

**Title:** Estimating the extinction date of the thylacine accounting for unconfirmed sightings

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## 1 **Summary**

2  
3 The thylacine, or Tasmanian tiger, was one of Australia’s most characteristic megafauna, and  
4 was the largest marsupial carnivore until hunting, and potentially disease, drove them to  
5 extinction in 1936<sup>1-3</sup>. Current knowledge suggests the thylacine became extinct on mainland  
6 Australia two millennia prior to its eradication on Tasmania, but recent “plausible” sightings on  
7 the Cape York Peninsula have emerged, leading some to speculate the species may have escaped  
8 extinction mostly undetected<sup>4</sup>. Here we show that sighting evidence indicates the continued  
9 survival of the thylacine would be entirely implausible based on current mathematical theories of  
10 extinction. We present a sightings dataset including physical evidence, expert-validated  
11 sightings, and unconfirmed sightings leading up to the present day, and use a Bayesian  
12 framework that takes all three types of data into account, by modelling them as independent  
13 processes, to evaluate the likelihood of the thylacine’s persistence<sup>5</sup>. Although the last captive  
14 thylacine died in 1936, our model suggests the most likely extinction date would be 1940, or at  
15 the latest the 1950s. We validated this result by analysing our dataset with other frequently used  
16 extinction estimator methods, all of which confirm that the thylacine’s extinction likely fell  
17 within the interval of 1936-1943. Even the most optimistic scenario suggests the species did not  
18 persist beyond the 1960s. The search for the thylacine, much like similar efforts to “rediscover”  
19 the Ivory-Billed Woodpecker and other recently extinct charismatic species<sup>6</sup>, is likely to be  
20 fruitless—especially given that persistence on Tasmania would have been no guarantee the  
21 species could reappear in regions that had been unoccupied for centuries. The search for the  
22 Tasmanian tiger may become a rallying point for conservation and wildlife biology in the  
23 coming years, and could indirectly help fund and support critical research in understudied areas  
24 like Cape York<sup>7</sup>. However, our results suggest that attempts to rediscover the thylacine will  
25 likely be unsuccessful.

## 26 **Estimating the extinction date of the thylacine accounting for unconfirmed sightings**

27  
28 The history of conservation biology has included a few exceptional errors, in which experts have  
29 pronounced a species extinct only to be later disproven by its reappearance. Perhaps most  
30 famous are “Lazarus” taxa known originally from the fossil record, like the coelacanth  
31 (*Latimeria* sp.) or the dawn redwood (*Metasequoia* sp.); but recent extinctions can also  
32 sometimes be overturned, like that of the Bermuda petrel (*Pterodroma cahow*). Just this year, the  
33 rarest dog in the world, the New Guinea highland wild dog (*Canis lupus dingo*), was  
34 rediscovered after an absence beginning in 1976 (with at least two unconfirmed sightings  
35 including unconfirmed evidence in the interim). Hope of rediscovering an “extinct” species can  
36 inspire volumes of peer-reviewed research, and sometimes a single controversial sighting<sup>6</sup> can be  
37 enough to reignite controversy and justify seemingly-endless field investigation, as in the  
38 ongoing search for the Ivory-Billed Woodpecker (*Campephilus principalis*) despite all odds.<sup>8</sup> In  
39 Queensland, a similar story is beginning, as two recent unconfirmed sightings have inspired a  
40 new search for the thylacine (*Thylacinus cynocephalus*).

41  
42 The thylacine, also frequently called the Tasmanian tiger or marsupial wolf, has been presumed  
43 extinct since the last captive specimen died on September 7, 1936.<sup>1</sup> Thylacines are believed to  
44 have gone extinct on the Australian mainland roughly two millennia ago, persisting as  
45 Tasmanian island endemics<sup>9</sup>. State-sponsored eradication in Tasmania began in 1886 and  
46 continued until 1909, driving a devastating population crash.<sup>1</sup> Theoretical models indicate that  
47 the eradication campaign, in combination with prey declines, could have been sufficient  
48 extinction pressure<sup>2</sup>; but other research strongly suggests a disease similar to canine distemper  
49 could have helped drive the species to extinction<sup>3,10</sup>. While its mechanism has been a topic of  
50 speculation, the status of the thylacine’s extinction has been essentially unchallenged in peer-  
51 reviewed literature. However, sightings have continued until as recently as late 2016 throughout  
52 Tasmania and mainland Australia, often gathering international media attention. Recently, two  
53 unconfirmed “detailed and plausible” sightings in the Cape York Peninsula of northern  
54 Queensland have sparked renewed interest in the thylacine’s persistence, particularly in the  
55 Australian mainland; researchers currently intend to investigate those sightings with a camera  
56 trap study beginning in Cape York later this year.<sup>4</sup>

57  
58 Is there empirical support for this most recent search? Extinction date ( $\tau_E$ ) estimators have been a  
59 key part of parallel debates about the Ivory-billed Woodpecker; what little work has been done  
60 on the thylacine places  $\tau_E$  in 1933-1935, with only one model (using temporally-subsetted data)  
61 suggesting the species might be extant.<sup>11</sup> These methods are sensitive to inaccurate data and false  
62 sightings, but more recently developed Bayesian models differentiate between the processes of  
63 accurate and false sightings explicitly, and allow researchers to include uncertain sightings in  
64 models as a separate class of data.<sup>5</sup> Here, we apply those models (and several other frequently  
65 used extinction date estimators) to 20<sup>th</sup> and 21<sup>st</sup> century thylacine sightings, and ask: what is the  
66 probability that the species might be rediscovered?

67  
68 Our study considers the only optimistic modeling scenario for the thylacine’s persistence, and  
69 includes valid sightings from Tasmania alongside highly questionable sightings from Australia,  
70 despite the species’ eradication two millennia earlier on the continent. (That scenario, in itself, is  
71 fairly implausible; in the supplement, we present an analysis using only confirmed sightings

72 from Tasmania, which could be considered a more realistic analysis of the probability the  
73 thylacine could have persisted in Tasmania alone). We used the sightings and specimens from  
74 Sleightholme & Campbell (2016) (1900-1982)<sup>1</sup>, sightings from Heberle (2004) (1939-1998)<sup>12</sup>,  
75 and records detailed on public websites of interested citizen groups ([www.tasmanian-tiger.com](http://www.tasmanian-tiger.com),  
76 [www.thylacineresearchunit.org](http://www.thylacineresearchunit.org), and [www.thylacineawarenessgroup.com](http://www.thylacineawarenessgroup.com)) supplemented by web  
77 searches for news media stories from 2007-2016. For each year between 1900 and 2016, we  
78 recorded the maximum level of certainty of records. Records were scored as confirmed  
79 specimens (e.g., from bounty records, museum specimens, or confirmed captures), confirmed  
80 sightings (sightings agreed as valid by experts), and unconfirmed sightings (sightings not  
81 considered valid by experts; **Figure 1**). Because there are also likely unreported unconfirmed  
82 sightings, we also ran models assuming that an unconfirmed sighting occurred in every year  
83 from 1940-2016 (**Supplementary Information**). For all analyses, we considered the species  
84 across its historical range (i.e., mainland Australia and Tasmania). All R code and more detailed  
85 data is available in the S.I.

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87 The Bayesian model we use, which explicitly differentiates sightings by certainty, suggests a  
88 negligible probability that the thylacine might have persisted later than the 1940s, with 1940 as  
89 the most likely value of  $\tau_E$ , and the posterior likelihood declining rapidly thereafter (**Figure 2**).  
90 Including unconfirmed sightings for years with no data did not change the probability  
91 distribution (**see S.I.**). Other, non-Bayesian estimators all strongly agreed with these findings.  
92 The optimal linear estimator (OLE) is considered the most robust of those tools<sup>13</sup>, and has been  
93 applied to other high-profile extinctions like that of the dodo (*Raphus cucullatus*).<sup>14</sup> Using only  
94 confirmed specimens provides an OLE extinction date of 1939 (95% confidence interval: 1937-  
95 1943); adding confirmed sightings did not change the estimated extinction date or confidence  
96 interval. Most other commonly used extinction estimators concur with these findings, with  
97 Robson & Whitlock's method<sup>15</sup> (producing by far the latest estimate) approaching the 1960s (**see**  
98 **S.I.**).

99  
100 In our assessment, there is only an extremely low probability that the thylacine could be extant  
101 (Bayes factor =  $6.21524 \times 10^{13}$ , or a probability of 1 in 1.6 trillion). Based on the results of our  
102 primary model, it remains fairly plausible that the thylacine's extinction could have occurred up  
103 to a decade later than believed. But for thylacines to appear in 2017, especially in an area where  
104 they are believed to have been absent for two millennia, is highly implausible. The two sightings  
105 from Cape York describe as "detailed" and "plausible" may be so, from a strictly zoological  
106 perspective; but from a modeling standpoint, they fit neatly into a pattern of ongoing, false  
107 sightings that follows nearly any high-profile extinction. Models can be wrong, and new data  
108 may overturn a century of common knowledge in what could be one of the most surprising re-  
109 discoveries in conservation history. But if the story of the Ivory-Billed Woodpecker offers any  
110 parallels, camera trap evidence is more likely to produce blurry evidence that might match the  
111 profile of a thylacine and sustain ongoing controversy, while producing little change in the state  
112 of scientific consensus.

113  
114 The hope to rediscover extinct species is one of the most powerful emotional forces in  
115 conservation biology, and can bring attention to threatened species and ecosystems while  
116 igniting public interest (and funding) in science<sup>7</sup>. The search for the thylacine may reap those  
117 benefits, and the proposed 2017 search has already gathered significant attention from journalists

118 and social media. Moreover, the camera trap data that will be collected during the search for the  
119 thylacine in Cape York will undoubtedly be valuable for many other conservation studies. But  
120 the ongoing search for extinct species, in the broader scheme, likely drains critical funds that the  
121 conservation of near-extinction species desperately requires. One estimate suggests 7% of some  
122 invertebrate groups may already have gone extinct—at which rate, 98% of extinctions would be  
123 going entirely undetected<sup>16</sup>. Globally, 36% of mammal species are threatened with extinction  
124 (classified as Vulnerable, Endangered or Critically Endangered), including 27% of native  
125 Australian mammals<sup>17</sup>, and often limited resources can be better spent reversing those declines,  
126 than chasing the ghosts of extinction past.

127  
128 **Supplementary Information** is linked to the online version of the paper at  
129 [www.nature.com/nature](http://www.nature.com/nature).

130  
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132 (2014), and A. Butler (Biomathematics and Statistics Scotland) for translating the Matlab code  
133 into R. We thank L. Bartlett for helpful criticism and feedback.

134  
135 **Author Contributions.** C.J.C. designed the study; A.L.B assembled the dataset. All authors  
136 developed code, analyzed the data, and wrote the manuscript.

137  
138 **Author Information.** Reprints and permissions information is available at  
139 [www.nature.com/reprints](http://www.nature.com/reprints). The authors declare no competing financial interests. Correspondence  
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## Methods.

### *Data Availability*

Our study utilizes a compendium of sightings gathered from previous studies on the thylacine (Table S1). The majority are taken from Sleightholme & Campbell's (2016) appendix<sup>1</sup>, which includes 1167 geo-referenced post-1900 sightings classified as a capture, kill, or sighting. For each year from 1900-1939, we used the sighting of the highest evidentiary quality, with captures or killed individuals being confirmed specimens. Additional sightings were taken from Heberle (2004)<sup>12</sup>, and Internet searches for recent news media reports.

### *Bayesian Extinction Estimators*

The primary model we employ in our paper is the latter of a pair developed by Solow & Beet<sup>5</sup> to address the independent process of accurate and inaccurate sightings. While the rate of valid sightings is likely to change leading up to an extinction event, after extinction that rate remains constant (at zero) and all sightings are presumed inaccurate. The sighting dataset  $t$  occurs over an interval  $[0, T)$ , where  $0 \leq \tau_E < T$ . During the interval  $[0, \tau_E)$ , valid sightings occur at rate  $\Lambda$  while invalid sightings occur at rate  $\Theta$ , meaning that valid sightings occur at proportion

$$\Omega = \frac{\Lambda}{\Lambda + \Theta}$$

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It is assumed further that certain sightings occur – at an independently determined rate – which divides the dataset of sightings  $t$  into certain sightings  $t_c$  and uncertain sightings  $t_u$ . The likelihood of the data conditional on  $\tau_E$  is given as

$$p(t|\tau_E) = p(t_c|\tau_E)p(t_u|\tau_E)$$

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These two values are calculated using  $n_c$  (the number of certain sightings, all before  $\tau_E$ ), and  $n_u$  (the number of uncertain sightings), where  $n_u(\tau_E)$  are the subset recorded before  $\tau_E$ , and  $\omega$  acts as a dummy variable replacing  $\Omega$ :

$$p(t_c|\tau_E) = \frac{(n_c - 1)!}{(\tau_E)^{n_c}}$$

171

$$p(t_u|\tau_E) = \int_0^1 \left[ \omega^{-n_u} (1 - \omega)^{n_u - n_u(\tau_E)} \left( \tau_E + \frac{1 - \omega}{\omega} T \right)^{-n_u} \right] d\omega$$

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In the main manuscript, we present that likelihood  $p(t|\tau_E)$  calculated as the product of those two terms; however, the likelihood a species is presently extinct can be calculated a Bayes factor, which can be treated as the odds that the species went extinct in the interval  $[0, T)$ , which they denote as an event  $E$  (with alternate hypothesis  $\bar{E}$ ). Based on some prior distribution set for  $p(\tau_E)$ , the posterior probability the species went extinct in the interval of observation is

$$p(t|E) = p(t|\tau_E)p(\tau_E)$$

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180 The alternate probability  $p(t|\bar{E})$  can be calculated by evaluating the same expression given  
181 above for  $p(t|\tau_E)$  at  $\tau_E = T$ . The Bayes factor is subsequently given as

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$$B(t) = \frac{p(t|E)}{p(t|\bar{E})}$$

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### 184 *Other Extinction Estimators*

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186 We also include several other non-Bayesian estimators, readily derived using the R package  
187 ‘sExtinct’ v1.1.<sup>18</sup> Were we to include every unconfirmed, controversial sighting continuing up to  
188 2016, all methods indicate that the species would likely be extinct. Consequently, we limit the  
189 implementation of other methods to two practical applications, examining how results change by  
190 either including (a) only confirmed, uncontroversial specimens and (b) both confirmed  
191 specimens and confirmed sightings (**Figure S1**).

192

193 Among the methods that we include, Robson and Whitlock<sup>15</sup> suggested a nonparametric method  
194 based only on the last two sightings:

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$$\tau_E = t_k + (t_k - t_{k-1})$$

196

197 In this study, that estimator consistently suggests the latest  $\tau_E$  (see **Figure S1**). A more middle-  
198 of-the-road estimator, the optimal linear estimator (OLE) method is typically considered the  
199 most robust non-parametric extinction estimator.<sup>14</sup> Based on a subset of the last  $s$  sightings of  $k$   
200 total:

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$$\tau_E = \sum_{i=1}^s w_i t_{k-i+1}$$

202

203 Where  $b$  is a vector of  $s$  1’s and

204

$$w = (b'\Lambda^{-1}b)^{-1}\Lambda^{-1}b$$

205

206 such that  $\Lambda$  is a square matrix of dimension  $s$  with typical element

207

$$\Lambda_{ij} = \frac{\Gamma(2\hat{v} + i)\Gamma(\hat{v} + j)}{\Gamma(\hat{v} + i)\Gamma(j)}$$

208

$$\hat{v} = \frac{1}{s-1} \sum_{i=1}^{s-2} \ln \frac{t_k - t_{k-s+1}}{t_k - t_{s+1}}$$

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210 The results of these analyses, as well as three other (weaker) extinction estimators, are presented  
211 in **Figure S1**.



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## 213 *Sensitivity Analysis*

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215 As there is likely an unknown number of unreported unconfirmed sightings after 1940, we also  
216 considered a case where we assumed unconfirmed sightings occurred annually from 1940–2016  
217 to ascertain the “best case” scenario in the absence of a confirmed sighting or specimen. The  
218 extinction date estimated using the Bayesian model was 1940 (Bayes factor:  $4.53 \times 10^{13}$ ), an  
219 identical date as our original model, and with a certainty in the same order of magnitude (**Figure**  
220 **S2**).

221

## 222 *Data Availability*

223

224 All sighting data is available in **Table S1**. All scripts in R to implement both sExtinct and the  
225 Solow & Beet method are available as a supplemental file. The authors declare that all data  
226 supporting the findings of this study are available within the paper and its supplementary  
227 information files.

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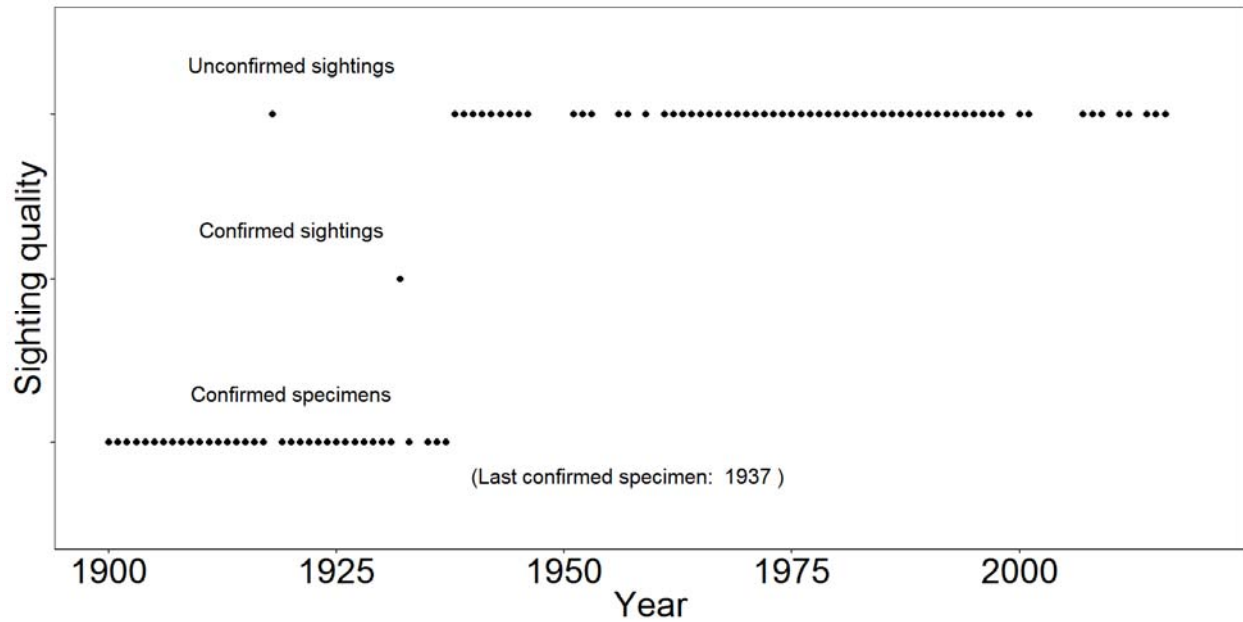


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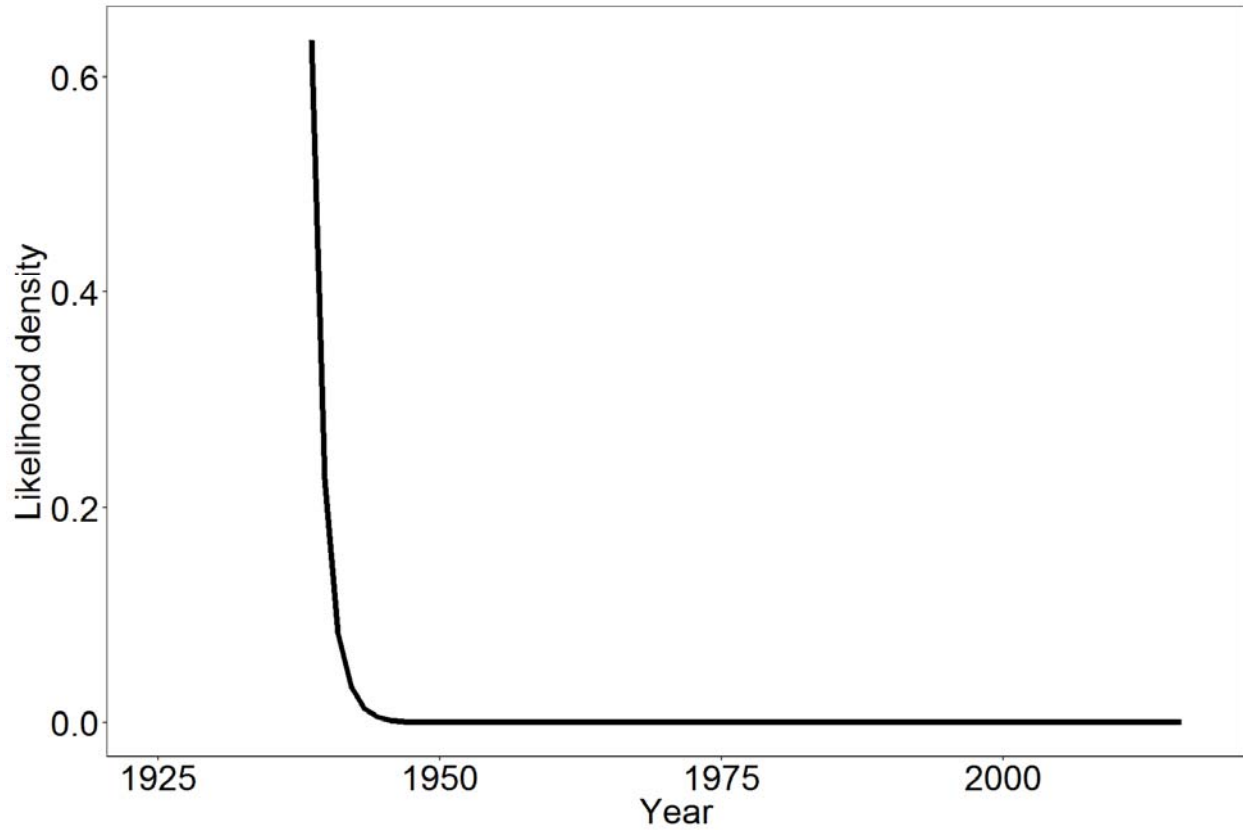
## Figures

**Figure 1. Thylacine sighting data.** Specimens are treated as an absolute, certain form of evidence, while expert-verified sightings are treated as an intermediate level of certainty. Controversial sightings, or indirect evidence based on scat or tracks, are classified as unconfirmed sightings, the weakest source of evidence. More detailed sighting data is available in **Table S1**.



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277 **Figure 2. The likelihood of thylacine persistence over time.** The figure presents the posterior  
278 probability of a given extinction date  $\tau_E$  scaled by the area under the entire likelihood curve. In  
279 Solow & Beet's model, specimen-based records are treated separately and as certain  
280 observations (see **Methods**); consequently evaluation begins in 1937, the year of the last certain  
281 sighting (i.e., extinction prior to that date is not considered).  
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