oaks showed bell-shaped curves with relatively high peak biomass in late spring, whereas spider abundance fluctuated in different patterns. In contrast, spider biomass and abundance on deciduous alder showed a similar pattern that remained at a low level from February to June and increased slightly in July and August. Seasonal fluctuation in spider biomass may be related to the dynamics of community composition over time (Hsieh & Linsenmair 2012; Neethling & Haddad 2013), activities of spiders corresponding to ambient temperature and changes in population size and biomass per capita (Turnbull 1960). The latter changes involve the life cycle of each species, including recruitment of spiderlings, maturing of overwintered sub-adults, and mortality of adults after reproduction (Turnbull 1960) of each dominant species. Due to the observational nature of our work, no cause-and-effect conclusions can be drawn. Further work is needed to ascertain community structure of spider assemblages to address the phenological difference between biomass and abundance.

In conclusion, our study demonstrates that use of shape-specific equations and incorporation of body width measurements produce the most accurate biomass estimates. Applying coefficients derived from the best equations, we describe for the first time the seasonal variation in spider biomass on five dominant tree species in mixed-oak forest and conifer plantation. Spider biomass and abundance varied by tree species. Moreover, phenological patterns of spider biomass differed from those of spider abundance on some tree species; therefore, the choice of spider biomass or abundance as an analytical unit needs to be made carefully in ecological studies. Our study provides the regression parameters appropriate for biomass estimation of spider assemblages in subtropical montane forest systems in Taiwan, and possibly in other geographic regions.

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