

1 **Lessons from COVID-19 for wildlife ranching in a changing world**

2 Hayley S Clements^{1,2}, Matthew F Child^{3,4}, Lehman Lindeque⁵, Kyra Lundstedt⁵, Alta De Vos⁶

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4 ¹Centre for Sustainability Transitions, Stellenbosch University, Stellenbosch 7600, South Africa

5 ²Helsinki Lab of Interdisciplinary Conservation Science, Department of Geosciences and Geography,
6 University of Helsinki, Helsinki FI-00014, Finland

7 ³South African National Biodiversity Institute, Kirstenbosch National Botanical Garden, Rhodes Drive,
8 Newlands, Cape Town 7735, South Africa

9 ⁴Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Private
10 Bag X20 Hatfield, Pretoria 0028, South Africa

11 ⁵United Nations Development Programme (UNDP), Pretoria, South Africa

12 ⁶Department of Environmental Science, P.O. Box 94, Rhodes University, Makhanda 6139, South
13 Africa

14

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24 **Author contribution**

25 HSC led the manuscript and performed most analyses. HSC, ADV and MFC contributed most of the
26 writing of the original manuscript draft. ADV led initial submission of the manuscript and contributed
27 to the analyses. All authors contributed to conceptualisation, design, framing, data collection, and
28 providing critical conceptual input.

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33 **Abstract**

34 The COVID-19 pandemic provided an opportunity to assess the impacts of a global disturbance on
35 conservation land uses and learn from responses to the crisis to enable more resilient conservation
36 systems. To understand socio-economic responses of diverse wildlife working lands to COVID-19, we
37 surveyed owners and managers of 78 private wildlife ranches (wildlife working lands), 23 agricultural
38 farms (conventional working lands) and six public protected areas (conventional conservation lands)
39 in South Africa. Most protected areas lost more than 75% of their revenues during 2020, while most
40 agricultural farms lost less than 10%. The impact on wildlife ranches was more varied. Ranches with
41 more diverse activities, particularly mixed wildlife-agriculture systems, lost less revenue, shifting
42 their activities from those heavily impacted (international ecotourism, trophy hunting) to those less
43 affected (e.g., wildlife meat, livestock). This adaptive capacity suggests that wildlife-based
44 enterprises could represent key ecosystem-based adaptations, providing lessons for integrated
45 global policies that seek to incorporate private land models in the 2030 Biodiversity Framework.

46

47 **Keywords:** private land conservation, adaptive capacity, other effective area-based conservation
48 measures, sustainable land management, agro-ecological systems

49

50

51 Curbing biodiversity loss requires transformative governance to strengthen the resilience of
52 conservation strategies in a rapidly changing world^{1,2}. Public protected areas remain the core global
53 conservation strategy³. However, their effectiveness and ability to meet the proposed 2030 Global
54 Biodiversity Framework target of 30% land conserved are impeded by limited resources (e.g., skills,
55 money and capacity), competing governmental interests, and social justice trade-offs^{4,5}. There is
56 thus a need for additional conservation strategies, with increasing recognition of the role that
57 private landholders and communities can play^{6,7}.

58

59 Private landholders and communities are involved in conservation through various models of
60 working lands – lands managed both for production and ecological function⁸. Working lands include
61 rangeland models such as silvopasture and holistic grazing management, which can contribute to
62 food security, job creation and biodiversity conservation simultaneously⁸. In Southern and Eastern
63 Africa, private and community wildlife and mixed wildlife-agricultural ranches provide one such
64 model, enabling innovative combinations of revenue-generating activities while also ‘rewilding’
65 habitats and increasing wildlife abundance^{9–12}. Assessing the ability of various wildlife working-land
66 models to adapt to global shocks is key to designing policies that unlock resilient wildlife economies
67 that benefit people and planet.

68

69 Diverse models that support conservation (i.e., protected areas, wildlife ranches, mixed farms) and
70 tenure types (i.e., state, private, community) can contribute diversity and redundancy in conserved
71 ecosystems, resources, knowledge systems and management strategies^{13–15}. Theory suggests that
72 there is a positive relationship between the diversity of elements in a system and its resilience¹⁶,
73 where resilience is defined as a system’s ability to retain its identity (critical structures, functions,
74 and feedbacks) in the face of disturbance and change through self-organisation, adaptation and
75 learning¹⁷. In more diverse ecosystems, for example, it is less likely that a disturbance that causes
76 species losses will cause the loss of entire ecosystem functions, due to diversity in species’ responses
77 to the disturbance¹⁸. Although this relationship is less well established in social-ecological systems, it
78 is predicted that systems with diverse management models and institutions, for example, may be
79 more effective at responding to change because diversity gives rise to higher levels of innovation,
80 adaptation, and resistance^{15,19,20}. Diversity in actors and tenure types may therefore strengthen the
81 resilience of conservation systems if it increases the ability to learn and adapt in response to
82 disturbance and change (i.e., adaptive capacity)²¹.

83

84 Diversity in conservation actors can however also bring potential vulnerabilities: many community or
85 privately conserved lands lack the institutional and financial safety nets afforded to public protected
86 areas. Additionally, conservation in such lands is often an emergent outcome of enabling conditions
87 (e.g., policy and economic environments that make wildlife a competitive land use), rather than an
88 objective in-and-of-itself^{7,10}. This raises questions about the ability of these working lands to
89 continue contributing to conservation when conditions change, given their need to remain
90 financially viable^{20,22}. The COVID-19 pandemic was a major global shock that tested the resilience of
91 conservation- and other sustainable land use systems around the world. The pandemic provided an
92 opportunity to assess not only the impacts of a global disturbance on the economic sustainability of
93 diverse conservation land uses, but also to consider what we can learn from how these land uses
94 adapted in the face of a crisis, for enabling more resilient conservation strategies going forward.

95

96 Wildlife-based tourism in Africa generates US\$29 billion annually (over a third of all tourism to the
97 region) and employs 3.6 million people²³. The continent also attracts considerable foreign support
98 for conservation via philanthropy and aid. The net conservation impacts of COVID-19 in Africa are
99 believed to be strongly negative, due to ailing economies and limited travel resulting in reduced
100 funding and tourism revenues, restrictions on the operations of conservation agencies, and elevated
101 human threats to nature²⁴⁻²⁷. In South Africa, tourism revenue in National Parks declined by 90%
102 during lockdowns in 2020, resulting in loss of community development revenues and educational
103 programmes, and cost curtailment measures to park management such as ranger patrols²⁸. These
104 severe impacts bring into question the resilience of conservation models based primarily on
105 managing for biodiversity conservation, which are dependent on revenue from ecotourism, or
106 external or state-subsidised funding^{24,29,30}.

107

108 Private wildlife and mixed wildlife-livestock ranches in South Africa provide a good opportunity to
109 explore response strategies of working lands to a major shock, and the relevance of the
110 hypothesized relationship between social-ecological diversity, adaptive capacity, and resilience. An
111 estimated 14-17% of South Africa's area comprises wildlife-based land-uses on private land³¹. Over
112 1,000 privately protected areas and 5,000 wildlife ranches play a central role in the country's
113 conservation estate, with demonstrated biodiversity conservation outcomes^{9,15}. Their socio-
114 economic contributions are also notable, with wildlife ranches providing on average more jobs per
115 hectare and higher quality jobs than both agricultural farms³¹ and public protected areas³². The
116 hunting and ecotourism industries contribute millions of dollars to the national economy each
117 year^{31,33}. Some of these wildlife working lands have also been criticised, however, in cases where

118 financial and conservation objectives are not aligned, leading for example to the persecution of
119 predators to protect valuable species for trophy hunting, or the stocking of high densities of
120 charismatic megafauna in response to ecotourist preferences³⁴. They are also owned predominantly
121 by minority white South Africans and foreigners, reflecting inequities in land ownership that stem
122 from the racially defined and discriminatory apartheid era that ended in 1994³⁵. Several authors
123 argue that the wildlife ranching industry has entrenched these inequities^{36–38}. Understanding the
124 response of wildlife working lands in South Africa to a major shock thus requires nuanced
125 consideration of their contributions to conservation and socio-economic development, which could
126 improve policy design that seeks to find equitable, sustainable solutions to biodiversity loss”

127

128 The proliferation of wildlife ranches over the past half-century is largely due to policies that enable
129 the use and ownership of wildlife on private land, and lucrative non-consumptive (ecotourism) and
130 consumptive (e.g., hunting, meat and live-wildlife sale) industries that make wildlife a competitive
131 land use^{10,31}. Similar trends in the expansion of wildlife working lands and their socio-economic and
132 conservation contributions are evident on community and private land in other Southern African
133 countries^{10,39}. These ranches are highly diverse in their motivations and business models (i.e., the
134 combinations of wildlife activities they undertake)^{12,31,40}. The reliance of many ranches on (often
135 international) visitors and the need to remain financially viable suggests that they may have been
136 heavily impacted by the COVID-19 pandemic. While the estimated financial impact of COVID-19 on
137 the private wildlife industry is severe⁴¹, we hypothesize that the diversity of wildlife enterprises led
138 to heterogeneity in impacts and responses to the crisis.

139

140 In this paper we consider if and how diverse South African wildlife ranches responded to the
141 pandemic (see Supplementary Material Figure S1 for a map of study sites). A clustering analysis of
142 wildlife ranches based on their revenue-generating activities reveals four unique business models,
143 with two being more specialised (focused on ecotourism or trophy hunting) and two being more
144 diversified (diverse wildlife activities, or mixed wildlife and agricultural activities). We assess whether
145 the business models adopted by wildlife ranches influenced the extent to which they were impacted
146 financially by the pandemic, compared with agricultural farms (as an example of more conventional
147 working lands) and public protected areas (an example of more conventional conservation lands).
148 Importantly, we then assess the strategies that wildlife ranches implemented to cope with these
149 impacts, highlighting the value of diverse business models for enhancing adaptive capacity. We
150 consider potential implications of this adaptive capacity for the socio-economic and conservation

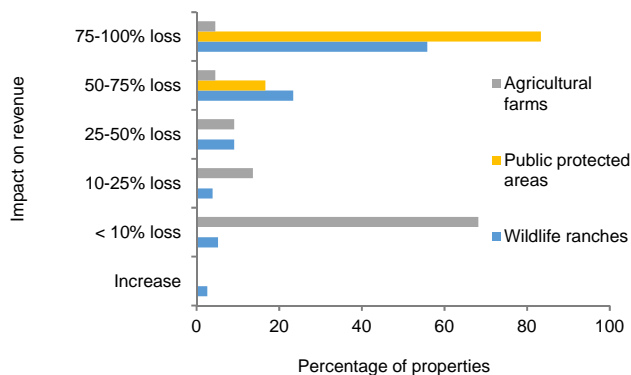
151 contributions of wildlife ranches, and conclude with lessons for building resilience in the wildlife and
152 conservation sectors more broadly.

153

154 Results

155 During the 2020/21 financial year, the majority of wildlife ranches lost more than half of their
156 expected revenue, while 9% lost less than a quarter and 3% experienced an increase in revenue
157 (Figure 1). Comparatively, nearly all public protected areas lost more than 75% of their expected
158 revenue, and most agricultural farms lost less than 10% ($X^2 = 57.83$, $df = 1$, $p < 0.001$; Figure 1).

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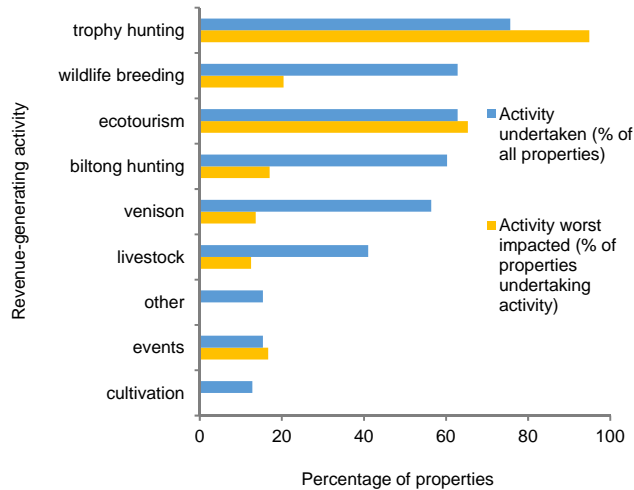
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161 **Figure 1.** Impact of the pandemic on expected revenues during the 2020/21 financial year, for 78
162 wildlife ranches, 6 public protected areas (PAs), and 23 agricultural farms.

163

164 On wildlife ranches, the most common revenue-generating activities were trophy hunting (sale of
165 hunting experiences where the hunter, usually a foreign tourist, retains some of the animal's body as
166 a trophy); wildlife breeding (sale of live animals with good genetics, usually to breed trophy animals);
167 and ecotourism (sale of wildlife viewing experiences) (Figure 2). Livestock farming (cattle, goats,
168 sheep) was also undertaken on 41% of the properties, with a smaller proportion of properties
169 undertaking cultivation. On average, 66% ($\pm 4\%$ SE) of visitors to these properties were foreign,
170 though it varied from 0% to 100%. Of the landholders undertaking trophy hunting, 95% stated it to
171 have been the activity worst impacted by the pandemic, while 65% of landholders undertaking
172 ecotourism stated it to have been the worst impacted activity (Figure 2). By contrast, less than 20%
173 of landholders undertaking other wildlife-based activities (e.g., biltong hunting, wildlife breeding,
174 venison) stated that these activities were the worst impacted by the pandemic. Biltong hunting
175 refers to hunting for meat, usually by South African hunters, and venison refers to the sale of wildlife
176 meat.

177



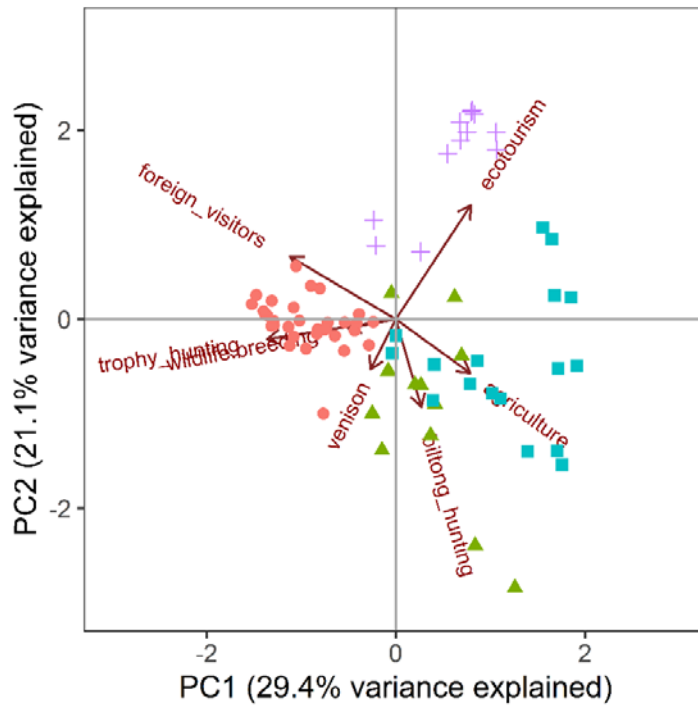
178

179 **Figure 2.** Percentage of 78 wildlife ranches undertaking different revenue-generating activities, and
 180 percentage of ranches undertaking a certain activity that reported it to have been worst impacted by
 181 the pandemic.

182

183 The combination of revenue-generating activities adopted by wildlife ranches before the pandemic
 184 (represented by two principal components - PCs; Figure 3 and Supplementary Material Table S1)
 185 predicted a quarter of the variation in the extent to which ranch revenues were impacted by the
 186 pandemic ($r^2 = 0.253$, $F = 13.25$, $df = 2$ and 70 , $p < 0.001$). Two combinations of activities resulted in
 187 significantly larger revenue losses. The first was a higher proportion of foreign visitors and revenues
 188 from trophy hunting and wildlife breeding, combined with a lower proportion of revenues from
 189 ecotourism and agriculture (livestock and/or cultivation) (depicted by the negative relationship
 190 between PC1 and revenue loss; Figure 3). The second combination was a higher proportion of
 191 foreign visitors and revenues from ecotourism, combined with a lower proportion of revenues from
 192 biltong hunting, venison sales and agriculture (depicted by the positive relationship between PC2
 193 and revenue loss; Figure 3).

194



195

196 **Figure 3.** Biplot depicting trends in the contributions of different activities to wildlife ranch revenues,
 197 based on the relative scores of seven activities on two principal components (PCs). Data points
 198 indicate the PC scores of 74 ranches, with shapes and colours corresponding to four distinct
 199 ‘business model’ clusters (pink circles - Trophy hunting focus; green triangles - Mixed wildlife; blue
 200 squares - Mixed wildlife-agriculture; purple plus signs - Ecotourism focus). Revenue losses during the
 201 pandemic were higher with lower values of PC1 ($\beta = -1.00$, $SD = 0.24$, $t = -4.15$, $p < 0.001$), and higher
 202 values of PC2 ($\beta = 0.74$, $SD = 0.24$, $t = 3.07$, $p = 0.003$).

203

204 Four distinct clusters of wildlife ranches were evident, based on the combinations of revenue-
 205 generating activities that they adopted before the pandemic (Figure 3; Mantel $r = 0.56$, $n = 74$).
 206 Trophy hunting focused ranches (45% of properties) generated two thirds of their revenues, on
 207 average, from predominantly foreign trophy hunters (Table 1). They undertook other wildlife-based
 208 activities and agriculture to a limited degree. By contrast, on mixed wildlife ranches (16% of
 209 properties), trophy hunting generated a third of revenues, closely followed by biltong hunting,
 210 venison sales and ecotourism. These properties had majority South African visitors. Mixed wildlife-
 211 agriculture ranches (23% of properties) generated just over half of their revenues from agriculture
 212 (mostly livestock), with largely South African ecotourism making up a fifth of revenues and other
 213 wildlife-based land uses comprising the remainder, on average. Finally, ecotourism focused ranches
 214 (16% of properties) generated over 80% of their revenues from ecotourism, on average, focusing

215 predominantly on foreign visitors. Other wildlife-based activities formed the remainder of their
 216 revenues, with almost no agriculture taking place, on average.

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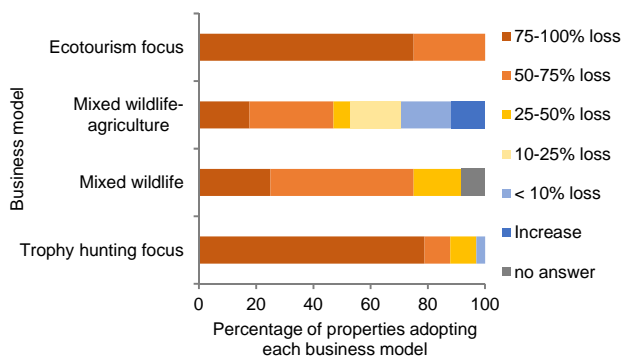
218 **Table 1.** Revenue-generating characteristics of wildlife ranches in four distinct ‘business model’
 219 clusters (mean ±SE). Colours and symbols refer to the respective clusters on Figure 3.

	Trophy hunting focus (Pink circles)	Mixed wildlife (Green triangles)	Mixed wildlife-agriculture (Blue squares)	Ecotourism focus (Purple plus signs)
Number properties	33	12	17	12
PC1	-0.52 (±0.21)	0.19 (±0.25)	0.65 (±0.37)	0.33 (±0.24)
PC2	-0.02 (±0.14)	-0.54 (±0.52)	-0.25 (±0.40)	1.00 (±0.31)
% Revenue from:				
Ecotourism	4.9 (±7.1)	15.6 (±15.3)	21.2 (±28.3)	83.1 (±21.7)
Biltong hunting	5.3 (±5.4)	22.3 (±26.3)	6.1 (±6.9)	1.7 (±3.3)
Trophy hunting	65.9 (±16.8)	31.3 (±20.4)	9.4 (±12.4)	6.3 (±11.9)
Venison	6.4 (±8)	17.1 (±20.6)	1.8 (±4.3)	1.1 (±1.9)
Wildlife breeding	9.8 (±8.8)	4.3 (±6.6)	5.1 (±7.7)	5.5 (±6.5)
Agriculture (livestock and cultivation)	5.8 (±9)	2.8 (±6.9)	55.3 (±21.6)	0.5 (±1.4)
Livestock	5.3 (±9.1)	2.4 (±6.9)	50.9 (±24.3)	0.5 (±1.4)
Cultivation	0.5 (±1.9)	0.4 (±0.8)	4.4 (±10)	0 (±0)
Events	0.2 (±0.9)	1.8 (±5.7)	0.1 (±0.2)	1.4 (±3.1)
Other	1.8 (±7.1)	4.7 (±14.3)	1.2 (±3.8)	0.5 (±1.4)
% Foreign visitors	87.2 (±12.9)	29.6 (±21.4)	35.8 (±37.2)	85.2 (±12.5)

220

221 These four business models differed markedly in the extent to which their expected revenues were
 222 impacted by the pandemic (Fisher’s $p < 0.001$; Figure 4). The majority of trophy hunting- and
 223 ecotourism-focused properties lost >75% of their revenues. By contrast, many mixed wildlife-
 224 agriculture properties lost less than half of their revenues, with 12% actually increasing their
 225 revenues. Half of mixed wildlife properties lost between 50 and 75% of their revenues.

226



227

228 **Figure 4.** Impact of the pandemic on expected revenues during the 2020/21 financial year, on 74
229 wildlife ranches adopting four business models.

230

231 The most common coping strategy, adopted by 40% of landholders in response to the impacts of the
232 pandemic, was to adapt their marketing strategies to attract local tourists and/or biltong hunters,
233 often by offering discounted rates (Table 2). Over a quarter of landholders adapted by cutting down
234 on running costs - decreasing staff numbers or salaries, pausing new projects, for example. Just
235 under a fifth of landholders adapted by shifting their focus to livestock (and to a lesser extent
236 cultivation), and a similar proportion shifted their focus to other wildlife-based activities, beyond
237 hunting and ecotourism, such as packaging and selling venison. Just over a tenth of landholders
238 mentioned their reliance on off-property income sources. Notably, 10% of landholders specifically
239 mentioned supporting their staff to cope with the pandemic.

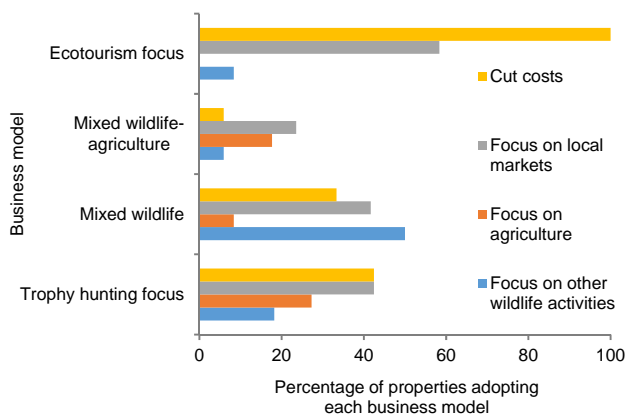
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241 **Table 2.** Summary of key strategies adopted by 78 wildlife ranches to cope with the pandemic.

Response	Details	Example Quote from interviewees	% of ranches
Focused on local markets	Shifted marketing to attract local visitors; advertised "isolation" appeal; offered local discounts; shifted from trophy hunting to biltong hunting.	"Every farmer in the country is trying to get to the local hunters" "Local hunters really pulled us through" "They put out some South African specials to at least try and attract some local trade" "Lockdown (COVID-19) increased our revenue as more locals wanted to "escape the city" and beaches were banned, so the mountains suddenly became very attractive"	40
Cut costs	Cut down on running costs; decreased staff salaries or time; retrenched staff; paused new projects; partially closed accommodation (closed some lodges or the enterprise over some weeks).	"That budget [to run land management operations] alone was cut by 75%...just down to essential services - they [employees] can still make sure the fence is working, but they can't now go and attack alien invasive species" "We got rid of unnecessary vehicles, equipment, just kept what we could work around with" "We had to lay some staff off. We had to make some retrenchments or temporary retrenchments"	28
Focused on agriculture	Focused more on livestock farming, using farming income to fund the property; introduced cattle and/or goats; diversified into tobacco, flowers, or nuts.	"I'm thankful that we diversified and made money out of the tobacco" "We increased cattle, goats and sheep to generate a second income" "We began farming with cattle and goats as soon as lockdown was announced"	17
Focused on other wildlife-based activities, beyond hunting or tourism	Venison processing, packaging, and sale to local markets; moved to events or horse riding; undertook wildlife culling; increased live wildlife sales.	"We moved to incorporate events and horseback safaris" "More biltong hunting and conferences. We also had to cull animals that would've been hunted, and sold their meat on the local market"	17
Relied on other income	Funded costs through other income or savings, a loan or insurance.	"We coped by transferring some of our employees to other businesses, and also relied on the income from some of our other businesses"	12
Supported staff	Avoided staff layoff by applying for government support for salaries; provided food parcels or venison to staff; changed staff roles e.g., from visitor guides to antipoaching or livestock.	"We were able to apply and receive UIF [Unemployment Insurance Fund] payments for staff, which enabled us to not permanently lose staff" "We cross-subsidised and used our income from cattle to fund the tourism staff"	10

242

243 Wildlife ranches with different business models differed significantly in their strategies to cope with
244 the pandemic ($X^2 = 19.25$, $df = 9$, $p = 0.02$; Figure 5). All ecotourism-focused ranches reported cutting
245 costs, and over half shifted their marketing focus to attract local tourists. No ecotourism-focused
246 ranches shifted their focus to agriculture and less than 10% focused on other wildlife-based
247 activities, beyond ecotourism. Just over 40% of trophy hunting ranches similarly cut costs and
248 focused on local markets. In addition, over a quarter reported shifting their focus to agriculture and
249 almost a fifth focused on other wildlife-based activities. The most common strategy among mixed
250 wildlife ranches was to focus on other wildlife-based activities beyond trophy hunting and
251 ecotourism, particularly venison, as well as to focus on local markets. All four coping strategies were
252 less common among mixed wildlife-agriculture ranches than the other three business models.
253



254

255 **Figure 5.** Percentage of 74 wildlife ranches adopting four business models that reported adopting
256 each of the most common responses to the pandemic.

257

258 Discussion

259 Many wildlife-based working lands demonstrated adaptive capacity in the face of a major global
260 shock. While the significant impact of the pandemic on their revenues must not be overlooked⁴¹,
261 lessons can be learned from patterns in the degree to which different wildlife-based land uses were
262 affected and the ways in which these enterprises responded to the crisis. Importantly, more
263 diversified business models and mixed wildlife-agriculture models were less impacted financially and
264 better able to adapt by shifting revenue-generating strategies away from those worst hit, namely
265 international ecotourism and trophy hunting. This supports the theory that diversity promotes
266 adaptive capacity, an important aspect of resilience^{16,19,21}. Adopting a specialised business model can
267 cause path dependence, through investment in specialised infrastructure, markets, and capacities

268 that constrain future options⁴². For example, specialised ecotourism areas were less able to adopt
269 more consumptive wildlife activities, perhaps due to their prior investment into an international
270 market that desires pristine, unutilized landscapes with high densities of charismatic megafauna^{43,44}.
271 Their high lodge start-up and running costs can also be a burden when revenues become limited⁴².

272

273 The ability to adapt to maintain financial viability is critical for many wildlife working lands, yet some
274 adaptations may not result in desirable socio-economic or ecological outcomes. For example,
275 ecotourism-focused areas were more likely than wildlife consumption-orientated areas to adapt by
276 cutting jobs in response to revenue losses. This has important implications for job security in rural
277 areas and reveals that investment strategies focused on establishing ecotourism ventures without
278 incorporating the capacity to switch to other wildlife economy revenue streams might undermine
279 their long-term socio-economic contributions. Cost cutting in response to revenue losses may also
280 undermine ecological outcomes, if it results in diminished mitigation of threats to biodiversity such
281 as alien invasive species or poaching⁴⁵. The least financially impacted wildlife economy model was
282 mixed wildlife-agriculture areas, as many were able to adapt to the pandemic and some even
283 increase their revenues. Notably, this model was able to adapt by scaling up less affected revenue-
284 generating activities rather than cutting costs. Not all of these activities were wildlife-based
285 however, and it will be important to monitor the long-term conservation implications of scaling up
286 other farming activities (largely livestock, as well as cultivation, which was less common but likely
287 more impactful to conservation). While models based on international visitors (ecotourism and
288 trophy hunting) can be lucrative activities in normal times^{12,31,40}, our results support the
289 recommendation by Lindsey et al.²⁴ that building resilience requires diversifying the revenue streams
290 from wildlife-friendly land uses, to include domestic and international tourism, sustainable use and
291 mixed land-use approaches.

292

293 *The importance of multi-tenure conservation systems in a changing world*

294 More generally, our results speak to the importance of diversified conservation systems for
295 promoting adaptive capacity (in this case, in the interest of retaining financial viability), which is
296 likely to be important for strengthening the resilience of conservation efforts in a changing world.
297 The private ranches in our study lacked the government support that allowed public protected areas
298 to sustain their identity through the pandemic, but because they were less institutionalized with
299 fewer constraints on activities, many of these private areas also had the capacity to adapt their
300 business models more easily. Although our public protected area sample size was small, these areas
301 showed similarly high revenue losses during the pandemic to those reported across South African

302 national parks by Smith et al.²⁸. Conservancies in Botswana²⁵ and Zimbabwe²⁶ also experienced large
303 losses because of over-reliance on a single income stream, but unlike South African national parks,
304 were able to adapt and strategize beyond non-consumptive wildlife uses. Protected areas like
305 national parks are not only constrained by what the law requires them to do, but also by public
306 perception and values around how “wild” and “untouched” these areas need to be²⁸. Whilst national
307 parks are important for national identity, heritage and conservation^{28,46,47}, the need to manage them
308 for optimizing a certain kind of biodiversity value can undermine economic sustainability²⁸. Strict
309 protected areas are often expensive for national treasuries and can therefore only represent a small
310 fraction of a sufficiently comprehensive, diverse, and resilient national conservation estate.

311

312 Beyond the COVID-19 pandemic, there are many more disturbances projected in the coming
313 decades. Drought, wildlife, stock and crop disease, conflict over water rights, recessions, political
314 instability, changes in agricultural subsidies, species range shifts, and global preference changes
315 could all have unpredictable impacts on the sustainability of individual protected areas and wildlife
316 areas (e.g.,⁴⁸⁻⁵⁰). Ensuring the resilience of healthy ecosystems to these disturbances requires
317 conservation networks with sufficient response diversity in economic and governance models^{15,51},
318 supported by diverse values and motivations¹. Such diverse systems will still experience
319 conservation losses – in our study, over a third of ranches cut operating costs (e.g., anti-poaching
320 and alien species control efforts) in response to the pandemic, and some increased crops on their
321 properties, possibly reducing biodiversity. The possible trade-offs associated with achieving
322 economic sustainability for wildlife-based systems require consideration⁶, recognising that some
323 trade-offs are inevitable under global change pressures. Enhancing the economic adaptive capacity
324 of individual areas translates into a greater probability of maintaining wildlife-based land uses³,
325 which should support ecological resilience relative to counterfactual land uses such as cultivation.
326 The nature of the relationship between economic and ecological sustainability on wildlife working
327 lands however requires further attention and will depend partially on landholder motivations to
328 manage for short-term profit over long-term land productivity and biodiversity, and if trade-offs can
329 be lessened by supportive policy.

330

331 *Policy implications*

332 Our results demonstrate that non-state actors on working lands are responsive to changing
333 environments. Such adaptive capacity was similarly evident in the transition of private landholders
334 and communities from livestock to wildlife in response to policy changes in Southern African
335 countries around the mid-20th century (including the introduction of wildlife property rights and the

336 cessation of agricultural subsidies)¹⁰; and in their diverse responses to the rhino poaching crisis²⁰. It is
337 important that policy is sufficiently flexible to allow for this adaptive capacity, while also seeking to
338 incentivise the types of land uses that are desirable to countries as they navigate sustainable
339 development. For example, governments could create enabling environments for more diverse land
340 uses that include wildlife-based models to thrive, such as access to land and tenure security,
341 avoiding over regulation, and increasing skills development programmes for managing both wildlife
342 and livestock simultaneously. These programmes should simultaneously emphasise sustainable land
343 management practices to ensure both wildlife and livestock production promote desirable ecological
344 outcomes on these working lands⁵².

345

346 As we have argued, and as the IPBES Global Assessment⁵³ emphasises, strategies to curb global
347 biodiversity loss require a mix of policies and funds that support a diversity of nature-positive
348 economic and governance models, maintained by pluralistic values and motivations¹. The 2030
349 Global Biodiversity Framework goals in sentiment support such a diverse portfolio of area-based
350 strategies through, for example, the emphasis on other effective area-based conservation measures
351 (OECMs)⁷. Many on-the ground assessments for establishing OECMs (e.g., Marnewick et al.⁵⁴),
352 however, still focus on protectionist ideas that favour single intrinsic values of nature as opposed to
353 adaptive and financially viable working lands. In many countries, conservation agencies still favour,
354 sometimes exclusively, policies that promote ecotourism enterprises akin to public protected area
355 models (e.g., South Africa's Biodiversity Stewardship programme, Conservation Covenants in
356 Australia). Such approaches may inhibit the adaptive capacity of these areas, potentially
357 undermining the resilience of national conservation systems. Similarly, policies that focus only on
358 enhancing the economic or ecological sustainability of conservation-positive land uses without
359 considering trade-offs for equity, may not only undermine social justice, but also the long-term
360 resilience of these systems.

361

362 From a sustainable land management perspective, the adaptive capacity of diverse wildlife-based
363 working lands suggests they may be good models of ecosystem-based adaptations (the use of
364 biodiversity and ecosystem services to adapt to life in a less predictable climate system⁵⁵). As such,
365 wildlife-based working lands should be a critical thematic focus of strategies and policies that seek to
366 align integrated commitments under the three Rio Conventions in the Decade of Ecosystem
367 Restoration. As wildlife-based working lands can also contribute substantially to sustainable
368 development goals such as reducing hunger, poverty, and providing employment³¹, but also

369 represent areas that may require societal transformation in ownership^{36–38}, they warrant strategic
370 attention for policies seeking to achieve equitable integration of the Sustainable Development Goals.

371

372 **Conclusion**

373 The adaptive capacity demonstrated by private wildlife ranches to mitigate revenue losses during
374 the global COVID-19 pandemic suggests that non-state conservation actors can play an important
375 role in building resilience in conservation and sustainable land use systems, given their diversity in
376 business models and associated strategies to cope with a major financial shock. Although various
377 trade-offs in managing for economic and ecological sustainability in working lands need
378 consideration, our study provides empirical evidence that wildlife working lands can be adaptive to a
379 changing world, particularly those with multiple revenue streams and thus options for responding to
380 change. Working lands with diverse wildlife-based activities or mixed wildlife-agriculture activities
381 thus represent potential ecosystem-based adaptations that can contribute to achieving multiple
382 global policy goals related to biodiversity conservation, economic development, restoration, climate
383 change adaptation and human well-being.

384

385 **Methods**

386 *Data collection*

387 We developed a semi-structured questionnaire survey as part of the “Sustainable Wildlife Economies
388 Project” (<https://www.wildeconomy.org>) to assess the socio-economic, sustainable land management
389 and conservation contributions of South African wildlife ranches, in comparison to agricultural farms
390 and public protected areas. An initial survey was designed by the authors at a workshop in December
391 2020 and distributed to the private wildlife ranch associations for comments. A revised version was
392 piloted at a workshop with members of Wildlife Ranching South Africa (WRSA), a private wildlife
393 ranching association with over 160 members in the Eastern Cape Province, and the survey revised
394 according to stakeholder feedback. Of relevance to this study, the survey included questions on the
395 proportion of visitors to the property that were foreign; the revenue-generating activities that were
396 undertaken on the property before the pandemic and how much each activity contributed to total
397 revenue; how severely total enterprise revenue for the 2020/21 financial year was impacted by the
398 pandemic relative to expected revenue; and which revenue-generating activities were worst
399 impacted. The survey asked wildlife ranchers what their key strategies were to cope with the effects
400 of the pandemic. Survey questions relevant to this study are included in Supplementary Material 2.
401 Ethical clearance was obtained from Rhodes University [no. 2021-2810-5892].

402

403 Twenty-three field assistants (recent graduates in Environmental Science-related disciplines) were
404 hired to conduct the interviews in teams of two to four. These assistants were trained by experts in
405 wildlife conservation and sustainable land management to conduct the survey. Training was
406 conducted during a week-long workshop in February 2021, covering the scientific background of the
407 project, social process learning techniques, conflict resolution and survey testing and practice.

408

409 In collaboration with WRSA and other private wildlife ranching associations, a media clip outlining the
410 project and requesting expressions of interest to be interviewed was distributed through landholder
411 networks estimated to reach at least 160 landholders. A project coordinator followed up with
412 respondents to confirm dates for the interview and field teams were assigned to each property.
413 Working with local associations and networks helped to ensure that the diversity of business models
414 was adequately sampled. A total of 112 surveys with landholders or managers in the Eastern Cape
415 Province of South Africa were conducted in-person between February and March 2021. Three-
416 quarters of these areas (82) were privately owned wildlife ranches (i.e., >10% of the enterprise's
417 revenue was generated from wildlife-based activities), 24 were private agricultural farms, and seven
418 were public protected areas. Mixed farms (that included wildlife-based and livestock activities) were
419 thus largely classified as wildlife ranches. We included agricultural farms (working lands which likely
420 generally experienced less impact from the COVID-19 pandemic since they are not reliant on tourism
421 or hunting), and public protected areas (the standard for area-based conservation), as reference
422 states. Surveys lasted between two and four hours. Respondents were made aware of the goals of the
423 project, that all questions were optional, and were assured of anonymity. No financial or in-kind
424 compensation was provided. Data were captured by a scribe in hardcopy during the interview and
425 later entered into the Open Data Kit (<https://opendatakit.org/>) application, which allows for
426 structured, distributed mobile data collection⁵⁶.

427

428 *Data analysis*

429 Five private properties and one public protected area were excluded because they provided
430 insufficient information. We assessed the extent to which 78 wildlife ranches, 23 agricultural farms
431 and six public protected areas were impacted by the pandemic, based on a categorical score of
432 revenue loss or gain over the 2020/21 financial year (March 2020 to February 2021, see
433 Supplementary Material 2). We further assessed which revenue-generating activities on wildlife
434 ranches were worst impacted, relative to the percentage of landholders undertaking each activity. If
435 landholders listed more than one activity as worst impacted (e.g., trophy hunting and ecotourism),
436 we counted both in the analysis.

437

438 To assess whether the combination of revenue-generating activities on a wildlife ranch influenced
439 the extent to which expected 2020/21 revenue was impacted by the pandemic, we performed a
440 principal component analysis (R package: vegan; function: rda) followed by a hierarchical
441 agglomerative cluster analysis. We included 74 wildlife ranches for which we had complete data on
442 revenue-generating characteristics. Characteristics included the proportion of revenue generated on
443 the property from the six most common activities: trophy hunting, wildlife breeding and live sales,
444 ecotourism, biltong ('meat') hunting, venison (meat) sales, and agriculture (livestock and/or
445 cultivation), as well as the proportion of visitors to the property that were foreign. The six revenue
446 impact categories were recategorized on an ordinal score from 1 (increase in revenue) to 6 (75% to
447 100% of revenue lost). We assessed the extent to which the two principal components representing
448 combinations of revenue-generating activities explained variation in the degree of revenue loss
449 using a linear model.

450

451 Distinct business models (i.e., combinations of revenue-generating activities adopted by wildlife
452 ranches) were identified using a cluster analysis, which employed Euclidean distance and Ward
453 linkages (R packages: vegan and stats; functions: vegdist and hclust)^{57,58}. We used a Mantel-based
454 comparison to identify the number of distinct clusters (R package: cluster; function: daisy)⁵⁹.
455 Differences between the business models identified by the cluster analysis were described according
456 to the mean values of revenue-generating characteristics within each group. We then compared
457 between business models the frequency of reported revenue losses/gains across categories, using a
458 two-sided Fisher's exact test.

459

460 Landholder responses to the question "What were your key strategies to cope with the effects of the
461 pandemic?" were categorised into broad themes, on an iterative basis, based on critical reading of
462 all interviews. We assessed how many landholders reported each strategy (strategies adopted by
463 10% or more of landholders are included in the results) and compared the frequency of four most
464 common strategies across business models using a two-sided Chi-squared test. Statistical analyses
465 were performed in R⁶⁰ at a significance level of $\alpha = 0.05$.

466

467 **Data availability statement**

468 All figures and tables in this study (Figures 1-5 and S1, Tables 1, 2, and S1) relate to the dataset
469 collected via semi-structured interviews, as described in the methods. As we are bound by ethical
470 considerations of the sensitivity of the data and committed to honour the trust placed in us by

471 interviewees to keep their data confidential, we cannot post the dataset publicly. We are, however,
472 similarly committed to transparent and open science, and anonymised data with all identifying
473 details removed can be requested from the corresponding author for the purpose of validating our
474 results independently, on the condition of signing a non-disclosure agreement.

475

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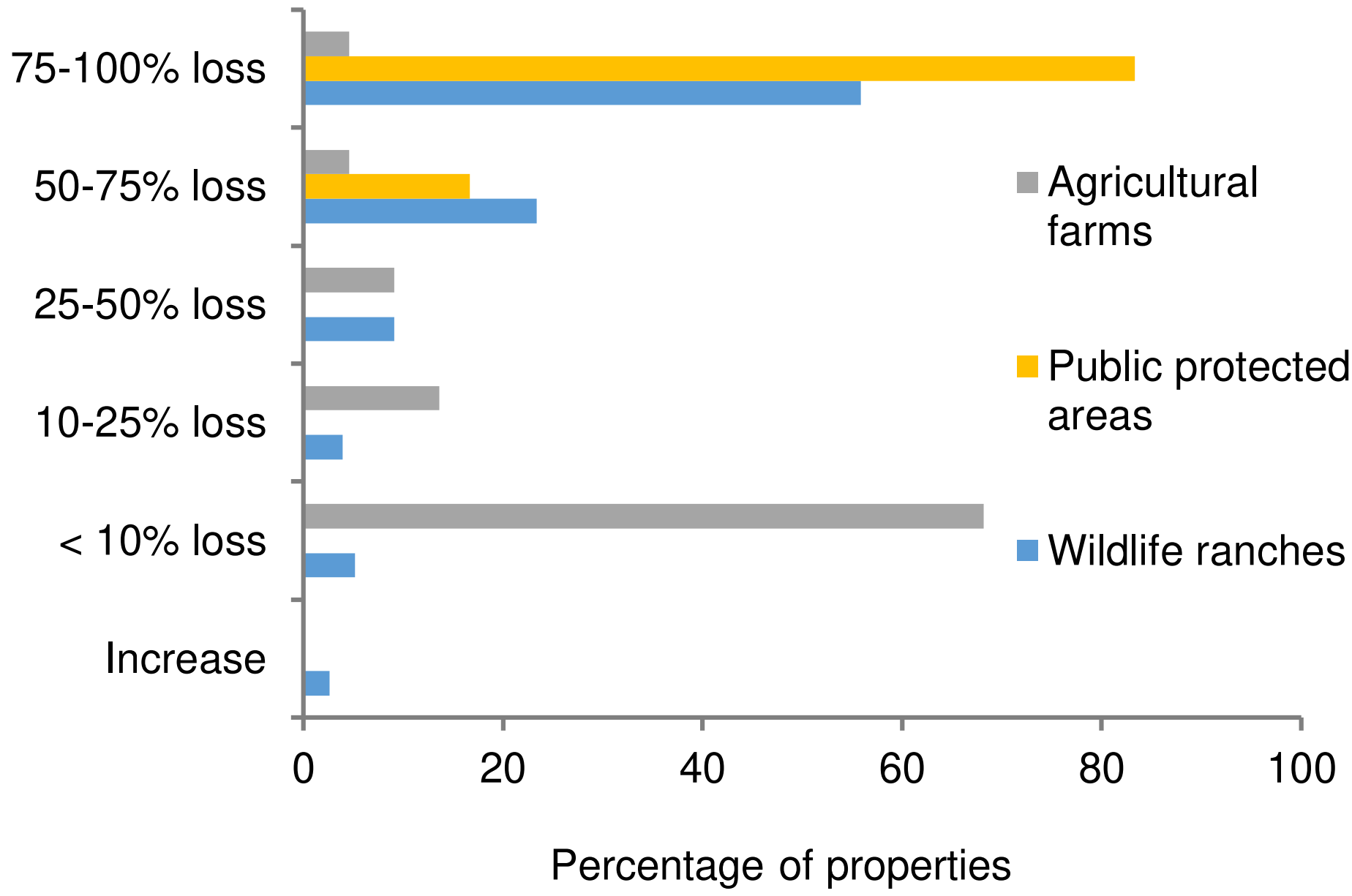
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605

Impact on revenue



Revenue-generating activity

