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# Can fire atlas data improve species distribution model projections?

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**Abstract.** Correlative species distribution models (SDMs) are widely used in studies of climate change impacts, yet are often criticized for failing to incorporate disturbance processes that can influence species distributions. Here we use two temporally independent data sets of vascular plant distributions, climate data, and fire atlas data to examine the influence of disturbance history on SDM projection accuracy through time in the mountain ranges of California, USA. We used hierarchical partitioning to examine the influence of fire occurrence on the distribution of 144 vascular plant species and built a suite of SDMs to examine how the inclusion of fire-related predictors (fire occurrence and departure from historical fire return intervals) affects SDM projection accuracy. Fire occurrence provided the least explanatory power among predictor variables for predicting species' distributions, but provided improved explanatory power for species whose regeneration is tied closely to fire. A measure of the departure from historic fire return interval had greater explanatory power for calibrating modern SDMs than fire occurrence. This variable did not improve internal model accuracy for most species, although it did provide marginal improvement to models for species adapted to high-frequency fire regimes. Fire occurrence and fire return interval departure were strongly related to the climatic covariates used in SDM development, suggesting that improvements in model accuracy may not be expected due to limited additional explanatory power. Our results suggest that the inclusion of coarse-scale measures of disturbance in SDMs may not be necessary to predict species distributions under climate change, particularly for disturbance processes that are largely mediated by climate.

*Key words:* California, USA; climate change; disturbance; fire; fire return interval; niche; species distribution model; transferability; vascular plant species.

## INTRODUCTION

Understanding the factors that determine biogeographic patterns has been a central tenet of ecological studies for decades (Grinnell 1917). Although early efforts to describe the relationships between species distributions and environmental factors were largely qualitative, ecologists today employ a wide variety of techniques for evaluating and describing these patterns (Elith and Leathwick 2009). In recent decades, species distribution models (SDMs) have become widely implemented for the study and description of biogeographic patterns. These models use observed species occurrences and spatially explicit environmental data to build probabilistic models of suitable habitat across the landscape (Austin 2002). Today these models are widely applied to a variety of topics, including invasive species biology (Urban et al. 2007), conservation planning (Araújo et al. 2011), and tests of ecological theory (Broennimann et al. 2007). However, perhaps the most common application of SDMs is in predicting the effects

of climate change on species distributions (Thuiller 2004). As the availability of species distribution and climate data continues to increase, it is likely that these models will continue to be widely used in ecological studies.

Although commonly used among ecologists, SDMs are also the subject of some criticism (Hampe 2004). This criticism focuses primarily on the failure of correlative SDMs to account for dynamic processes such as dispersal, biotic interactions, or disturbance (Austin 2002, Pearson and Dawson 2003, Hampe 2004). Because the results of SDMs are often used to guide conservation planning or climate change mitigation efforts, it is not surprising that substantial efforts have been made to understand the factors affecting SDM performance (Araújo and Luoto 2007, Thuiller et al. 2008). Yet despite these criticisms, SDMs are still considered to be an appropriate tool for many ecological studies (Pearson and Dawson 2003). For example, SDMs have been used to identify previously undiscovered locations for rare species (Williams et al. 2009), to understand the dynamics of biological invasions (Broennimann et al. 2007), and to aid in conservation planning efforts (Wilson et al. 2005). Thus it is clear that SDMs have great potential for applied ecological investigations

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and that additional research into factors affecting their performance is warranted.

One criticism that could limit the predictive accuracy of SDMs, and one whose effects have rarely been investigated, is that they typically fail to incorporate disturbance processes that can strongly influence biogeographic patterns (Austin 2002). It has been suggested that disturbance can disrupt the relationship between species occurrence and environmental factors (Cassini 2011) and that accounting for such processes is critical for the field of conservation biogeography (Franklin 2010). Fire is one such disturbance that is often strongly related to the spatial patterns of vascular plants on the landscape (Franklin et al. 2004). In systems where fire represents the dominant natural disturbance process, such as in many of the mountain ranges of California, fire differentially affects the survival and recruitment of individual species, with some succumbing to fire-induced mortality while others require the occurrence of fire to facilitate germination (Hickman 1993). Fire occurrence has also been linked to patterns of vegetation community shifts in portions of California (Callaway and Davis 1993), further indicating its influence on plant communities. There is abundant indirect evidence from studies in regions with mediterranean climates, such as California, to suggest that metrics of fire regimes could influence SDM predictions. For example, previous studies have shown that species-specific adaptation to fire is strongly related to SDM accuracy when using internally validated (i.e., within a single time period) or temporally independent data (Syphard and Franklin 2010, Dobrowski et al. 2011b). Similarly, simulations of potential vegetation indicate that fire occurrence strongly influences broadscale vegetation distribution and structure in mediterranean climates and across the globe (Bond et al. 2003, 2005). However, in one of the few studies to empirically assess the influence of fire-related covariates on SDMs, Tucker et al. (2012) found that the inclusion of fire-related covariates in SDMs provided relatively little additional explanatory power for species occurrence in plant communities in South Africa, a mediterranean climate region with strong ecological and evolutionary impacts of fire.

Metrics of fire occurrence may act as proxies of successional trajectories and thus prove useful in predicting species distributions across the landscape. However, a potential confounding factor when considering the occurrence of fire as a covariate in SDMs is that in many regions, the current fire regime differs substantially from the historical fire regime. In regions with altered fire regimes, contemporary occurrence of fire is likely not representative of the long-term fire conditions under which local species evolved. This means that, especially for species with distributions tightly coupled to historical patterns in fire occurrence, current fire regimes may overlap only the periphery of, or be entirely beyond, the fundamental niche of these species (i.e., Hutchinson's [1957] "*n*-dimensional hyper-

volume"). This issue may be exacerbated by the use of observational data, which rely on models of the realized niche. Because SDMs assume that species are at equilibrium with their environments, such departures from long-term disturbance dynamics may strain the ability of SDMs to account for disturbance processes. These departures in fire regime can be the result of change in climatic factors influencing fire occurrence and/or changes in anthropogenic influences on the fire regime, toward either longer or shorter return intervals (Whitlock et al. 2003), yet it is largely unknown as to how these departures may affect SDMs. For example, California has experienced large changes in fire regime, including ignition rates, fire frequency, and area burned, resulting from anthropogenic activities (Syphard et al. 2007). Thus in some systems, it is reasonable to assume that incorporating departure from historical fire regimes into SDMs may prove more useful than incorporating contemporary fire occurrence.

Despite previous research efforts and the extensive literature debating the utility of correlative SDMs, to date no studies have addressed the following basic question: Does including covariates describing disturbance patterns improve SDM projections under climate change? No work has been done to address this question directly, and what little related work has been done using empirical data has focused on a single time period, making inferences related to future climate projections impossible. Previous studies investigating species' response to fire have provided ancillary evidence to suggest that the inclusion of fire as a predictor in SDM development could improve projections (Dobrowski et al. 2011b), but a direct assessment of this is still lacking. Thus we have little information on how the inclusion of fire-related covariates influences SDM projections through time. We would expect that the inclusion of fire occurrence would provide additional power to identify occurrences of species that require fire for germination. Conversely, for species that are maladapted to fire we might expect the inclusion of fire occurrence as a covariate to improve our ability to identify absences, as fire may lead to mortality for such species. Thus our objectives are to (1) quantify the relative influence of fire occurrence as a covariate in climatic envelope models of vascular plant distributions, (2) quantify the relative influence of a measure of departure from long-term fire frequency as a covariate, and (3) determine if the inclusion of either variable as an additional covariate improves the projection accuracy of SDMs through time.

## METHODS

### *Study area*

Our study area encompasses the entire state of California, although the majority of our data comes from the mountainous regions of the state (Fig. 1). This area is characterized by less anthropogenic land use than other parts of the state, such as the agriculturally

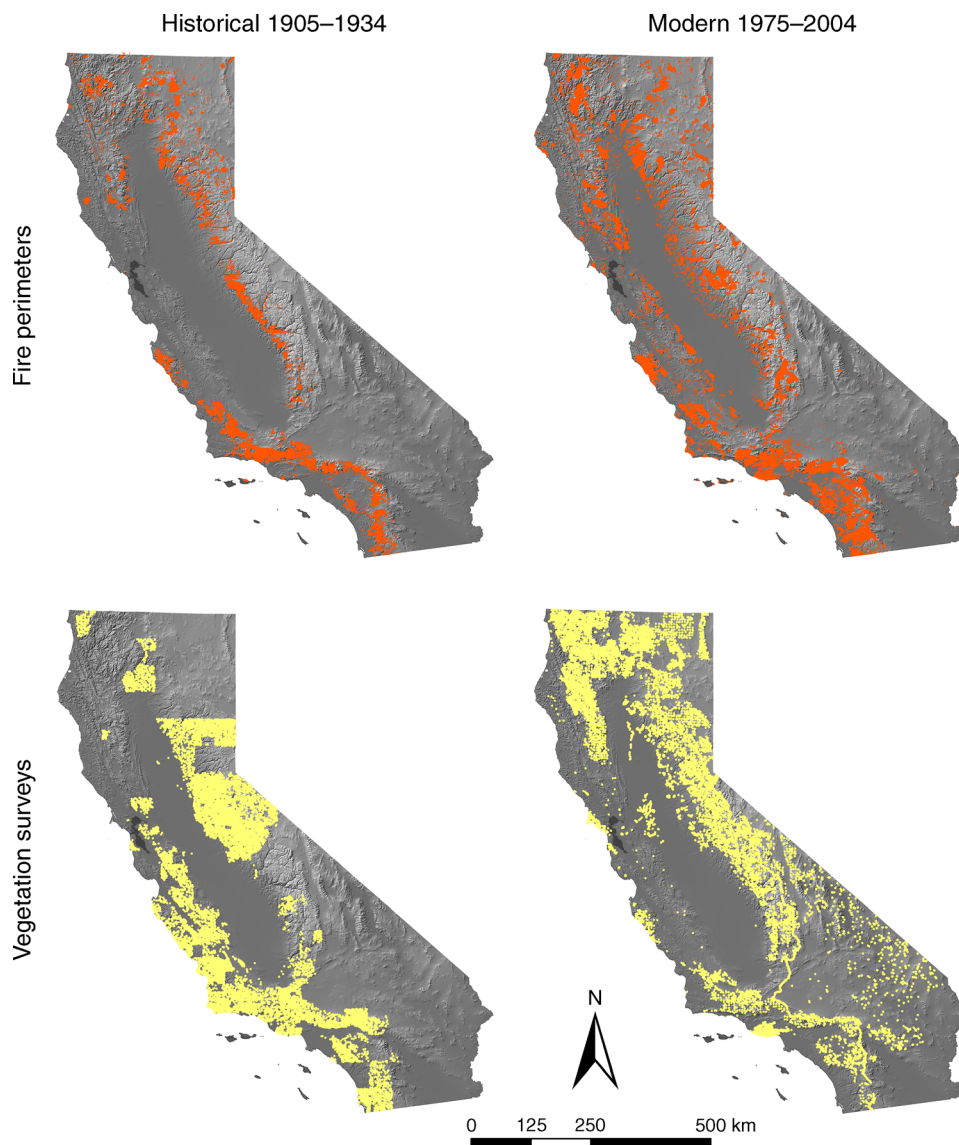


FIG. 1. Map of study area in California, USA, showing fire perimeters (orange) and vegetation survey locations (yellow) from historical (1905–1934) and modern (1975–2004) time periods.

dominated central valley. This region has experienced substantial and spatially variable changes in climate and hydrology and contains major elevational, latitudinal, and longitudinal gradients (Crimmins et al. 2011, Dobrowski et al. 2011a). The region has been identified as a global biodiversity hotspot, and predicting the effects of climate change on the region's endemic flora is of great conservation concern (Loarie et al. 2008). There is evidence to suggest that species distributions within this region have shifted as a result of recent climate change (Tingley et al. 2009, Crimmins et al. 2011). Additionally, fire represents arguably the most important natural disturbance process to plant species in this region (Fig. 1), with more than 65 000 km<sup>2</sup> burned (including areas with multiple fires) in the state during

our two primary study periods. Vegetation communities in California have adapted to vastly different fire regimes, with lower montane forests adapted to high-frequency but low-intensity fires while many chaparral communities are adapted to lower frequency, high-intensity fires (Sugihara et al. 2006, Safford and Van de Water 2013). Additionally, both fire suppression and increased human ignitions have greatly altered the current fire regimes across most of the state, resulting in divergent patterns of change in fire return intervals (Safford and Van de Water 2013).

#### *Species data*

We used two temporally independent data sets of vascular plant species distributions from our study area

to develop and test species distribution models (SDMs), both of which were statewide in coverage. The first data set is a collection of ~14 000 survey locations collected in the 1930s as part of the U.S. Forest Service's Vegetation Type Map (VTM) Project (Wieslander 1935a, b). VTM plots were 800 m<sup>2</sup> in size, and plot locations have been digitized and georeferenced with an accuracy of ±200 m (Kelly et al. 2005). The second data set represented ~33 000 survey locations compiled from a variety of sources that have been collected since 2000. Further details about these inventories are provided in Crimmins et al. (2011) and Dobrowski et al. (2011b). Hereafter we refer to these as "historical" and "modern" data. For both data sets, survey locations were included only if they were far enough apart to occur in different climate grid cells. We extracted species presence-absence data from both data sets for a suite of tree and shrub species that were sufficiently represented (≥30 occurrences) in each data set. This left us with 144 species for which we were able to build and evaluate SDMs. The number of occurrences per species averaged 402 (range 30–3044) in our historical data and 1161 (range 37–10 940) in our modern data.

We categorized species by their adaptation to fire, the primary natural disturbance agent in our study area. We used published studies of species' ecology and expert opinion to assign each species to one of three adaptation levels: (1) fire evaders, (2) fire resisters, and (3) fire endurers and avoiders (Agee 1998; we refer to group 3 as "avoiders" throughout). Fire evaders are species that exhibit regeneration syndromes that are thought to have evolved in response to fire, including fire obligate seeding and serotiny; these are mostly species adapted to high-intensity fire regimes, where the adult plant is often killed. Fire resisters are species that tend to survive fire through adaptations conferring resistance to low- or moderate-intensity fires, such as thick bark or self-pruning of lower branches; resisters do not possess specialized regeneration syndromes tied to fire, and they tend to be rare or absent in areas characterized by high-intensity fires. Fire endurers are resprouting species whose aboveground parts are usually killed by moderate- or high-intensity fire; the ability to resprout is considered a generalized adaptation to a variety of disturbances that remove or consume aboveground biomass (Bond and van Wilgen 1996). Fire avoiders are species without any adaptations to fire or similar disturbances; these species are rare in mediterranean climate regions like California. In the fire evader group, we included species that exhibit both fire-stimulated germination and postfire resprouting ("facultative" species), and in the resisters group we included fire-resistant species that sprout (e.g., *Quercus* spp.) or not (e.g., *Pinus* spp.).

#### *Climate and fire data*

We developed a suite of four climatic predictor variables that we hypothesized would exhibit direct

influence on species distributions. We used 800-m resolution climate data from two time periods representing ~30-year time frames prior to vegetation data collection (1906–1935, 1976–2005). We used two climatic variables from the Parameter-elevation Regression on Independent Slopes Model (PRISM; Daly et al. 2008) data set, maximum temperature and minimum temperature. We also used two hydrologic variables that have been shown both theoretically and empirically to affect vascular plant distributions: actual evapotranspiration and annual climatic water deficit (Stephenson 1990, 1998). These variables were estimated at a monthly time-step and then summed within each year and averaged across the 30-year periods to represent average annual conditions for the entire time period. The hydrologic variables were developed using a modified climatic water balance model (Lutz et al. 2010) that accounts for atmospheric demand, snowmelt, and soil moisture storage on a monthly time step. Climate and hydrologic variables were available at a nationwide level and clipped to our study region. For additional information on hydrologic data see Dobrowski et al. (2013). Fire perimeters were acquired from the California Department of Forestry and Fire Protection's Fire and Resource Assessment Program (FRAP; *available online*).<sup>5</sup> This database contains mapped fire perimeters for most fires >0.04 km<sup>2</sup> dating back to 1878 within the entire state of California. The database is not comprehensive, as it does not include most small fires or many on private lands. However, because most of our vegetation survey locations were from publicly owned lands, and because there are few examples of more accurate or comprehensive fire atlas data available, we felt the use of these data were justified. For each vegetation survey location, we determined if a fire perimeter from the same 30-year time periods used in our climate summaries overlapped the survey location. We also tabulated the total number of fire occurrences at each sampling location during the 30-year time periods and used this value as a covariate in SDMs. However, these results did not differ from those when including simple binary occurrence of fire (Appendix A). To evaluate the effects of departure from historical fire regime on SDMs, we used a recently developed data set on the departure in fire return interval between the 20th-century and pre-European settlement conditions for all national forests in California (Safford and Van de Water 2013; U.S. Forest Service, Pacific Southwest Region; *available online*).<sup>6</sup> These data cover the 18 U.S. Forest Service (USFS) National Forests in California and all adjacent lands and quantify the extent, in percent, to which contemporary fires (since 1908) are burning at frequencies similar to those prior to European settlement. These data range from –100 to 100, with negative values representing current return intervals that are

<sup>5</sup> <http://frap.cdf.ca.gov>

<sup>6</sup> <http://www.fs.fed.us/r5/rs/clearinghouse/r5gis/frid/>

shorter than presettlement intervals, and positive values representing intervals that are longer than presettlement intervals (Appendix C; see Safford and Van de Water [2013] for more details). This represented our only source of data that was not statewide in extent. From these data we extracted the percent departure in mean fire return interval (FRID) for all modern survey locations that occurred on USFS and adjacent lands. Because these data did not cover the entire state of California, analyses based on FRID were conducted using a subset ( $n = 116$ ) of the 144 species for which we had sufficient occurrence data within the area covered by the FRID maps.

#### *Hierarchical partitioning*

We evaluated the influence of covariates, including fire, on explained deviance in species distributions using hierarchical partitioning (Chevan and Sutherland 1991). Hierarchical partitioning is an approach that quantifies the contribution of a given explanatory variable to the explanation of a dependent variable, in our case species presence or absence. Importantly, it allows for the contribution to be partitioned into the component that is shared jointly with other explanatory variables and the individual component that is unique to that predictor. The independent contribution of the variable is calculated by quantifying the effect of the variable in all possible models that can be constructed from the entire set of explanatory variables, while the joint contribution is that contribution that is shared among explanatory variables. We conducted hierarchical partitioning using the *hier.part* package in the R programming language (R Development Core Team 2011). We used generalized linear models (GLMs) with a binomial distribution and calculated the contribution of each explanatory variable to goodness-of-fit, using log-likelihoods as our measure of fit. We modeled each species separately in each of the two time periods when including fire occurrence as a covariate and in the modern time period when including FRID. We compared explanatory power for each variable between time periods using  $z$  tests.

#### *Species distribution models*

Although our hierarchical partitioning allows us to decompose the influence of individual covariates on measures of model fit, it does little to describe how incorporation of new covariates affects actual prediction accuracy of SDMs. Because we sought to explore the influence of fire on various classes of SDMs, we used a suite of different model algorithms to build our predictive models. First, we developed GLMs of species presence-absence using logistic regression. We used an all-subsets stepwise variable selection procedure based on minimization of Akaike's information criterion (AIC) scores (Burnham and Anderson 2002). Using this procedure, each variable could be dropped or fit as a linear, second-order, or third-order polynomial. Second,

we developed generalized additive models (GAMs) as an example of a semiparametric regression approach (Hastie and Tibshirani 1990). We again used a stepwise variable selection procedure based on AIC scores where each variable could be dropped, fit as a linear term, or fit as a cubic spline with three degrees of freedom. Third, we developed boosted regression trees as an example of a relatively new machine-learning approach (De'ath 2007). Boosted regression tree models were built using 2000 trees with a shrinkage parameter of 0.01, a 0.5 bag fraction, and an interaction depth of 3 (Elith et al. 2008). We derived out-of-bag estimates of the optimal number of boosting iterations, which we then used to predict probability of occurrence. Finally, we developed random forest models as another example from the machine-learning community (Breiman 2001, Cutler et al. 2007). Random forest models were developed using independent bootstrap samples to grow 750 trees for each species (Cutler et al. 2007). For each species, the probability of occurrence was determined as the proportion of presence votes from the 750 trees. We built one set of models using only our four climatic variables, and one set of models that also included fire occurrence or FRID as a predictor in addition to climatic variables. We developed models using 75% of the historical data and tested the models on the remaining 25% of the historical data and all of the modern data. We refer to results from tests using the withheld 25% of the historical data as internal evaluations, and results using data from the modern time frame as independent evaluations. Because of the temporal scale of our FRID data, we were not able to develop models in the historical time period using these data and thus could not evaluate their effects on model projections across time (i.e., independent evaluations). However, we were able to evaluate the influence of FRID on internal evaluations in our modern data using a randomly selected 75% of the modern data to build models and testing it on the remaining 25%. Because these data did not cover our entire study area, we were able to conduct these evaluations only for a subset ( $n = 116$ ) of our overall group of species.

We evaluated SDMs using multiple criteria. First, we used the area under the receiver operating characteristic curve (AUC) as a threshold independent measure of SDM accuracy (Fielding and Bell 1997). Area under the curve is a commonly used metric for describing SDM accuracy (Elith et al. 2006) because it avoids the somewhat arbitrary issue of choosing a prediction threshold. However, it has been suggested that AUC may be a misleading measure of SDM accuracy (Lobo et al. 2008). Therefore, we also chose to use binary classifications of species presence or absence and confusion matrices to assess model accuracy. We used the sensitivity-specificity equality approach to select our prediction thresholds (Cantor et al. 1999). This approach places equal weight on sensitivity (proportion of occurrences correctly classified) and specificity (propor-

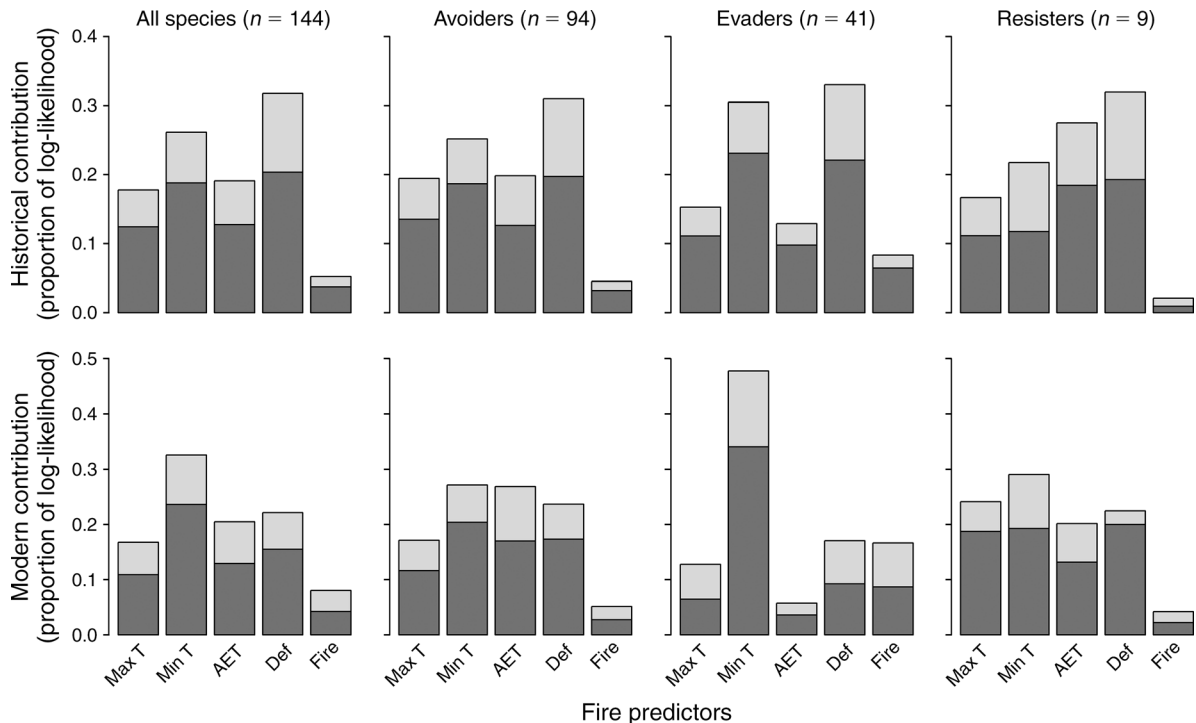


FIG. 2. Stacked bar plots of joint (light gray) and individual (dark gray) contributions (proportion of total log-likelihood) of predictors from hierarchical partitioning. Models were calibrated with historical (1905–1934) and modern (1975–2004) data for all species and within fire adaptation groups. Fire category represents binary fire occurrence. Avoiders are species with no adaptations to fire, evaders are species adapted to high-intensity fire regimes, and resisters are species that survive fires but exhibit no specialized regeneration strategy. All species are vascular plants. Abbreviations are as follows: Max T, maximum temperature; Min T, minimum temperature; AET, actual evapotranspiration; Def, climatic water deficit; Fire, binary fire occurrence.

tion of absences correctly classified) and performs well when compared to other commonly used threshold selection criteria (Liu et al. 2005). We converted our predicted probabilities of occurrence into binary presence-absence predictions for each species at each sampling location and assigned each prediction one of the four possible entries into a confusion matrix. We expressed false-positive (FP; errors of commission) and false-negative (FN; errors of omission) error rates as the proportion of true absences or presences that were incorrectly classified. These correspond to 1 minus sensitivity and 1 minus specificity for FP and FN, respectively. We quantified the effect of fire on SDM projection accuracy by calculating the change in each accuracy metric (AUC, FP rate, FN rate) when going from a model without fire as a predictor to one including fire as a predictor using both internal and external model evaluations. Because previous research has indicated that species' response to fire can influence SDM projection accuracy (Dobrowski et al. 2011b), we summarized results from hierarchical partitioning and SDM evaluations within each of the three fire response groups. We compared accuracy metrics between models with and without fire occurrence or FRID using paired *t* tests.

## RESULTS

### *Hierarchical partitioning*

In general, the occurrence of fire provided little explanatory power relative to the climatic variables used in species distribution models (SDMs). When examined across all 144 species, the joint and individual contributions of fire occurrence to the log-likelihood were the lowest of all explanatory variables, a pattern that was evident regardless of time period (Fig. 2). The individual explanatory power of fire occurrence was similar between time periods ( $P = 0.99$ ), in each case accounting for <6% of the total variation explained by the model. The patterns in explanatory power among other predictors differed between time periods but were consistently greater than fire (Fig. 2). Patterns of explanatory power differed when examined within individual fire adaptation groups. For fire avoiders and resisters, fire occurrence yielded the least explanatory power in either time period (Fig. 2). For fire evaders, the occurrence of fire provided the least explanatory power in the historical time period, but the third strongest in the modern time period, surpassing the explanatory power of actual evapotranspiration and maximum temperature (Fig. 2). For all fire adaptation groups in both time periods, the individual contribution of fire occurrence amounted to <10% of the total

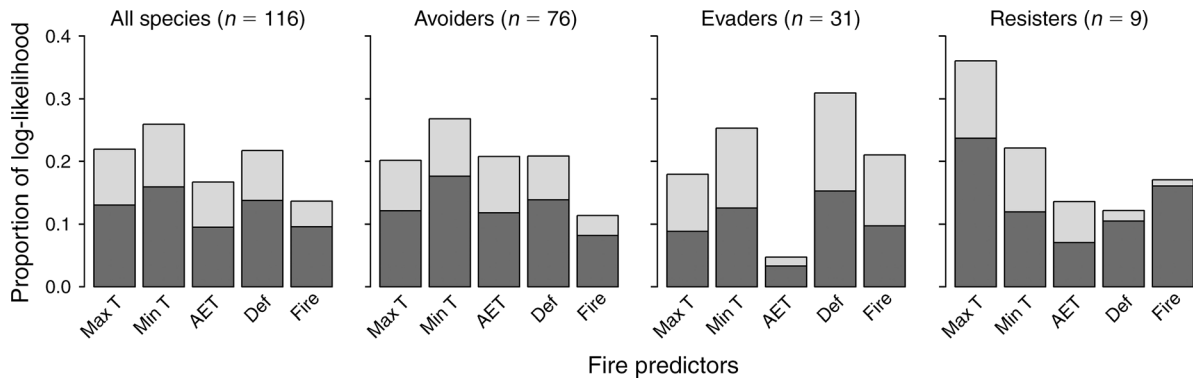


FIG. 3. Stacked bar plots of joint (light gray) and individual (dark gray) contributions (proportion of total log-likelihood) of predictors from hierarchical partitioning. Models were calibrated with modern (1975–2004) data from national forest lands in California for a subset of species with sufficient data. Fire category represents fire return interval departure (FRID). Abbreviations are as follows: Max T, maximum temperature; Min T, minimum temperature; AET, actual evapotranspiration; Def, climatic water deficit; Fire, fire return interval departure (FRID).

explanatory power. Patterns of explanatory power for other variables differed between time periods within each of the fire adaptation groups, with temperature-related variables showing a general increase in predictive power while hydrologic variables showed a general decrease (Fig. 2).

Compared to fire occurrence, fire interval departure did offer additional explanatory power, with an individual contribution to the total explained variability of ~10% when examined across all species. However, as with fire occurrence, this was the lowest among all predictors (Fig. 3). Patterns of explanatory power for the avoiders and evaders groups were similar to those found when using fire occurrence, with the explanatory power of departure in mean fire return interval (FRID) exceeding that of AET and maximum temperature for the evaders while retaining the lowest explanatory power among the avoiders. For the resisters, FRID yielded the second highest individual contribution to total model likelihood, explaining ~16% of the total variation in species occurrence.

*Species distribution model accuracy*

Our models that excluded fire occurrence performed well when evaluated internally, with an average area

under the curve (AUC) of 0.91 across all five model algorithms (Table 1). When validated with contemporary data, average AUC of models excluding fire occurrence dropped to 0.80. The random forest model exhibited the largest decrease in AUC when projected into the modern time period (Table 1). False-positive (FP) and false-negative (FN) error rates both increased when SDMs were projected into the future, with FP rates increasing to a larger degree than FN rates (Table 1).

Because our results were qualitatively similar across SDM algorithms (Appendix B), hereafter we present results only from our generalized additive models unless otherwise noted. When evaluated internally, models including fire occurrence yielded small but nonsignificant ( $P > 0.1$ ) increases in overall model accuracy compared to models excluding fire across all 144 species (Table 1). Changes in accuracy metrics varied among model algorithms but in each case were not significant (Table 1). When evaluated with temporally independent data, the inclusion of fire occurrence in SDMs had no discernible effects on model accuracy, with no significant changes in any accuracy metric when examined across all 144 species (Table 1). When examined within fire adaptation categories, the inclusion of fire generally did

TABLE 1. Accuracy statistics for 144 species distribution models with and without fire occurrence as a predictor variable.

Model	Fire not included						Fire included as binary predictor					
	Internal evaluation			External evaluation			Internal evaluation			External evaluation		
	AUC	FP	FN	AUC	FP	FN	AUC	FP	FN	AUC	FP	FN
GLM	0.888	0.176	0.209	0.829	0.383	0.210	0.891	0.171	0.209	0.826	0.377	0.214
GAM	0.895	0.172	0.199	0.834	0.279	0.268	0.898	0.167	0.197	0.830	0.318	0.237
BRT	0.925	0.202	0.174	0.803	0.284	0.349	0.926	0.186	0.175	0.804	0.284	0.347
RF	0.975	0.209	0.056	0.781	0.536	0.152	0.975	0.181	0.056	0.788	0.493	0.168
CT	0.877	0.298	0.162	0.742	0.439	0.230	0.878	0.302	0.168	0.742	0.444	0.223

Note: Abbreviations are: AUC, area under curve; FP, false-positive error rate; FN, false-negative error rate; GLM, general linear model; GAM, generalized additive model; BRT, boosted regression tree; RF, random forest; CT, classification tree.



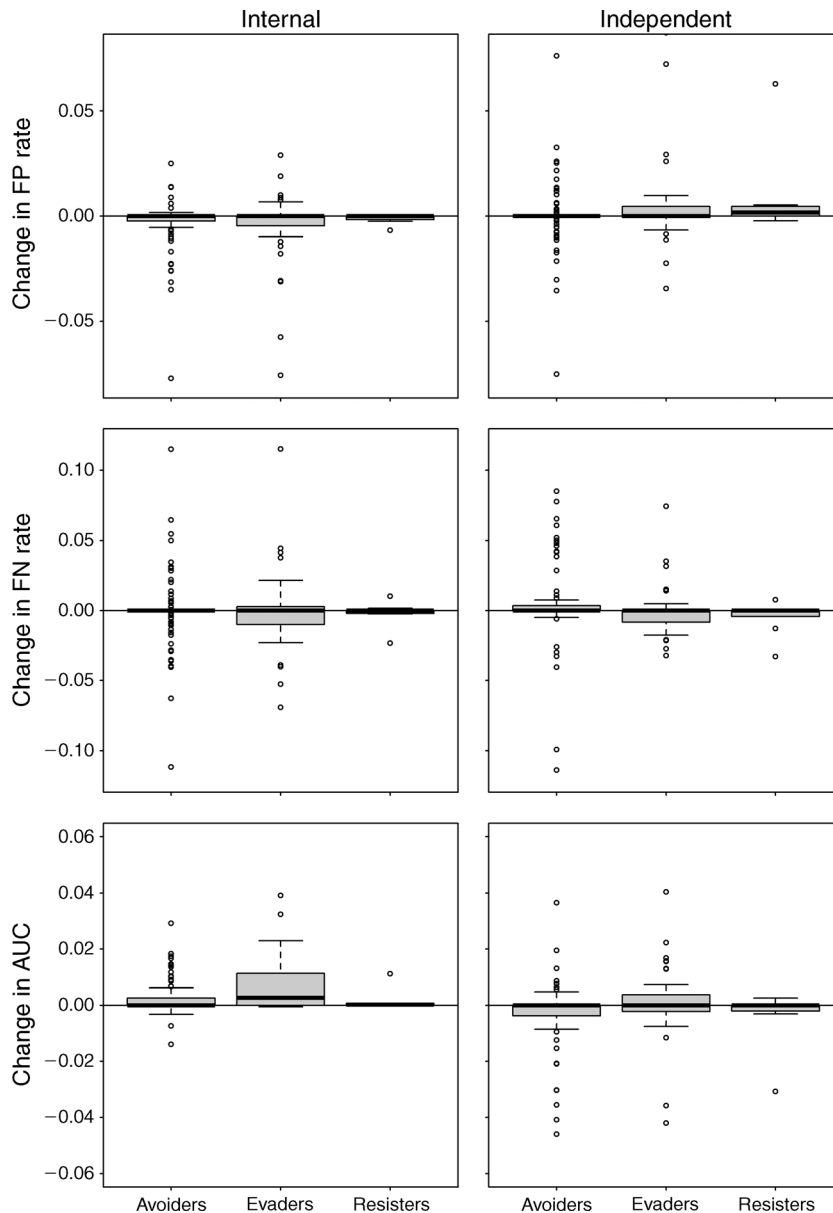


FIG. 4. Change in species distribution model (SDM) accuracy metrics from internal ( $t_1$  models against  $t_1$  data) and independent ( $t_1$  models against  $t_2$  data) evaluations within fire response groups when adding fire occurrence as a binary predictor variable in a generalized linear model (GLM). Results were similar across SDM algorithms (Appendix B). The black line in the box represents the mean, the box width represents inner quartile range, whiskers extend 1.5 times the inner quartile range from the mean, and outlying points represent individual species occurring outside the bounds of the whiskers. Abbreviations are: FP, false-positive error rate; FN, false-negative error rate; AUC, area under curve.

not improve any metric of projection accuracy (Fig. 4). The lone exception was AUC for the evaders group, which exhibited a small ( $\sim 0.01$ ) but significant ( $P < 0.01$ ) increase. When evaluated against temporally independent data, the inclusion of fire occurrence yielded no discernible changes in any accuracy metric within any of the fire adaptation groups (Fig. 4). The inclusion of FRID yielded no discernible changes in any accuracy metric within any of the fire adaptation groups (Fig. 5).

## DISCUSSION

Disturbance-related variables are typically absent from species distribution models (SDMs), a point that has been highlighted in critical evaluations of SDMs (Austin 2002). Although SDMs are often criticized for this lack of disturbance processes, empirical evaluations of the effects of failing to include disturbance history on model accuracy are rare. We conducted our study in a region with a dominant natural disturbance process

(fire) that is generally thought to exert a strong influence on plant distributions (Keeley and Fotheringham 2001). Because of this we hypothesized that fire occurrence would be an important predictor of species distributions and that its inclusion would improve SDM projection accuracy. Contrary to our expectations, we found that fire occurrence yielded very little additional explanatory power relative to climatic variables and generally did not improve model accuracy. We had also hypothesized that using a metric of departure from presettlement fire return interval as a covariate in our models might yield additional explanatory power compared to observed fire occurrence. Our hierarchical partitioning results confirmed this hypothesis, with a combined individual and joint contribution to total explanatory power nearly double that of fire occurrence (15% compared to 8%). However, this increase in explanatory contribution had little effect on metrics of model accuracy. For fire evaders, species for which the explanatory power of fire occurrence and departure in mean fire return interval (FRID) exceeded that of some climatic metrics, inclusion of these disturbance variables yielded small improvements ( $\sim 0.01$  increase in area under the curve [AUC]) in model projection accuracy. Thus for species for which we have evidence to suggest that disturbance regimes influence distributions, we were unable to improve our predictions by accounting for disturbance.

In a related study, Tucker et al. (2012) found that variables related to fire regime yielded little explanatory power. Their study was conducted in the Cape Floristic Region of South Africa, an area with similar climatic patterns and evolutionary forces as much of our study area, which may help explain the similarity in our results. Tucker et al. (2012) found that the influence of fire-related variables on SDMs was not related to species' adaptation to fire, which they attributed to limited statistical power due to a small number of species included in their analysis ( $n=27$ ). Our results are similar to those of Tucker et al. (2012) in that we generally found that fire occurrence yielded little explanatory power. Although the improvement in model accuracy for fire evaders was not statistically significant, the pattern does match what we would expect for species that are dependent upon fire for regeneration and is consistent with the results of Syphard and Franklin (2010), who found that species with pyrogenic seeding had higher SDM accuracy than other species in southern California. This suggests that SDMs for such species may benefit from the inclusion of alternative fire regime metrics not included in our study (Tucker et al. 2012). Interestingly, nearly all species studied by Tucker et al. (2012) were sclerophyllous shrubs typical of fynbos, a region dominated by species adapted to high-frequency fire regimes (i.e., fire evaders). Our suite of species represented a much greater breadth of life forms, suggesting that the overall lack of effect that we observed may be present across numerous vegetation communities. Despite coming from a single study

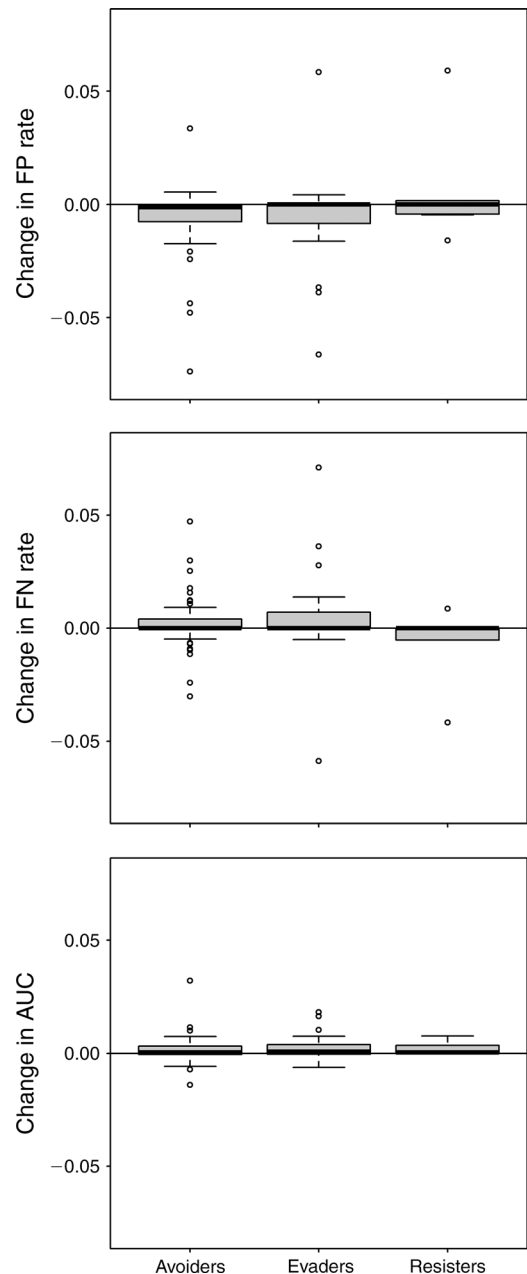


FIG. 5. Change in SDM accuracy metrics from internal ( $l_2$  models against  $l_2$  data) evaluations for a subset of species within fire response groups when adding FRID as a predictor variable in a GLM. Results were similar across SDM algorithms (Appendix B). Abbreviations and boxplot components are as in Fig. 4.

region, the fact that our study area comprises several climatic/disturbance regimes also suggests that our results may be applicable to other regions.

An explanation for the general lack of influence of fire occurrence on species distributions is that the occurrence of fire itself is not independent of climate. Wildfire regimes are largely determined by climatic factors

(Westerling et al. 2003), which likely limit their predictive power in our models. For example, using the same climatic variables as in our SDMs to build logistic models (general linear models) of fire occurrence at the vegetation survey locations yields an AUC value of  $>0.78$  in both time periods, suggesting that the occurrence of fires in our study area was largely determined by the climatic parameters used in our SDMs. This is not entirely surprising, as previous research has documented the strong influence of long-term climate on the relative probability of fire occurrence in the western United States (Parisien et al. 2012). Similarly, climatic models of FRID yielded relatively high levels of predictive power ( $r^2 = 0.5$ ) as well. Even though FRID is driven primarily by fire suppression efforts, the success of these efforts is dependent to a great extent on variables related to weather and climate, such as drought, fuel moisture, temperature, precipitation, and wind patterns (Miller et al. 2012). The fact that FRID generally yielded greater explanatory power than fire occurrence is likely the result of departures from environmental equilibrium. Such departures from equilibrium would more readily be captured by our FRID data than short-term occurrence of fire. It is entirely possible that other disturbance processes unrelated to long-term climate may prove useful for SDM studies, however our results suggest that, particularly for relatively short-term projections ( $\sim 80$  years), climatologically mediated disturbance processes may be of limited utility in improving SDM projections.

Although fire was prevalent in our study area, with 15.6% and 17.6% of our historical and modern plots having at least one fire occurrence during our 30-year time frames, respectively, our data come from a time period in which both fire suppression and human-caused fire ignitions were widespread. Thus the fire regimes represented in our data do not represent the natural, long-term fire regimes that developed in the region prior to large-scale anthropogenic alterations of the system and the fire regime under which many of these species have adapted. This effect of human influence on fire regimes is largely captured with our FRID data, which motivated our use of these data in addition to our fire atlas data. Because of this, it is not entirely surprising that including contemporary fire occurrence data in our models had little effect on their accuracy, particularly given the limited time frame over which fire occurrence was measured (30 years). Given that both large-scale fire suppression and increased human ignitions are likely to continue in the near future, our results are very pertinent to short-term predictions of future species distributions. The lack of influence of FRID on SDM accuracy, despite its increased contribution to explained variation, may be an artifact of the relatively short time frame (30 years) used in our analysis. Fire regimes, and species adaptations to them, have developed over evolutionary time scales. Thus altered fire regimes may have a strong influence on species distribution, but at a time scale

greater than that of our study. Paleoecological studies may prove informative for understanding the long-term influence of altered disturbance regimes on species distributions (Svenning et al. 2011). Other metrics related to fire regime, such as time since last fire, may prove more informative than the metrics used here.

Another issue to consider regarding the inclusion of disturbance-related covariates in SDMs is that of large-scale distributional patterns vs. small-scale occupancy dynamics. Although we found that disturbance had little effect on broadscale species distributions in this study, as evidenced by similarities in model accuracy and in spatial patterns of predicted probability of occurrence (Appendix D), disturbance may be important when considering temporal changes in site-level occupancy patterns. For example, propagules of fire-evading species dispersing into previously unoccupied habitat cannot generally germinate in the absence of a fire event, regardless of climatic suitability. Thus the actual occurrence of a fire at a specific site can serve as the mechanism determining whether or not a site is occupied by a particular species, for example by resetting the succession process, despite the site being climatically "suitable" habitat. This dynamic would be very important at range margins, where transient metapopulation dynamics that are poorly represented by correlative SDMs may exhibit stronger influence on site-level occupancy dynamics than long-term climatic conditions. Thus it is important to consider issues of both temporal and spatial scale when developing SDMs using disturbance-related covariates. For instance, we were not able to differentiate between plots that had burned 30 years prior to sampling or two years prior. If a fire occurred at a plot near the beginning of our 30-year window, this would allow ample time for regeneration of any species that were killed by fire. Thus the timing of vegetation sampling relative to that of fire occurrence may have substantial consequences for understanding site-level occupancy dynamics, further emphasizing the need for additional studies focused on the effects of alternative fire regime metrics. Our results, when using the count of the total number of fires during our 30-year time frames (results not shown), did not differ from those when using binary fire occurrence, suggesting that our analysis is likely robust to this issue. Hybrid modeling approaches that incorporate climate envelope models with dynamic models (e.g., Anderson et al. 2009, Conlisk et al. 2013) may be more appropriate for incorporating dynamic disturbance processes into predictions of species distribution under climate change, as would explicit consideration of other metrics related to disturbance regimes. Additionally, explicit consideration of spatial nonstationarity in the relationship between species occurrence and fire regimes should also be considered, as small-scale alterations to fire regimes may have direct effects on species distributions at localized scales.

The motivation behind including disturbance-related variables in SDMs is that they represent dynamic

processes that can directly affect the survival and reproduction of organisms, whereas many long-term climatic factors commonly used in SDMs (e.g., mean annual temperature) do not. An important yet overlooked caveat to this discussion is that it presumes that patterns of disturbance, both spatially and temporally, carry information that is independent of the climate factors used in SDM development. It is nearly impossible to argue that fire does not have a direct influence on plant distributions through its differential effects on mortality and regeneration. Yet in some situations, SDMs that do not include variables related to disturbance yield accurate predictions of species distributions (see Table 1). Although our study area has historically been dominated by fire as a disturbance, the inclusion of fire-related predictors yielded no discernible improvement on SDM performance. Because the disturbance process of interest in our system is largely governed by the same climatic parameters used in SDM development, it may be unnecessary to include it in modeling broadscale species distributional patterns. For other disturbance processes that are not related to climate, the decision of whether to include them in SDMs will depend upon a variety of factors, including the availability of spatially explicit disturbance data and the accuracy of future projections of disturbance regimes.

There are several practical limitations to including disturbance processes into SDMs used for conservation planning. First, it requires a detailed knowledge of the life history requirements of the species of interest in order to properly incorporate the disturbance process into the model (Franklin 2010). For example, it has been suggested that fire occurrence in fire-dominated systems is more likely to affect demographic patterns and abundances of vascular plants than their broadscale distribution patterns (Tucker et al. 2012). Many species that require the occurrence of fire for germination also have life spans longer than the interval between our two study periods. For these species, it seems reasonable to assume that areas that frequently burn may support higher densities, but that because of their longevity, these species can occur in many areas that have not experienced recent fire activity. This also relates to the issue of detectability, as many of these species can lay dormant in seed banks for extended periods of time until fire occurrence promotes germination. Second, it requires spatially explicit estimates of the disturbance process and ideally, projections of the disturbance into the future. For many disturbance processes such data are difficult to attain, and projections of disturbance processes into the future carry large uncertainty in their predictions and are inherently difficult to validate (Flannigan et al. 2009, Moritz et al. 2012). In the absence of such data, it has been suggested that modeling demographic ratios rather than simple occurrences in nonequilibrium environments can accurately capture the effects of disturbance by separating its

differential effects on survival and recruitment (Cassini 2011). However, this approach requires information that is typically unavailable in most data sets. Obviously, the inclusion of anthropogenic disturbance processes will be critical for building accurate SDMs in regions with a rapidly expanding human footprint. However, our results indicate that in certain situations, SDMs that do not include disturbance processes can yield accurate projections of species distributions under climate change.

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## SUPPLEMENTAL MATERIAL

### Appendix A

Hierarchical partitioning and species distribution model (SDM) accuracy results when considering number of fires as an ordinal predictor ([Ecological Archives A024-061-A1](#)).

### Appendix B

Change in model accuracy metrics for alternative SDM algorithms ([Ecological Archives A024-061-A2](#)).

### Appendix C

Twentieth-century fire return interval departure on public lands in California, USA ([Ecological Archives A024-061-A3](#)).

### Appendix D

Predicted probability of occurrence maps in historical and modern time periods for models with and without fire occurrence for three example species ([Ecological Archives A024-061-A4](#)).