that determine fire spread success (Weise et al. 2005). The contribution of dead fuel is particularly important for fire spread since the low moisture levels of dead fuel may allow fire to spread through live fuels (Countryman & Dean 1979).

In a broad sense, the total amount of dead fuel increases with time as branches die back due to light limitation (Mahall & Wilson 1986), drought stress (Davis et al. 2002) or pathogens (Riggan et al. 1994), or as entire shrubs die during stand development (Schlesinger et al. 1982; Riggan et al. 1988). However, the proportion of dead fuel is highly variable. Even for a single species and over large areas, stand age is likely not the most important factor in determining the proportion of dead fuel (Paysen & Cohen 1990). Dead remnant stems from the last fire are also an important source of dead fuel. In young stands without high live biomass, these dead remnant stems may represent a high percentage of total biomass (Regelbrugge & Conard 1996). Large remnant stems, when burned, may not contribute greatly to stand ignitability or fire behaviour, but would contribute to overall energy release and some ecological fire effects, such as soil heating.

Since the time scales of biomass accumulation are so long, it is usually impossible to track a single stand through time. Instead, researchers typically take measurements from multiple stands to reconstruct a chronosequence of temporal change in fuel (e.g. Specht 1969; Black 1987). Due to the large areas commonly consumed by wildfires, stands that make up each age group are often composed of heterogeneous vegetation, soil types and terrain characteristics. Also, areas that remain unburned for long periods of time may fundamentally differ in their landscape characteristics from those that frequently burn or have recently burned.

Previous studies have found variability in chaparral biomass at fine spatial scales (Black 1987). Such variability could affect the characteristics of fire, although more data are needed to link fine-scale fire behaviour patterns to the broad scales of interest to fire managers (Hiers et al. 2009). One source of variation is due to the species composition of a given stand. *Adenostoma fasciculatum* (chamise), the most common chaparral shrub in California (Hanes 1971), has been relatively well studied in terms of shrub-scale fuel properties. It has fine, needle-like leaves, with a high proportion of small diameter stems (Countryman & Philpot 1970). It retains dead stems in the canopy, which contributes to increased fire intensity (Schwilk 2003). The percentage of dead biomass is highly variable even in stands of the same age, and might be related to site productivity (Countryman & Philpot 1970; Riggan et al. 1988). *A. fasciculatum* is commonly found on south-facing slopes (Hanes 1971). *Quercus berberidifolia* (scrub oak) is also often present in California chaparral, typically on north-facing slopes (Hanes 1971). It has relatively broad leaves, and accumulates only low levels of standing dead biomass (Riggan et al. 1988). It has a comparatively lower proportion of small diameter stems (Riggan et al. 1988) and is usually taller, with higher fuel volume than *A. fasciculatum* (Green 1970). Regardless of this variation, fuel mapping efforts typically focus on relatively coarse groupings of fuel types rather than species-specific measurements (Arroyo et al. 2008). In addition to specific fuel mapping projects, fire managers have information such as previous fire perimeters, vegetation type and fire threat readily available for the entire state of California from the Fire and Resource Assessment Program (http://frap.fire.ca.gov/, accessed 10 Jul 2015).

The objective of this study is to measure the fine-scale changes in fuel properties that occur over long time periods as southern California chaparral ages. Understanding how fuel properties such as total and dead biomass and their spatial arrangement across the landscape change with age has the potential to improve fire modelling and inform fuel management policies.

We address the following research questions using detailed measurements of chaparral field plots and high-resolution species group mapping: (1) how do stand-level biomass and percentage of dead material vary as a function of stand age; and (2) how do the landscape properties of aggregation index and patch size vary in each of the dominant species groups as a function of stand age?

Methods

Study site

The site for this study is located near Kitchen Creek Road on southern Laguna Mountain in San Diego County, CA, US (Fig. 1). Chaparral there experiences a typical mediterranean-type climate with hot, dry summers and cool, wet winters. The soils are classified as being in the Bancas series, which are fine loamy, mixed, mesic and mollic haploxeralfs derived from quartz diorite and mica schist (http://websoilsurvey.nrcs.usda.gov/, accessed 19 Dec 2014). Average annual precipitation is 66 $cm \cdot yr^{-1}$ (http://www.prism.oregonstate.edu/, accessed 4 Apr 2014). *Adenostoma fasciculatum*, a facultative seeder and *Quercus berberidifolia*, an obligate resprouter, are dominant species on the site, although *Arctostaphylos glandulosa* and *Ceanothus perplexans* (formerly *Ceanothus greggii* var. *perplexans*) are also commonly found. The general study location has previously served as the field site for a study of chaparral community development (Riggan et al. 1988).

The entire study area burned in 1944. Three strips were burned as part of an experimental burn in 1979, then additional areas were burned in the early 1980s, creating one burned area approximately 300 m north of another

Doi: 10.1111/avsc.12209

included. The Af/Ag class included the species *A. fasciculatum* and *A. glandulosa*. We treated these species as a separate class since they featured a lower biomass per area than the other shrub species. The sub-shrub category was mostly composed of *Salvia apiana,* but also included small amounts of *Trichostema lanatum*, *Keckiella ternata*, *Hazardia squarrosa* and *Eriogonum fasciculatum.* The bare category was mostly composed of granite outcroppings in the 28- and 68-yr-old areas, and a combination of granite outcroppings and bare ground in the 7-yr-old area. The dead category included only shrubs that were entirely dead. Dead biomass attached to living shrubs was included within the appropriate species group. We were unable to classify dead cover in the 7-yr-old area due to the relatively coarse resolution of the imagery and small quantity of dead material in this area. We collected calibration/validation samples from 1 m × 1 m plots in the Kitchen Creek study area (68- and 28-yr-old vegetation) along the trail using the Trimble GeoXM GPS unit. Eighteen of the plots were used to train the classifier, and 42 were used for validation.

We used eCognition, an object-based image analysis (OBIA) software package, for image-based classification of vegetation types (eCognition Developer 8.9, http://www.ecognition.com/). OBIA segments an image into groups of adjacent pixels (objects) and then assigns these objects to the categories of the classification scheme based on a set of user-defined rules. We used an iterative segmentation/classification approach, re-segmenting several times to create objects of the appropriate size for the class of interest. A multi-resolution segmentation algorithm with scale parameters of 10 and 15 was implemented, as well as the chessboard segmentation algorithm with object sizes of 1 and 10. The multi-resolution segmentation algorithm works by iteratively merging adjacent pixels based on criteria of spectral and shape homogeneity, and the scale parameter modifies the size of the final image objects. The chessboard segmentation algorithm simply divides the image into equally sized square objects. After each round of segmentation, we used properties such as texture, brightness, colour, adjacency and NDVI to classify the objects in the class of interest, then merged the unclassified objects so they could be re-segmented with appropriate parameters for the next class of interest. Although we made minor manual corrections to the vegetation type maps in the primary study area, the accuracy assessment was based on the uncorrected classification results.

Landscape analysis

Vegetation cover percentages of each field plot were extracted from the image classification product. We calculated biomass per m^2 using biomass measured in the field and species category cover taken from imagery classification. We used the average biomass per m^2 of the two plots from each age and species category with the highest field measured biomass for a given species category. Since the plots were composed of a mixture of species, samples of some plots were not representative of the species category of interest. In order to reduce the error associated with these plots, we based our calculation on only the plots in which the species category of interest was abundant. In order to provide a more cautious estimate of biomass, we also calculated the average biomass per m^2 for the combined 68- and 28-yr-old areas. We did not include the 7-yr-old area in this calculation because these values were much lower than those found in the older burn areas.

There were not enough areas of sub-shrub in the 68-yr-old plots to calculate an average, so the values for these plots were estimated from the 28-yr-old plots. Dead biomass per area values fluctuate so widely that it was not possible to calculate realistic values with the procedure used for the rest of the species groups. We simply used a value of 2 kg·m^{-2} to approximate dead vegetation. This approximation is based on half the value calculated for the combined 68- and 28-yr-old Af/Ag coefficient.

We selected six 60 m × 60 m study areas within each age class for a total of 18 large study areas. We selected this size because it was the largest area that would fit in the burn perimeters of the 7-yr-old area. We clustered the study areas into three northern and three southern study areas, each separated by at least 200 m (Fig. 1). The aspect of the 60 m × 60 m study areas, based on a 10 m spatial resolution digital elevation model, is shown in Appendix S1. In each of these study areas, we randomly selected five 8 m × 8 m plots for a total of 30 plots per burn age (90 plots total).

The landscape properties of aggregation index and patch size were derived from vegetation-class patches from the 18 large study areas using the software program Fragstats (v 4.1, http://www.umass.edu/landeco/research/fragstats/fragstats.html). The aggregation index is calculated by dividing the cell adjacencies of a given class by the total number of possible cell adjacencies for that class. It is given as a percentage, such that a given class clumped in a single, compact patch would have a value near 100. Patch size for each species group was calculated using the area-weighted patch mean size, in which each patch is weighted by its proportional area representation. We also examined species composition by calculating the percentage cover of each species group. Since the vegetation map of the 7-yr-old age class was produced using 0.5 m imagery, we reduced the resolution of the 68- and 28-yr-old age classes (originally 4 cm) to match this lower resolution of 50 cm. In order to more closely examine the differences in the 68- and 28-yr-old age classes, we also calculated the same met-

area present in each plot. We made every effort to sample shrubs from the full range of basal area values found in the field plots, but it was not always possible to locate large enough shrubs for the destructive sampling. A maximum of 4% (and usually much less) of all stems in the field plots were so large as to require an extrapolation of the regression equation to estimate biomass.

Biomass measurements from the field survey ranged from 7.5 kg·m^{-2} in one of the oldest plots to 1.1 kg·m^{-2} in one of the youngest plots (Appendix S3). The highest biomass values were found in the 68-yr-old stand, particularly in plots dominated by *Q. berberidifolia*. Despite these much higher values in the oldest plots, there was considerable overlap in the total biomass values in the 68- and 28-yr-old plots. Total biomass values were much lower in the 7-yr-old plots, as expected. Charred stems were found only occasionally in the older areas, but were abundant in the 7-yr-old area. Charred stem biomass ranged from about one-third to nearly equivalent to the amount of post-fire growth in these plots, although the regression relationship for calculating charred stem biomass exhibited a high degree of scatter, meaning that actual values of charred biomass may vary substantially from what we estimated.

The percentage of dead biomass varied substantially, but was generally higher in *A. fasciculatum* than other species, and overall much lower in the 7-yr-old area. Since partially dead stems were categorized as 'live' if green leaves were still present, these values represent the lower bound of percentage dead biomass. Biomass from entirely dead shrubs was also highly variable and almost completely absent in the 7-yr-old area.

The image classification product of species groups was assessed to have an overall accuracy of 71% (Table 1), based on reference data from the 1 m × 1 m field-based validation sample plots. Accuracy was higher in the more abundant categories of broad-leaf and Af/Ag, and particularly low in the dead biomass category.

Estimated biomass per area ranged from 6.2 kg·m^{-2} in the oldest age class of broad-leaf vegetation to 0.4 kg·m^{-2} in the youngest age class of sub-shrub vegetation (Table 2). The biomass per area coefficients provided a good approximation of the two major categories of shrub species (Af/Ag and broad-leaf) and of overall biomass (Fig. 4a–c). The predicted Af/Ag biomass values based on the mapped cover tended to yield a closer agreement with the field-measured plot biomass values, while the broad-leaf and the combined total calculations were more variable.

We found a significant difference in mean biomass in the three age classes when using age-specific biomass coefficients ($F_{2,87}$ = 326, P < 0.001), and the post-hoc Tukey test revealed that all three means were significantly different (Table 3, Fig. 5). The calculated biomass values showed a clear trend of accumulation through time (Fig. 5). However, the differences between age classes were not as clear when using the biomass values calculated using pooled coefficients (average of 28- and 68-yr-old areas). Although the overall ANOVA was significant ($F_{2,87}$ = 243, P < 0.001), the post-hoc Tukey test revealed that the 28- and 68-yr-old areas were not significantly different (Table 3, Fig. 5). An overall trend of increasing biomass through time was evident, but when using these pooled coefficients, the difference between the 68- and 28-yr-old areas was not significant (Fig. 5). Both the results from the age-specific and pooled coefficients revealed a

Table 2. Above-ground biomass per unit area based on classification.

Veg type	Age class	kg·m^{-2}
Broad-leaf	68	6.2
Broad-leaf	28	4.2
Broad-leaf	7	2.4
Broad-leaf	68/28	5.2
Af/Ag	68	4.3
Af/Ag	28	3.6
Af/Ag	7	1.4
Af/Ag	68/28	4
Sub-shrub	68/28	1.5
Sub-shrub	7	0.4

Table 1. Error matrix from field-based accuracy assessment of the classified high spatial resolution map.

	Field classification							
		Af/Ag	Bare	Broad-leaf	Dead	Sub-shrub	Total	User accuracy
Remote sensing classification	Af/Ag	10	1	4	0	0	15	0.67
	Bare	0	2	0	0	1	3	0.67
	Broad-leaf	3	0	17	2	0	22	0.77
	Dead	1	0	0	0	0	1	0.00
	Sub-shrub	0	0	0	0	1	1	1.00
	Total	14	3	21	2	2	42	
	Producer accuracy	0.71	0.67	0.81	0.00	0.50		Overall accuracy 0.71

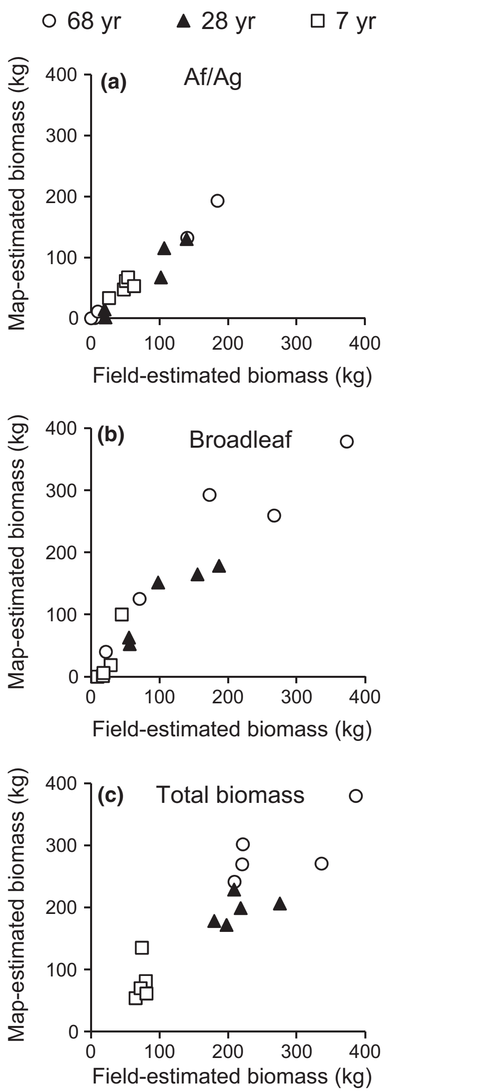

Fig. 4. Field-estimated biomass vs biomass estimated using age-specific biomass coefficients in each field plot for (**a**) Af/Ag, (**b**) broad-leaf, and (**c**) total biomass. The dotted line is the 1:1 line.

Table 3. Mean, range and ANOVA results for stand-level biomass comparisons using age-specific and pooled biomass coefficients. *df* = 2,87, *n* = 30

	7 yr	28 yr	68 yr	*F*	*P*
Age-specific					
Mean (kg·m^{-2})	1.3	3.4	5.1	326	<0.001
range	0.5–2.2	1.6–4.0	3.8–6.0		
Pooled					
Mean (kg·m^{-2})	1.3	4.0	4.4	243	<0.001
range	0.5–2.2	1.9–4.9	3.5–5.1		

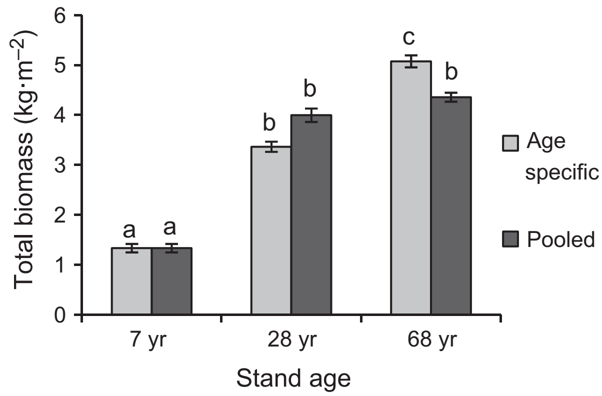

Fig. 5. Total biomass means using age-specific biomass coefficients and pooled biomass coefficients. Error bars indicate SE and letters indicate post-hoc Tukey tests. Bars with different letters are significantly different ($P < 0.05$)

wide range in biomass values for each stand age calculated for the 30 sampling plots (Table 3).

Landscape properties

The general trend of average percentage cover in the 60 m × 60 m study areas within each burn area indicates that broad-leaf percentage cover was higher in the older areas, sub-shrub cover was lower, and bare was not different (Fig. 6). Af/Ag cover was higher in the 28- than 7-yr-old area, and was similar in the 28- and 68-yr-old areas. However, closer inspection of the associated ANOVA results indicated that while there was a significant cover difference among several of the vegetation classes in each age class (e.g. broad-leaf, $F_{2,15} = 10.2$, $P = 0.0016$), post-hoc Tukey tests revealed that only the youngest age class was significantly different from the two older age classes (Table 4, Fig. 7a). The post-hoc Tukey tests showed the same pattern for the Af/Ag category and in the sub-shrub category, only the youngest and oldest age classes were significantly different (Fig. 7a).

In general across stand ages, the aggregation index (landscape pattern metric) is higher (more aggregated) in the broad-leaf and Af/Ag classes, and lower (more dispersed) for the sub-shrub and bare categories. Within the three age classes, only in the Af/Ag and sub-shrub categories are there significant differences in aggregation index with age (Af/Ag $F_{2,15} = 6.8$, $P = 0.0079$, sub-shrub $F_{2,15} = 6.9$, $P = 0.0077$; Table 4). Post-hoc Tukey tests show that in the Af/Ag category, only the 7- and 28-yr-old age classes are significantly different from one another, and in the sub-shrub category, only the 7- and 68-yr-old age classes are significantly different (Fig. 7b).

Area-weighted patch mean area is higher for the older age classes in the broad-leaf category, with only the differ-

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Doi: 10.1111/avsc.12209

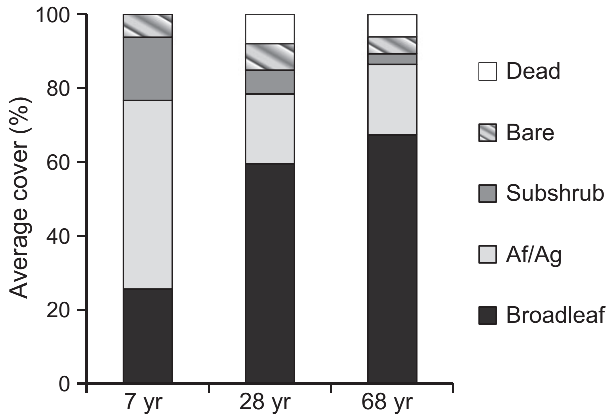

Fig. 6. Average percentage cover in the three age classes. Note that dead cover could not be estimated in the 7-yr-old age class.

ence between the youngest and oldest age class being significant ($F_{2,15}$ = 8.0, P = 0.0042; Table 4). Patch mean area was lower in the youngest age class in the Af/Ag category, and the youngest area is significantly different than the two older areas ($F_{2,15}$ = 15.8, P = 0.0002; Fig. 7c).

The series of *t*-tests of landscape metrics generated from the higher resolution (4 cm) classified imagery comparing the two older age classes indicate that the only significantly different classification/landscape metric combination is percentage cover of sub-shrub, which is higher for the 28-yr-old area (*df* = 9.561, P = 0.009; Table 5).

Discussion

Stand-level biomass

We could not make statistical inferences regarding the overall stand composition based on the field data. This was due to the sampling of plots that represented the range of variability found in our study area rather than random plots. We instead presented general observations about the species composition and overall biomass present in the field plots. For this reason, we did not present averages or estimates of error associated with plot biomass values.

We found a high degree of variability in biomass in the study area due to species composition and stand age. Older stands had higher levels of biomass per area, and coefficients of the tall, dense species that make up the broad-leaf category were highest, followed by the more sparse Af/Ag category species, and finally by the much smaller sub-shrub species category. The regression equations calculated in this study were similar to those calculated in a previous study of the same area for the corresponding species and age (Riggan et al. 1988). The resulting biomass per area values were higher for each age than found by Riggan et al. (1988), but similar to those found in other studies within southern California (Black 1987; Riggan et al. 1988). Although the exact biomass per area coefficient values is not necessarily applicable to areas outside of this field site, these values provide valuable field data to more accurately map and estimate stand-level biomass across the study area. The high spatial resolution of the mapping effort allowed non-shrub cover (such as large rock outcrops) to be efficiently removed from the estimates of biomass per area. This means that caution must be used when applying the biomass coefficients from this study to mapping efforts based on lower resolution imagery, in which rock outcrops might not be reliably separated from shrub cover. Field-based biomass sampling is often too time consuming and logistically difficult to be conducted over large study areas (Lu 2006). Using remotely sensed imagery allows for biomass estimation over of much larger areas in an efficient manner. Our approach of using high spatial resolution imagery with object-based methods is reasonably successful for mapping fine-scale variation in species composition. Considering all the potential sources of error and uncertainty due to geolocation accuracy, field measurement error and other possible sources, it is promising

Table 4. ANOVA results for class metrics for the classified standardized resolution (0.5 m) data set. Bold *P*-values indicate significant results ($P \leq 0.01$). *df* = 2,15, *n* = 6.

Class	Metric	Mean 7-yr-old	Mean 28-yr-old	Mean 68-yr-old	*F*	*P*
Broad-leaf	Aggregation	83	86	89	3.0	0.0816
Af/Ag	Aggregation	81	65	70	6.8	**0.0079**
Sub-shrub	Aggregation	53	39	31	6.9	**0.0077**
Bare	Aggregation	44	63	53	3.8	0.0477
Broad-leaf	% of landscape	26	60	67	10.2	**0.0016**
Af/Ag	% of landscape	51	19	19	13.9	**0.0004**
Sub-shrub	% of landscape	17	6	3	6.7	**0.0083**
Bare	% of landscape	6	7	5	0.9	0.4315
Broad-leaf	Mean patch area (m^2)	321	1514	2155	8.0	**0.0042**
Af/Ag	Mean patch area (m^2)	1293	173	127	15.8	**0.0002**
Sub-shrub	Mean patch area (m^2)	79	5	3	4.1	0.0378
Bare	Mean patch area (m^2)	6	20	10	1.8	0.2059

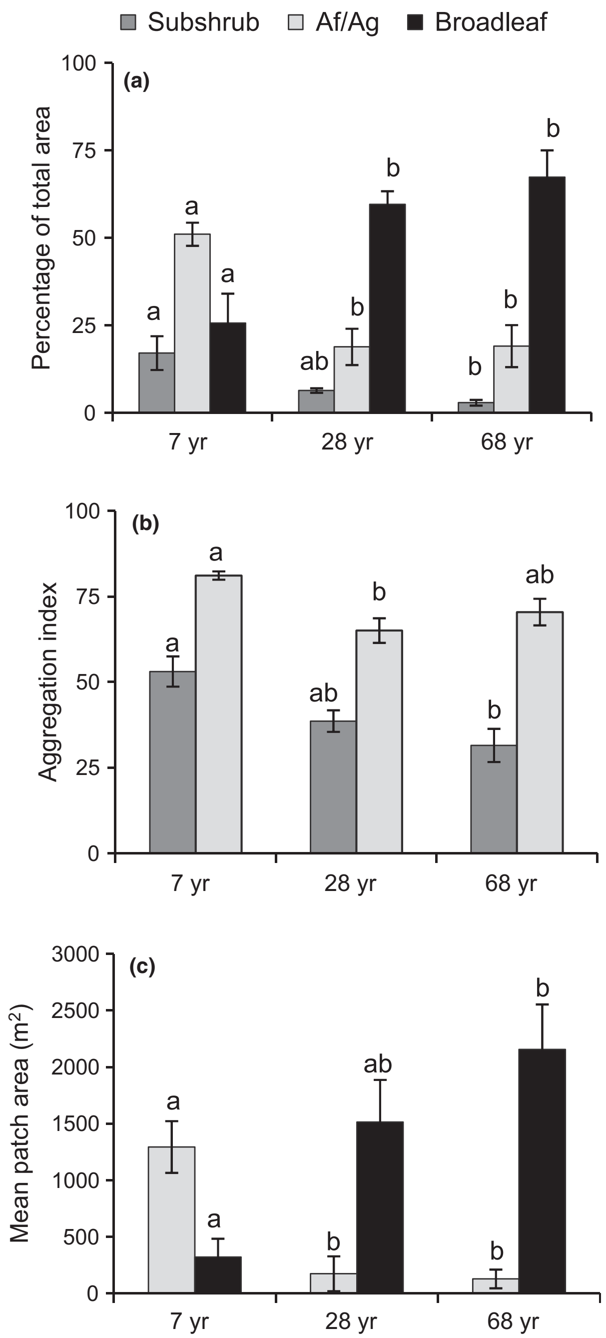

Fig. 7. (**a**–**c**) Mean and SE of significantly different age classes for the: (**a**) percentage of total area for sub-shrub, Af/Ag and broad-leaf categories, (**b**) aggregation index for Af/Ag and broad-leaf categories, and (**c**) mean patch area for Af/Ag and broad-leaf categories from the standardized resolution (0.5 m) data set. Letters indicate post-hoc Tukey comparisons. Bars with different letters are significantly different ($P \leq 0.05$).

that coefficients based on just two plots per stand age and species category yield such close agreement between field-estimated and map-estimated biomass. Mapping success at the species category level (and by extension, biomass) could likely be further improved by using high spatial resolution colour infrared imagery.

It is more challenging to derive reliable maps of dead biomass based on image-based classification. This is partly due to the tendency of dead biomass to be located beneath plant canopies composed mostly of live biomass, either as dead stems within a single shrub or as an entirely dead shrub surrounded by live shrubs. This means that although dead biomass is often spread uniformly throughout stands of chaparral, it is only occasionally visible from above (which would allow it to be measured through aerial imagery). These small patches of dead biomass are not representative of the total dead biomass found in an area and make it more difficult to derive a relationship for biomass per unit area.

We calculated stand-level biomass in two ways to provide a more cautious estimate for the older sites. While results for the age-specific coefficients show a substantially higher biomass for the 68-yr-old areas, the results from the pooled coefficients indicate that the difference is not statistically significant. It is possible that if the 68-yr-old area had substantially more broad-leaf cover than the 28-yr-old area, the broad-leaf coefficient (higher than the Af/Ag coefficient in both the age-specific and pooled calculations) might have resulted in a higher biomass value in both calculations. However, it appears that differences are not that dramatic. Regardless of whether biomass continues to accumulate, it is clear that biomass levels remained high in the oldest stand of chaparral, consistent with the findings of previous studies (Specht 1969; Black 1987). Unsurprisingly, there was a large difference in biomass between the 7-yr-old and 28-yr-old stands. Shrub growth is rapid during this early phase of post-fire recovery and shrubs quickly expand in both cover and stature (Rundel & Parsons 1979; Keeley & Keeley 1981). While there were site differences between the 7-yr-old site and the older sites, the measurements of biomass per unit area for each species were based on areas in which each species is dominant.

Although it is still uncertain whether or not biomass continues to appreciably accumulate at older stand ages, the high number of plots examined through the scaling approach revealed a wide range of biomass values within a single age class. It is noteworthy that biomass varied so widely at the plot level (8 m × 8 m) within a relatively constrained spatial extent in an even-aged stand. This fine-scale spatial variation is typically difficult to map and might be important in understanding fire behaviour (Keane et al. 2001).

The scaling approach used in this study is based on two separate relationships, which has advantages and disadvantages. The final biomass values depend on both the stem-to-biomass regression relationship and the field-measured biomass-to-mapped cover category relationship. The

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Doi: 10.1111/avsc.12209